From Behaviour to Brain Dynamics

Allen Cheung

Queensland Brain Institute
School of Information Technology and Electrical Engineering,
The University of Queensland, QLD 4072, Australia
acheung@itee.uq.edu.au

Abstract. It is well accepted that medium to long range navigation requires the use of an external directional reference i.e. a compass. Cheung et al (2007) recently demonstrated through theory and simulation the quantitative significance of the compass. It was shown that navigating agents using and not using a compass could be differentiated on the basis of the population behaviour. In the current work, theory and simulation results will be presented on ways to characterize individual paths on the basis of whether the system was using an external directional reference. Thus it is demonstrated that important information concerning the neural input used by a navigating animal may be inferred probabilistically from its behaviour.

1 Population-Based Behaviour

It is an age old problem to understand the behaviour of a control system e.g. the brain, based on its input and output, and yet that is often the challenge facing a neuroethologist. One particular behavioural output which is of interest is animal navigation. Current technology is capable of tracking with unprecedented precision the position and orientation of animals. However, it is only in strict laboratory conditions that such behaviour may be measured concurrently with neurodynamics. It has been shown that the behavioural characteristics of a population of navigating agents differed quantitatively and qualitatively depending on whether a compass (allothetic directional cue) is available to the population (Cheung et al 2007). In particular, the expected displacement of an agent has a finite upper limit if it did not use a compass (using only idiothetic cues)! This is accompanied by a positional uncertainty which asymptotically increases more rapidly than that of a Pearson's random walk (Pearson 1905). Using a compass, however, an agent could travel arbitrarily far along any predefined direction (axis of intended locomotion), with relatively small positional uncertainty. With such a dichotomy in population behaviour, it stands to reason that if it is feasible to obtain population estimates such as the positional mean and variance along and perpendicular to the axis of intended locomotion, then it should be possible to determine with some confidence what class of directional sensory cue was used (idiothetic or allothetic). The expected properties are summarized in Table 1.

M. Marinaro, S. Scarpetta, and Y. Yamaguchi (Eds.): Dynamic Brain, LNCS 5286, pp. 91–95, 2008.

Table 1. Population-based characteristics of different forms of directed walks

Type of Directed Walk	
Idiothetic	*Allothetic*
$\overline{x_{total}} < E_{max} < n\overline{x_1}$	$\overline{x_{total}} = n\overline{x_1}$
$s^2_{total} > n^2 > ns^2_1$	$n^2 > s^2_{total} = ns^2_1$
$\lim_{n\to\infty} s^2_x(n) = s^2_y(n)$	$\lim_{n\to\infty} s^2_x(n) \neq s^2_y(n)$

The average displacement after n steps along the axis of intended locomotion is denoted $\overline{x_{total}}$, while s^2_{total} denotes the sample variance in position along any particular axis. The Y direction is designated as being perpendicular to the axis of intended locomotion. The asymptotic limit for $\overline{x_{total}}$ during a simple idiothetic directed walk is denoted E_{max} and was shown by Cheung et al (2007) to be

$$E_{max} = \lim_{n\to\infty} \langle X_{total} \rangle = \mu_L \frac{\beta}{1-\beta} \tag{1}$$

where $\beta = \langle \cos \Delta \rangle$. These characteristics allow populations of navigating agents undergoing IDWs or ADWs to be differentiated.

2 Individual-Based Behaviour

Despite the analytical rigour of the population-based results, it may be difficult in practice to obtain a sufficient sample size to be confident of the estimates of population parameters. Furthermore, repeated trials can only be pooled with confidence if the axis of intended locomotion is known for each trial and therefore aligned.

A very different approach is currently being developed to quantify the IDW vs ADW character of an individual directed walk (see Fig 1), without a priori knowledge of the axis of intended locomotion, magnitude of random errors, or existence of bias. The geometric construct is analogous to the simple directed walks presented in Cheung et al (2007). The angular error at step t is denoted Δ_t. Hence for a simple idiothetic directed walk, the allocentric heading Θ_t following t steps is the sum of all preceding Δ's. In contrast, for the ideal allothetic directed walk, a compass is used to reset heading errors at each step such that by the $t'th$ step, errors from step 1 to $t-1$ are zero. In contrast, the turn angle θ depends only on the difference between the successive headings i.e. $\Theta_{t+1} - \Theta_t$. It is then possible to define a pair of ideal covariance functions.

