Estimation of D

12/27-31/13. I have some concerns regarding the estimation of the diffusion constant as reported in the Curr. Biol. 2012 Appendix and its relation to the way MA estimates in this study. The Appendix in CB states:

> Eq.1 enables closed-form estimation of the input power spectrum when the eye movement process is two-dimensional Brownian motion. In this case, the probability distribution of retinal displacement obeys the diffusion equation:
>
> $$\frac{\partial}{\partial t}q(x,y,t) = \frac{1}{2}D\nabla^2 q(x,y,t) \tag{9}$$
>
> where D is the diffusion constant.
>
> For the initial condition that q is concentrated at the origin at $t = 0$, the solution of Eq. 9 is well-known:
>
> $$q(x,y,t) = \frac{1}{2\pi Dt}\ \exp(-\frac{x^2+y^2}{2Dt}). \tag{10}$$
>
> This function has Fourier Transform
>
> $$q(k_x,k_y,\omega) = \frac{(k_x^2+k_y^2)\,D}{(k_x^2+k_y^2)^2\,\frac{D^2}{4}+\omega^2}. \tag{11}$$
>
> Substitution of $q(k_x,k_y,\omega)$ from Eq. 11 into Eq. 1 gives the power spectrum of the retinal stimulus, as plotted in Figs.2$b-d$. To obtain the value of D from the recorded eye movement data, we measured the empirical standard deviation of the eye displacement as a function of time, for intervals from 0 to 500 ms. We then chose the value of D for which the standard deviation of the probability distribution $q(x,y,t)$ in Eq. 10, namely $\sqrt{2Dt}$, provided the least-squares best fit to the data. This yielded $D = 40$ arcmin^2/s.

Eq. 10 is a bivariate normal distribution with the assumptions of (1) zero correlation between the two variables and (2) equal standard deviation on the two axes $\sigma_x = \sigma_y = \sigma$. It implies $Dt = \sigma^2$. Therefore, I don't understand the statement above: "We then chose the value of D for which the standard deviation of the probability distribution $q(x,y,t)$ in Eq. 10, namely $\sqrt{2Dt}$." The standard deviation of the distribution on each axis is $\sqrt{Dt}$, not $\sqrt{2Dt}$. $\sqrt{2Dt}$ would be the standard deviation of the variable $x+y$, but I doubt that is what is meant here. An oversight?

MA noted also that one has to be careful in using the term "diffusion coefficient", because the D in Eq. 9 is not the standard way to define the diffusion coefficient of Brownian motion D_B. This is explained in JV's notes. In general, a random walk in any dimensions is defined by the diffusion equation:

$$\frac{\partial q}{\partial t} = D_B\nabla^2 q \tag{12}$$

where the second term becomes $\frac{\partial^2 q}{\partial x^2}$ in the one-dimensional case. Note the difference with Eq. 9, where $D = 2D_B$. This equation leads to the power spectrum, which seems to be valid in all dimensions:

$$\frac{2|\mathbf{k}|^2 D_B}{|\mathbf{k}|^4 D_B^2 + \omega^2} \tag{13}$$

For consistency with the 1-D case, we defined D in 2-D as in Eq. 10, so that the mean of the squared distance is $2Dt$ in both 1-D and 2-D. But one should remember that the D in Eq. 10 is NOT the standard 2-D diffusion coefficient of Brownian motion: $D_B = D/2$. MA's data are the values D_B, and this has created confusion in comparing to previous data from CB.

<u>*CB 2012:*</u> XK estimated the D value in Eq. 9, NOT D_B, as consistently pointed out in the paper. He estimated D by calculating the σ of the best fitting circular 2D Gaussian as in Eq.10 (function fit_prob_gaussian2d). The D value was then given by linear regression of σ^2, $D =< \sigma^2/t >$. Since $\sigma^2 = Dt$, this correctly gives D. Indeed the CB Appendix concludes "This yielded $D = 40$ arcmin^2/s" and everything seems consistent.

