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Letter to Editor

Sensory and update errors which can affect path integration

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Path integration (PI, also called dead reckoning) is a computational process whereby displacements are summed over time to provide an estimate of the net displacement from some reference location. Numerous studies have reported evidence that animals from across multiple phyla can carry out this process, e.g., see reviews by Maurer and Seguinot (1995), Vickerstaff and Cheung (2010). Mathematically, the exact formulation of PI is trivial:

$$\mathbf{z} = \int d\mathbf{z} \quad (1)$$

where **z** denotes the net displacement vector, which is the integral of the infinitesimally small displacements over the journey of interest. Perhaps not surprisingly, PI and related behaviours can be expressed in a number of mathematically equivalent ways in the absence of noise (i.e., random, non-systematic errors) (Vickerstaff and Cheung, 2010). It was shown that PI-related phenomena including PI update per se, steering, searching and even some forms of systematic errors (i.e., deterministic deviations from (1)), can all be equivalently modelled in an egocentric or allocentric coordinate system, using either Cartesian or polar coordinates, as long as there is no noise. Furthermore, transformations between coordinate systems, as well as models in continuous and discrete time, can all be expressed exactly and equivalently in the absence of error (e.g., Tables 1–5 of Vickerstaff and Cheung, 2010).

Subsequently, it was shown by Cheung and Vickerstaff (2010) and more recently by Cheung (2014) that both sensory input and PI update noise have significantly different effects on the PI system, depending on the coordinate system used.

These results were challenged recently by Benhamou (2014), the author reporting that there is no difference in the way that errors accumulate when different coordinate systems are used to update the PI system, despite the presence of noise. Based on computer simulation examples using recurrent PI update equations, the author concluded that resultant PI errors do not depend on the coordinate system used.

We certainly agree that, by definition, noise-free PI can be expressed equivalently in any coordinate system and reference frame, however, the author also erroneously states that "Cheung and Vickerstaff (2010) showed that only Cartesian exocentric coding can prevent PI fed with *noisy movement estimates* from accumulating errors very fast" (emphasis added). This is a significant mischaracterisation, as we clearly dealt with a broader class of noise than that which only affects movement estimation. Indeed, the differing performances of the various coordinate systems shown by Cheung (2014), Cheung and Vickerstaff (2010) are largely a consequence of noise which *cannot be considered* to originate from movement estimation alone, but rather from noise within the brain itself, a type of noise which is nowhere represented by the equations of Benhamou (2014). Neither is any notice of or justification for this omission given, nor any indication as to its effect on the conclusions reached.

Detailed examples, explanations, computer simulations, mathematical derivations and discussions have been provided previously for why and how noise may affect PI (Cheung, 2014; Cheung and Vickerstaff, 2010; Cheung et al., 2007, 2008; Vickerstaff and Cheung, 2010). These papers considered a wide range of important issues including: modelling PI-related behaviours (Vickerstaff and Cheung, 2010), developing generalized coordinate systems to account for diverse published PI models (Cheung and Vickerstaff, 2010), the effect of tortuous trajectories on PI error accumulation (Cheung, 2014), continuous time models (Cheung, 2014; Vickerstaff and Cheung, 2010), complex error interactions during locomotion (Cheung and Vickerstaff, 2010; Cheung et al., 2008), and potential advantages or disadvantages of different coordinate systems other than those related to cumulative error (Vickerstaff and Cheung, 2010). Instead of reiterating the same points, we focus here specifically on possible reasons for the different conclusions drawn by Benhamou (2014). Based on the equations and arguments of Benhamou (2014), we point out key areas where misunderstandings and/or inappropriate simplifications of the PI update problem may lead to differences from previously reported results. We show degenerate cases where critical error terms are neglected, which are consistent with the conclusions of Benhamou (2014).

For this paper, we use the term 'allocentric' to denote the spatial reference frame of the navigator's environment, and 'egocentric' to denote the spatial reference frame of the navigator (Benhamou, 2014; Cheung and Vickerstaff, 2010; Vickerstaff and Cheung, 2010). Although this terminology is consistent with a large body of published literature, Benhamou (2014) noted that there is inconsistency in the etymological

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origin of these two terms. While there may be etymological reason to update the nomenclature, for the examples in this paper, the reader may consider the terms 'allocentric', 'geocentric' and 'exocentric' to be synonymous. In all analyses in this paper, the hat notation, e.g., $\widehat{W}$, denotes the estimate of the true value, which is W here.