The ideal allocentric covariance function is defined as

$$\begin{aligned} Cov_{allo} &= Cov(\Theta_t, \Theta_{t+1}) \\ &= \langle \Theta_t \Theta_{t+1} \rangle - \langle \Theta_t \rangle \langle \Theta_{t+1} \rangle . \end{aligned} \tag{2}$$

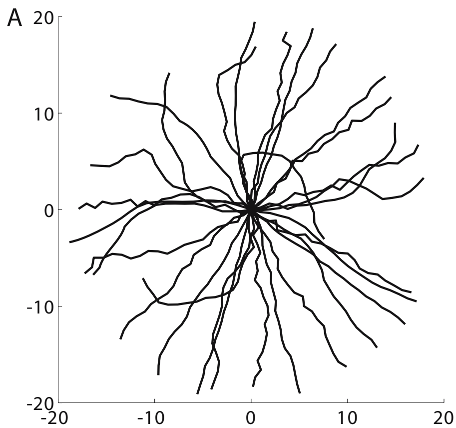

Fig. 1. (A) Graphical example of an unknown mixture of simulated (unbiased) idiothetic and allothetic directed walks with varying magnitudes of random angular displacement errors, and unknown axes of intended locomotion. (B) In this set of 30 paths of 20 steps, the decision function (Eqn 6) made the correct decision in 28 out of 30 paths (ADWs = solid lines, IDWs = dotted lines), being unable to decide in the remaining two (dashed lines). There were no incorrect decisions in this sample set.

Table 2. Angular components and covariance results of directed walks

	Type of Directed Walk		Covariance Result	
Function	*IDW*	*ADW*	*Cov|IDW*	*Cov|ADW*
Cov_{allo}	$\Theta_t = \sum_{j=1}^{t} \Delta_j$	$\Theta_t = \Delta_t$	$tV(\Delta)$	0
Cov_{ego}	$\theta_t = \Delta_t$	$\theta_t = \Delta_{t+1} - \Delta_t$	0	$-V(\Delta)$

The ideal egocentric covariance function is defined as

$$\begin{aligned} Cov_{ego} &= Cov(\theta_t, \theta_{t+1}) \\ &= \langle \theta_t \theta_{t+1} \rangle - \langle \theta_t \rangle \langle \theta_{t+1} \rangle . \end{aligned} \tag{3}$$

The pair of ideal covariance functions can be shown to have distinct angular error components and therefore different values when the directed walk is idiothetic or allothetic in nature. These results are summarized in Table 2. This implies that the pair of covariance values can be used to determine whether the directed walk was more likely to have been idiothetic or allothetic in nature.

3 Practical Application

In practice, systematic bias is removed by letting $\Theta'_t = \Theta_t - \overline{\Theta}$, which doesn't affect the turn angle $\theta'_t = \Theta'_{t+1} - \Theta'_t$. The following covariance estimates are used as inputs to the decision function (Eqn 6):

$$\widehat{Cov}_{allo} = \frac{1}{n-2} \sum_{t=1}^{n-1} \left(\Theta'_t - \overline{\Theta'}\right) \left(\Theta'_{t+1} - \overline{\Theta'}\right) \tag{4}$$

and

$$\widehat{Cov}_{ego} = \frac{1}{n-3} \sum_{t=1}^{n-2} \left(\theta'_t - \overline{\theta'}\right) \left(\theta'_{t+1} - \overline{\theta'}\right). \tag{5}$$