One should not be confused by the fact that, in order to compare the power spectrum of Brownian motion to that obtained by Welch, XK decided to use D_B. In the function plotPSStatDyn_RW_paper XK set $D_B = D/2 = 20$ and then used the D_B formula in Eq. 13, which—he noted—could be directly integrated to give the total power above ω_o (function powerintegral):

$$\int_{\omega}^{\infty} \frac{2|\mathbf{k}|^2 D_B}{|\mathbf{k}|^4 D_B^2 + \omega^2}\, d\omega = \pi - 2\arctan\left(\frac{\omega^2}{|\mathbf{k}|^2 D_B}\right)$$

So, everything is consistent in CB, and the value $D = 40$ refers to the D defined as in Eq. 9, not D_B.

<u>*This paper:*</u> MA decided to estimate D_B using the standard equation Eq. 12, as explained in the file MuratComments_Jan6-13, following Berg's notation (book chapter on file). He has been using an approach based on the mean of $d^2 = x^2 + y^2$, the squared 2D distance. Under the assumption of zero means and independence, $E(d^2) = 2\sigma_x^2$. In a random walk with $\sigma_x^2 = Dt = 2D_B t$, we obtain $E(d^2) = 2Dt = 4D_B t$. MA takes the linear regression of this divided by 4: $E(d^2)/4t$, therefore obtaining $D_B = 2D$.

What is not clear is MA's direct comparison of his values to XK's previous values. From XK's $D = 40$, I expect $D_B = 40/2 * 1.42^2 \sim 43$, not 82 as MA claims. This is a large discrepancy. I have been trying to understand how this is possible, but so far without success.

<u>1/7/13.</u> MA explains the discrepancy with two errors. The first one from XK in the procedure of fitting, possibly caused by discretization of space before fitting a Gaussian. According to MA (MuratComments_Jan6-13) analysis of XK's data with the $E(d^2)/4t$ method gives: $D_B = 29.4$ which converts on the retina to $D_B = 63$. So according to MA, $D = 40$ in the CB paper should have been $D \sim 60$. The second issue, MA noted an error in his own code, revising the average D_B estimate for the head-free paper to 260, a bit lower than before.

Methods for estimating D. This has implications on the estimate of D from a simulated trace. One approach is to estimate D via the individual σ_x and σ_y. This involves calculating the distributions of displacements $\{x_t\}$ and $\{y_t\}$ at all delays t and estimating the standard deviations as a function of delay. In a random walk the product of these two standard deviations should increase linearly as Dt. The value of D will be given by linear regression of this function. I have implemented this approach in a simple simulation that compares the spectra obtained via Welch to those given by the formula for a random walk. The code is in CompareWelchTheory_BM in Martina/Projects/PowerSpectrum.

MA has been using an approach based on the mean of $d^2 = x^2 + y^2$, the squared 2D distance. Assuming zero means and independence, $E(d^2) = 2\sigma_x^2$. In a random walk with $\sigma_x^2 = Dt$, we obtain $E(d^2) = 2Dt$. Therefore, an alternative approach to estimate D is to compute the linear regression of $E(d^2)/2$. The two methods are obviously equivalent.

Methods for estimating D_B. Since $D_B = 2D$, the previous methods obviously apply to the estimation of D_B followed by multiplication by 2. MA has been using two main methods: (1) The mean of the squared 2D distance, $d^2 = x^2 + y^2$. Since $E(d^2) = 2Dt$ and $D = 2D_B$, $E(d^2) = 4D_Bt$ and $D_B = E(d^2)/(4t)$. (2) Use PCA to estimate the standard deviations on the two uncorrelated axes: σ_x and σ_y. Since $\sigma_x\sigma_y = Dt = 2D_Bt$, we obtain $D_B = \sigma_x\sigma_y/2t$.