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The Turning of Magnetotactic Bacteria

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A magnetotactic bacterium aligns itself along the magnetic field. When the field is reversed the bacterium makes a U-turn in the surrounding water. The turning is described by a Fokker–Planck equation for the angle ϑ, which is singular at the endpoints $\vartheta = 0$ and $\vartheta = \pi$. The time needed for turning can be found exactly as a first-passage time. The probability distribution itself can be found in terms of an approximation for low temperature. To cover the regions near the endpoints singular perturbation theory is needed.

KEY WORDS: Bacteria; singular Fokker–Planck equation.

1. THE EXPERIMENTAL SITUATION

For our purpose a bacterium is a body immersed in water propelled by a flagellum at its tail end. A magnetotactic bacterium contains a magnet, consisting of crystals of Fe_3O_4 or Fe_3S_4, inside the body and in line with the tail. An external magnetic field will turn the bacterium parallel to the field, so that the flagellum has the effect of propelling the bacterium along the field line.[(1)] Experiments were done in which the magnetic field was suddenly reversed, so that the bacteria had to turn around. The time it took to complete the turn was measured, because it provides information about the strength of the magnet and the friction with the fluid.[(2, 3)]

Take the z-axis in the direction of the original field and let ϑ, ψ be the direction of the magnet. At $t = 0$ the field B is reversed into the direction $-z$, and then exerts a torque $mB \sin \vartheta$, where m is the magnetic dipole moment. The torque acts to increase ϑ; the turning is overdamped due to the friction with the water, so that

$$\dot{\vartheta} = \frac{mB}{8\pi\eta R^3} \sin \vartheta \tag{1}$$

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Here η is the viscosity of the water and R is the radius of the bacterium in case it is spherical, and otherwise some phenomenological effective radius. This is the macroscopic equation, i.e., the equation of motion ignoring fluctuations. It yields for the time needed to rotate from ϑ_1 to ϑ_2

$$t_2 - t_1 = (8\pi\eta R^3/mB)(\log\tan\tfrac{1}{2}\vartheta_2 - \log\tan\tfrac{1}{2}\vartheta_1) \tag{2}$$

To obtain the total turning time we ought to take $\vartheta_1 = 0$ ("north pole") and $\vartheta_2 = \pi$ ("south pole"), but both give infinity. The reason for the infinity at the north pole is that it is an equilibrium point, albeit unstable, at which the torque vanishes. The reason for that at the south pole is that it is a stable equilibrium, toward which the angle ϑ creeps infinitely slowly. In the experiments therefore the turning time between $\vartheta_1 = \delta$ and $\vartheta_2 = \pi - \delta$ was measured, where δ was taken equal to 10°.

In this work the thermal fluctuations, linked to the dissipation in (1), are included by means of a Fokker–Planck equation. The solution for low temperature can be obtained without infinities, but near each of the poles a special treatment is required. The contributions of these polar caps to the total turning time is not negligible. That was the reason why in the experiments the caps were excluded.

2. THE FOKKER–PLANCK EQUATION

In the absence of a field the direction ϑ, ψ of the magnet performs a Brownian motion on the unit sphere. The probability density $p(\vartheta, \psi, t)$ on the surface of the sphere obeys the diffusion equation

$$\frac{\partial p}{\partial t} = D\left(\frac{1}{\sin\vartheta}\frac{\partial}{\partial\vartheta}\sin\vartheta\frac{\partial p}{\partial\vartheta} + \frac{1}{\sin^2\vartheta}\frac{\partial^2 p}{\partial\psi^2}\right)$$

The diffusion constant D will be determined presently. In our case p does not depend on ψ, and it is enough to know the probability density, $P(\vartheta, t)$ of ϑ alone. The area of a zone on the unit sphere is proportional to $\sin\vartheta$, so that $P(\vartheta, t) = 2\pi p(\vartheta, t)\sin\vartheta$ and

$$\frac{\partial P}{\partial t} = D\frac{\partial}{\partial\vartheta}\sin\vartheta\frac{\partial}{\partial\vartheta}\frac{1}{\sin\vartheta}P$$

Here $0 < \vartheta < \pi$, and at the boundaries $P = 0$.

