Different forms of optimal cue integration
Supplementary Information

From the Central Limit Theorem, positions estimated via the process of path integration are expected to follow bivariate Gaussian distributions [S1]. Combining with Bayes' theorem, the inverse covariances of two independent estimates sum linearly, i.e.,

$$\boldsymbol{\Sigma}_{opt}^{-1}=\boldsymbol{\Sigma}_1^{-1}+\boldsymbol{\Sigma}_2^{-1} \tag{1}$$

where $\boldsymbol{\Sigma}_i^{-1}$ denotes the inverse covariance matrix of cue *i*, and $\boldsymbol{\Sigma}_{opt}^{-1}$ is the inverse covariance matrix of the optimally combined positional estimate. The inverse covariance can be interpreted as a measure of positional 'certainty', analogous to the directional uncertainty considered in [1].

The center of the combined estimate's Gaussian positional uncertainty is given by the relationship

$$\boldsymbol{\mu}_{opt}\boldsymbol{\Sigma}_{opt}^{-1}=\boldsymbol{\mu}_1\boldsymbol{\Sigma}_1^{-1}+\boldsymbol{\mu}_2\boldsymbol{\Sigma}_2^{-1} \tag{2}$$

The derivations of (1) and (2) can be found in many standard texts, but is outlined briefly below for bivariate Gaussians. The bivariate positional uncertainty distribution can be written as

$$f(x,y)=f(\boldsymbol{z})=\frac{1}{2\pi\sqrt{|\boldsymbol{\Sigma}|}}\exp\left(-\frac{1}{2}(\boldsymbol{z}-\boldsymbol{\mu})\boldsymbol{\Sigma}^{-1}(\boldsymbol{z}-\boldsymbol{\mu})^T\right) \tag{3}$$

where $\boldsymbol{z}=[x \quad y]$ is the 2D position variable, $\boldsymbol{\mu}=[\mu_x \quad \mu_y]$ is the mean of the distribution (and also position of maximum likelihood), and $\boldsymbol{\Sigma}$ is the standard covariance matrix of two variables, i.e.,

$$\boldsymbol{\Sigma}=\begin{bmatrix}\sigma_x^2 & \sigma_{xy}\\ \sigma_{xy} & \sigma_y^2\end{bmatrix} \tag{4}$$

Bayes-optimal integration of two estimates with bivariate Gaussian uncertainty, f_1 and f_2, yields another estimate with bivariate Gaussian uncertainty f_{opt}:

$$\begin{aligned}
f_{opt}(x,y)&\propto f_1(x,y)\cdot f_2(x,y)\\
&\propto\exp\left(-\frac{1}{2}(\boldsymbol{z}-\boldsymbol{\mu_1})\boldsymbol{\Sigma_1}^{-1}(\boldsymbol{z}-\boldsymbol{\mu_1})^T-\frac{1}{2}(\boldsymbol{z}-\boldsymbol{\mu_2})\boldsymbol{\Sigma_2}^{-1}(\boldsymbol{z}-\boldsymbol{\mu_2})^T\right)\\
&=\exp\left(-\frac{1}{2}(\boldsymbol{z}(\boldsymbol{\Sigma}_1^{-1}+\boldsymbol{\Sigma}_2^{-1})\boldsymbol{z}^T-2(\boldsymbol{\mu}_1\boldsymbol{\Sigma}_1^{-1}+\boldsymbol{\mu}_2\boldsymbol{\Sigma}_2^{-1})\boldsymbol{z}^T)+C\right)\\
&=\exp\left(-\frac{1}{2}(\boldsymbol{z}-\boldsymbol{\mu}_{opt})\boldsymbol{\Sigma}_{opt}^{-1}(\boldsymbol{z}-\boldsymbol{\mu}_{opt})^T+C'\right)
\end{aligned} \tag{5}$$

noting that $\boldsymbol{z}\boldsymbol{\Sigma}^{-1}\boldsymbol{\mu}^T=\boldsymbol{\mu}\boldsymbol{\Sigma}^{-1}\boldsymbol{z}^T$ since $\boldsymbol{\Sigma}$ is always symmetric. Note also that the constants *C* and *C'* do not affect the form of f_{opt} since it is normalized. Hence (5) shows that f_{opt} is bivariate Gaussian with mean and covariance given by (1) and (2).

Importantly, μ_{opt} is the both maximum likelihood estimate of position (peak of distribution), and also the position where most search effort should be applied [5].