Careful examination reveals that the sample estimate of the allocentric covariance function in the case of IDWs is not an unbiased estimator (in contrast to the other three conditions). Nonetheless, it will be used for its practicality and simplicity. Using these values as inputs, it is then possible to decide whether the path travelled was more likely to be idiothetic (I), allothetic (A), or cannot be reliably decided (U). The decision function $\Lambda()$ is defined as follows:

$$\Lambda\left(\widehat{Cov}_{allo}, \widehat{Cov}_{ego}\right) = \begin{cases} A & if \left(\left|\frac{\widehat{Cov}_{allo}}{\widehat{Cov}_{ego}}\right| < 0.2\right) \cap \left(\widehat{Cov}_{ego} < 0\right) \\ I & if \left(\left|\frac{\widehat{Cov}_{allo}}{\widehat{Cov}_{ego}}\right| > 1\right) \cup \left(\widehat{Cov}_{ego} > 0\right) \\ U & Otherwise \end{cases} \tag{6}$$

Ideally, if the spatiotemporal resolution is sufficiently high to record each locomotory unit in detail, then it should be possible to distinguish each cycle of locomotion. It is then trivial to apply the decision function presented. However, if that is not practical, then it is better to undersample rather than oversample points along the journey. The main reason is to avoid the problem of a strong

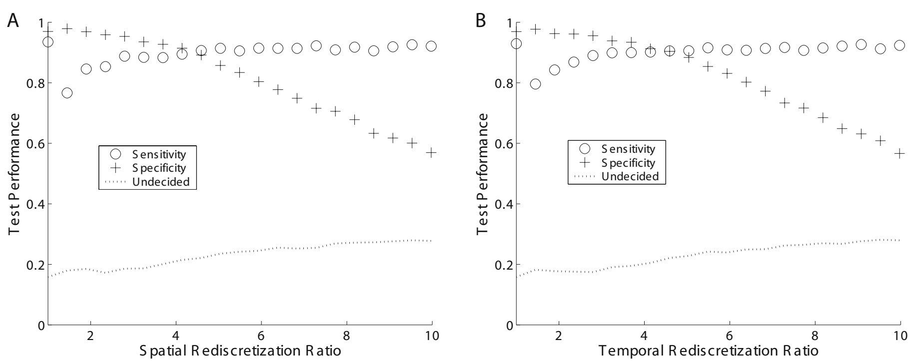

Fig. 2. Test performance of the decision function (Eqn 6) using simulated IDWs and ADWs. A range of spatial (A) and temporal (B) rediscretization ratios were used to downsample paths, keeping only the first 20 steps in each path. Simulation parameters: normally distributed Δ where σ_Δ was randomly chosen from the interval [0.1,0.5] rad; Δ_{bias} was also normally distributed with $\sigma_{bias} = 0.1$ rad. The performance results at each rediscretization ratio were calculated from 10,000 simulated paths. Note 'sensitivity' and 'specificity' were defined with respect to the ADW.

but spurious negative correlation between components within one locomotory unit. For example, if a leftward error is always followed by a rightward error within one elementary step, this would bias the statistics in favour of a decision of 'allothetic', irrespective of the directional cue used. In other words, the paths have to be rediscretized (Bovet and Benhamou 1988). In principle, this may be done either spatially or temporally as shown in Fig 2.

It can be seen from the simulation results that the method presented here can cope with a range of spatial (Fig 2A) and temporal (Fig 2B) rediscretization ratios, as well as tolerate noise and biases of varying magnitudes. It is noteworthy that performance (sensitivity and specificity) was always above chance with only 20 steps in each path sample, and yet the failure to make a decision rarely exceeded 20%.

4 Conclusions

1. *Population − based* statistical behaviours have already been described, and should be used where possible to determine the class of sensory input being used during animal navigation.
2. A novel method for quantifying *individual − based* statistical behaviour is under development and shows useful characteristics in simulations and early experimental trials (data not shown).

Acknowledgements. This work was supported by an NHMRC/ARC Thinking Systems grant and a COSNet Overseas Travel grant (COSNet Proposal number 93).

References

1. Bovet, P., Benhamou, S.: Spatial analysis of animals' movements using a correlated random walk model. J. Theor. Biol. 131, 419–433 (1988)
2. Cheung, A., Zhang, S., Stricker, C., Srinivasan, M.V.: Animal navigation: the difficulty of moving in a straight line. Biol. Cybern. 97, 47–61 (2007)
3. Pearson, K.: The problem of the random walk. Nature 72, 294 (1905)