When the field is added an additional term appears, which must have the form of a drift:

$$\frac{\partial P}{\partial t} = D\frac{\partial}{\partial\vartheta}\sin\vartheta\frac{\partial}{\partial\vartheta}\frac{P}{\sin\vartheta} - \frac{\partial}{\partial\vartheta}F(\vartheta)P \tag{3}$$

We know that the equation is satisfied by the equilibrium distribution

$$P^{\mathrm{eq}}(\vartheta) = C \sin \vartheta \exp\left[-\frac{mB\cos\vartheta}{kT}\right]$$

and we find

$$F(\vartheta) = D\frac{mB}{kT}\sin\vartheta$$

On the other hand, if the diffusion term in (3) is neglected, i.e., in the limit $T \to 0$, the equation must reduce to the Liouville equation that goes with (1), hence

$$F(\vartheta) = \frac{mB}{8\pi\eta R^3}\sin\vartheta$$

This yields the Einstein relation

$$D = \frac{kT}{8\pi\eta R^3}$$

Thus the coefficients of (3) are entirely expressed in the constants B, m, η, R, kT.

It is convenient to divide the right-hand side of (3) by $mB/8\pi\eta R^3$ and absorb this factor into t. The rescaled diffusion constant is

$$D\frac{8\pi\eta R^3}{mB} = \frac{kT}{mB} \equiv \varepsilon$$

ε is the ratio of the fluctuation energy kT to the potential energy mB. Our approximations will be based on small ε. In the experiments it was about 1/16.[2] The Fokker–Planck equation (3) now takes the form

$$\begin{aligned}\frac{\partial P}{\partial t} &= \varepsilon\frac{\partial}{\partial\vartheta}\sin\vartheta\frac{\partial}{\partial\vartheta}\frac{1}{\sin\vartheta}P - \frac{\partial}{\partial\vartheta}\sin\vartheta\, P\\ &= \varepsilon\frac{\partial^2 P}{\partial\vartheta^2} - \frac{\partial}{\partial\vartheta}(\varepsilon\cot\vartheta + \sin\vartheta)P \qquad (4)\end{aligned}$$

3. THE MEAN FIRST-PASSAGE TIME

Take $0 < \Theta < \pi$. Let $\tau(\Theta\,|\,\vartheta)$ be the average time for a point starting out at some ϑ between 0 and Θ to reach Θ for the first time. This mean first-passage time obeys[4]

$$\varepsilon\frac{d^2\tau}{d\vartheta^2} + (\varepsilon\cot\vartheta + \sin\vartheta)\frac{d\tau}{d\vartheta} = -1$$

One obvious boundary condition is $\tau(\Theta\,|\,\Theta)=0$. The solution is elementary,

$$\tau(\Theta\,|\,\vartheta)=\int_{\vartheta}^{\Theta}\{Ae^{\cos\vartheta'/\varepsilon}-1\}\,\frac{d\vartheta'}{\sin\vartheta'}\qquad(\vartheta\leqslant\Theta)$$

The remaining integration constant A is determined by the requirement that $\tau(\Theta\,|\,0)$ should be finite, and one finds

$$\tau(\Theta\,|\,\vartheta)=\int_{\vartheta}^{\Theta}\{1-e^{-(1-\cos\vartheta')/\varepsilon}\}\,\frac{d\vartheta'}{\sin\vartheta'}\tag{5}$$

Another way of justifying this choice of A is by imagining a boundary at $\vartheta=\eta$ with the reflecting boundary condition $d\tau/d\vartheta=0$, and then taking the limit $\eta\to0$.