1. PI update error is more than sensory error

An explicit assumption was made in Cheung and Vickerstaff (2010) and Section 3.6 of Cheung (2014) that the PI update process itself is prone to random error. This error is distinct from sensory error, such that even in the presence of perfect measurements of displacement in the current step, the update of the net PI vector per se leads to PI error. This can be illustrated using an allocentric polar coordinate system. We first consider the degenerate case where PI update error is assumed to be zero.

From Eqs. (2a) and (2b) of Benhamou (2014), exact allocentric polar PI update is given by

$$D_i = \sqrt{D_{i-1}^2 + l_i^2 + 2D_{i-1} l_i \cos(\theta_i - \Phi_{i-1})} \tag{2}$$

for the radial component, and

$$\Phi_i = \Phi_{i-1} + \text{atan}_2\left(\sin(\theta_i - \Phi_{i-1}), \frac{D_{i-1}}{l_i} + \cos(\theta_i - \Phi_{i-1})\right) \tag{3}$$

for the angular component, and where D_i is the exact polar modulus following the ith step, l_i is the true step length of the ith step, θ_i is the exact movement direction (heading) of the ith step, Φ_i is the exact polar argument following the ith step, and $\text{atan}_2(\cdot)$ denotes the four-quadrant arctangent function. It should be noted that (2) and (3) provide mathematically equivalent PI update to the exact geocentric polar (GP) discrete equations using an allothetic directional cue in Table 5 of Vickerstaff and Cheung (2010). In order to understand how (Benhamou, 2014) has diverged from our subsequent analyses in Cheung and Vickerstaff (2010) and Cheung (2014), we will use the notations of Benhamou (2014). Based on this notation, we will write the update angle of (3) as

$$\Delta\Phi_i = \Phi_i - \Phi_{i-1} \tag{4}$$

Clearly, (3) shows that the change in the polar coordinate Φ at a given step is a function of the radial distance D. It is straightforward to show that

$$\lim_{D_{i-1}\to\infty} \Delta\Phi_i = \lim_{D_{i-1}\to\infty} \text{atan}_2\left(\sin(\theta_i - \Phi_{i-1}), \frac{D_{i-1}}{l_i} + \cos(\theta_i - \Phi_{i-1})\right) = 0 \tag{5}$$

Therefore, as an animal moves further from its starting position, the magnitude of polar argument update must decrease. In the limit, the magnitude of update approaches zero.

If it is assumed that the only source of error is in the sensory input, then

$$\begin{aligned}\widehat{\Phi_i} &= \widehat{\Phi_{i-1}} + \Delta\widehat{\Phi_i^{TypeI}} \\ &= \widehat{\Phi_{i-1}} + \text{atan}_2\left(\sin\left(\theta_i + \delta_i - \widehat{\Phi_{i-1}}\right), \frac{D_{i-1}}{l_i + \lambda_i} + \cos\left(\theta_i + \delta_i - \widehat{\Phi_{i-1}}\right)\right)\end{aligned} \tag{6}$$

where $\widehat{\Phi}$ is the estimated polar argument, δ is the compass error, λ is the linear step size estimation error, and $\Delta\widehat{\Phi_i^{TypeI}}$ is the estimated argument update assuming sensory noise only. Similar to (5),

$$\begin{aligned}\lim_{D_{i-1}\to\infty} \Delta\widehat{\Phi_i^{TypeI}} &= \lim_{D_{i-1}\to\infty} \text{atan}_2\left(\sin\left(\theta_i + \delta_i - \widehat{\Phi_{i-1}}\right), \frac{D_{i-1}}{l_i + \lambda_i}\right. \\ &\quad \left. + \cos\left(\theta_i + \delta_i - \widehat{\Phi_{i-1}}\right)\right) = 0\end{aligned} \tag{7}$$

which means that $\widehat{\Phi}$ has to be updated by a vanishingly small amount as D becomes large. Thus, the contribution of sensory error terms δ and λ to the update of $\widehat{\Phi^{TypeI}}$ also becomes vanishingly small.