To gain more insight into why there is a difference between directional and positional cue integration, we can take advantage of a simple relationship between bivariate Gaussian distributions and univariate von Mises distributions. For a cue with a circularly symmetric Gaussian uncertainty distribution ($\sigma_x^2=\sigma_y^2=\sigma^2$ and $\sigma_{xy}=0$), its directional uncertainty is well approximated by a von Mises distribution whose mean is the direction of the Gaussian peak, and with concentration

$$\kappa\approx\frac{r^2}{\sqrt{|\boldsymbol{\Sigma}|}}=\frac{r^2}{\sigma^2} \tag{6}$$

where κ is the concentration of the von Mises directional uncertainty distribution, *r* is the distance between the observer and the cue, $|\boldsymbol{\Sigma}|$ and σ^2 are the determinant of the covariance matrix and marginal variance of the Gaussian, respectively. This useful approximation arises from the property of von Mises distributions being equivalent to the hitting density on a circle following Brownian motion which begins at the circle's center, and with some constant drift [S2]. If an observer is at the circle's center, the hitting density is the directional distribution from the observer's viewpoint. Furthermore, since simple Brownian motion results in a circularly symmetric bivariate Gaussian distribution with some marginal variance σ^2, and the constant drift determines the radial distance r at which the directional distribution is computed, the directional distribution of a circularly symmetric bivariate Gaussian distribution at distance r is given by (6). Thus, Bayes-optimal directional integration cannot distinguish entire classes of positional uncertainty distributions, e.g.,

$$\boldsymbol{z} = [x \quad y] \sim N\left([r \quad 0], \begin{bmatrix} \frac{r^2}{\kappa} & 0 \\ 0 & \frac{r^2}{\kappa} \end{bmatrix}\right) \tag{7}$$

where any constant ratio of r^2 and σ^2 leads to a constant κ despite substantially different distances r. Hence optimal directional cue integration results in practically identical combined directional estimate for all r in this class of positional uncertainty distributions (e.g., Fig 1A, initial headings of red paths). In contrast, both the center and covariance of the positional uncertainty varies with r which signficantly affects the optimal estimate of goal position and direction.

Similar principles apply to non-Gaussian uncertainties but do not always have simple closed form solutions or approximations. Nevertheless, it is straightforward to perform empirical positional and directional Bayesian integration to quantify their differences.

Figure 1A parameters

Cue uncertainty parameters:

$$\boldsymbol{z}_{LM} \sim N\left([0 \quad 2], \begin{bmatrix} \frac{1}{4} & 0 \\ 0 & \frac{1}{4} \end{bmatrix}\right) \tag{8}$$

$$\boldsymbol{z}_{PI1} \sim N\left([2 \quad 0], \begin{bmatrix} \frac{1}{4} & 0 \\ 0 & \frac{1}{4} \end{bmatrix}\right) \tag{9}$$

$$\boldsymbol{z}_{PI2} \sim N\left([4 \quad 0], \begin{bmatrix} 1 & 0 \\ 0 & 1 \end{bmatrix}\right) \tag{10}$$

$$\boldsymbol{z}_{PI3} \sim N\left([7 \quad 0], \begin{bmatrix} \frac{49}{16} & 0 \\ 0 & \frac{49}{16} \end{bmatrix}\right) \tag{11}$$

$$\mathbf{z}_{PI4} \sim N\left(\begin{bmatrix} 11 & 0 \end{bmatrix}, \begin{bmatrix} \frac{121}{16} & 0 \\ 0 & \frac{121}{16} \end{bmatrix} \right) \quad (12)$$

Start position was $[0 \quad 0]$. To generate paths using directional integration, (6) was combined with the von Mises path integration model of [1] at each step to compute the goal direction, at a step size of 0.01 units. To generate paths using positional integration, (1) and (2) were used.

Figure 1B parameters

The empirical probability of successfully locating a goal whose uncertainty distribution is *f*(*x*, *y*) is given by

$$P(success) \approx \sum_{x,y} f(x,y)\left(1-e^{-\gamma\phi(x,y)}\right)\Delta x \, \Delta y \quad (13)$$

where search success parameter γ = 0.2, discretized grid resolution Δx = Δy = 0.1, and search effort distribution $\phi(x,y)$. The optimal search distribution for a circularly symmetric bivariate Gaussian uncertainty distribution is from [5]:

$$\phi(x,y) = \begin{cases} \sqrt{\frac{\Phi}{\pi\sigma^2}} - \frac{x^2+y^2}{2\sigma^2} & x^2+y^2 \leq 2\sigma\sqrt{\frac{\Phi}{\pi}} \\ 0 & otherwise \end{cases} \quad (14)$$

where Φ denotes the cumulative total search effort, ranging from 0 to 200 units in Fig 1B.

Figure 1C parameters

For each of three true paths of 100 steps, there were 10^4 repetitions with i.i.d. random compass error

$$\varepsilon \sim VM(0,2) \quad (15)$$

where *VM* denotes the von Mises distribution. The true paths were: straight (Fig 1C left), circular arc with a total turn angle of 7π/4 radians (Fig 1C middle), and a correlated random walk with independent random turn angles of the same distribution as ε (Fig 1C right). For display purposes, path integration position estimates were all scaled by $1/\langle\cos(\varepsilon)\rangle = I_0(2)/I_1(2)$, where I_ν denotes the modified Bessel function of the first kind of order ν, to correct for the proportionate underestimation of distance travelled due to compass error [S1].

Supplementary References

[S1] Cheung A (2014) Animal path integration: A model of positional uncertainty along tortuous paths. *J Theor Biol* 341:17–33.

[S2] Gordon L, Hudson M (1977) A characterization of the von Mises distribution. *Ann Stat* 5: 813-814.