If one considers the 'PI update error' to be entirely due to sensory error, then Eqs. (5)–(7) seem valid. Indeed, computer simulations (see later) show equivalence between PI update using allocentric Cartesian and allocentric polar coordinates, consistent with the arguments of Benhamou (2014).

However, the degenerate case above neglects a critical error term, i.e., error during the update of $\widehat{\Phi}$ itself. To update the polar argument, it must be changed by some amount depending on the sensory input and previous state of the argument. However, it is implausible that the change itself can be made with absolutely zero error in an animal's brain. Both Cheung and Vickerstaff (2010) and Cheung (2014) found that any PI update error has substantially different effects on PI output depending on whether a Cartesian or Polar coordinate system is used.

Mathematically, a critical difference between Eq. (28) of Cheung (2014) and Eq. (2b) of Benhamou (2014) is that the former assumed the PI update process itself has error, while the latter did not. Based on the assumptions of Cheung and Vickerstaff (2010) and Cheung (2014), (6) can be written as

$$\begin{aligned}\widehat{\Phi_i} &= \widehat{\Phi_{i-1}} + \text{atan}_2\left(\sin\left(\theta_i + \delta_i - \widehat{\Phi_{i-1}}\right), \frac{D_{i-1}}{l_i + \lambda_i}\right. \\ &\quad \left. + \cos\left(\theta_i + \delta_i - \widehat{\Phi_{i-1}}\right)\right) + \varepsilon_i^{\Phi}\end{aligned} \tag{8}$$

where ε_i^{Φ} is a random error whose variance is finite, and which does not vanish with radial distance of the path during PI. Hence,

$$\begin{aligned}\lim_{D_{i-1}\to\infty} \Delta\widehat{\Phi_i^{TypeII}} &= \lim_{D_{i-1}\to\infty} \text{atan}_2\left(\sin\left(\theta_i + \delta_i - \widehat{\Phi_{i-1}}\right), \frac{D_{i-1}}{l_i + \lambda_i}\right. \\ &\quad \left. + \cos\left(\theta_i + \delta_i - \widehat{\Phi_{i-1}}\right)\right) + \varepsilon_i^{\Phi} = \varepsilon_i^{\Phi}\end{aligned} \tag{9}$$

Even though the error ε_i^{Φ} may be small in absolute value, the fact that the ideal update of $\widehat{\Phi}$ approaches zero with large D means that the ratio

$$\lim_{D_{i-1}\to\infty} \left| \frac{\varepsilon_i^{\Phi}}{\Delta\widehat{\Phi_i^{TypeII}}} \right| = 1 \tag{10}$$

Hence for large D, the polar angular update, $\Delta\widehat{\Phi_i^{TypeII}}$, is dominated by the error ε_i^{Φ}. Therefore, a polar PI system effectively amplifies the PI error attributed to ε_i^{Φ}, by a factor approximately scaled by D_{i-1}. Consequently, the seemingly subtle difference between (6) and (8) has a profound cumulative effect on the PI output, as detailed previously (Cheung, 2014; Cheung and Vickerstaff, 2010). Contrary to the claim by Benhamou (2014), the PI output error using a polar coordinate system is substantially larger than a Cartesian coordinate system, given PI update errors of the same magnitude.

To graphically illustrate the substantial difference between having and not having PI update error when using a polar coordinate system, we used the path and noise parameters of Table 1 in Benhamou (2014) to simulate PI outputs using either an allocentric Cartesian or allocentric polar coordinate system. We directly compared the degenerate recurrent equations of Benhamou (2014) which are free of PI update error (Fig. 1A, black ◊ and red x), and the same equations with PI update error (Fig. 1A, black □ and red ∗). It is clear that the presence of PI update error had a significant effect on the PI output error, and that the size of the effect depended on the coordinate system. Not surprisingly, the PI output error was substantially larger using an allocentric polar coordinate system in the presence of PI update error—entirely consistent with our previous work and the analysis above. Therefore, it is clear that the claim by Benhamou (2014) that 'the resultant PI errors … do not depend on the coordinate system used' is wrong in general.