The divergence of the macroscopic equation (2) at $\vartheta=0$ has now been overcome thanks to the fluctuations. Starting from $\vartheta=0$, the mean time to reach a prescribed value Θ is

$$\tau(\Theta\,|\,0)=\int_{0}^{\Theta}\{1-e^{-(1-\cos\vartheta)/\varepsilon}\}\,\frac{d\vartheta}{\sin\vartheta}\tag{6}$$

This is to be compared to (2), which involves the cutoff δ:

$$\tau(\Theta\,|\,\delta)=\log\tan\frac{1}{2}\,\Theta-\log\tan\frac{1}{2}\,\delta=\int_{\delta}^{\Theta}\frac{d\vartheta}{\sin\vartheta}\tag{7}$$

The difference between (6) and (7) is

$$\int_{0}^{\delta}\{1-e^{-(1-\cos\vartheta)/\varepsilon}\}\,\frac{d\vartheta}{\sin\vartheta}-\int_{\delta}^{\Theta}e^{-(1-\cos\vartheta)/\varepsilon}\,\frac{d\vartheta}{\sin\vartheta}\tag{8}$$

Let δ run from 0 to Θ. The first integral increases monotonically from 0 to the value (6). The second integral decreases monotonically from $+\infty$ to 0. Hence there is one δ_0 at which (8) vanishes. Note that δ_0 cannot be small, because the first integral is small only for $\delta^2\ll2\varepsilon$, while the second is small for $1-\cos\delta\gg\varepsilon$. Yet δ_0 cannot be empoyed as a cut-off, as it cannot be found without the use of the exact result (6). Moreover it depends on Θ, because the second integral in (8) increases with Θ. A cutoff δ can be used if the experimental observations also are done between the angles δ and $\Theta-\delta$.

4. THREE COMMENTS

One comment is that the mean first-passage time is not identical with the actual turning time. The reply is that once ϑ has left the neighborhood of the unstable equilibrium point it moves with negligible fluctuations according to the macroscopic equation (1), so that both times are the same. If the fluctuations are too large for this identification, the concept of turning point itself is not well defined.

A second comment is that the bacterium does not start at $\vartheta = 0$, but is initially dispersed about the north pole according to the equilibrium distribution belonging to the field before its reversal,

$$P(\vartheta, 0) = C \sin \vartheta \, e^{\varepsilon^{-1} \cos \vartheta}, \qquad C^{-1} = 2\varepsilon \sinh \varepsilon^{-1} \tag{9}$$

The mean first-passage time at Θ, when averaged over this initial distribution of the starting ϑ, is

$$\begin{aligned}\overline{\tau(\Theta, \vartheta)} &= \int_0^\pi \tau(\Theta, \vartheta)\, P(\vartheta, 0)\, d\vartheta \\ &= C \int_0^\pi \sin \vartheta \, e^{\varepsilon^{-1} \cos \vartheta}\, d\vartheta \int_\vartheta^\Theta \left\{1 - e^{-\varepsilon^{-1}(1 - \cos \vartheta')}\right\} \frac{d\vartheta'}{\sin \vartheta'}\end{aligned}$$

Actually this expression makes no sense for $\vartheta > \Theta$, but for small ε those values of ϑ do not contribute perceptibly. Integrating and using $C\varepsilon = \exp(-\varepsilon^{-1})$ gives

$$\overline{\tau(\Theta, 0)} = \int_0^\Theta \left\{1 - e^{-\varepsilon^{-1}(1 - \cos \vartheta)}\right\}^2 \frac{d\vartheta}{\sin \vartheta} \tag{10}$$

In the same way as before one may show that this cannot be approximated by (2).

The third comment is that both our results (6) and (10) diverge for $\Theta = \pi$; since they are exact, this means that it actually does take an infinite time to reach the south pole. [To put it differently: the endpoint $\vartheta = \pi$ is a "natural repulsive boundary" of the diffusion equation (4); see ref. 4, p. 313.] To give a precise meaning to the concept of "turning time" one therefore has to agree on a value for Θ at which one considers the turning completed, for instance at $\Theta = \pi - \delta$. It seems more natural to average the endpoint over the ultimate equilibrium distribution. With this definition one finally obtains for the turning time

$$\begin{aligned}\tau &= C \int_0^\pi e^{-\varepsilon^{-1} \cos \Theta} \sin \Theta \, d\Theta \int_0^\Theta \left\{1 - e^{-\varepsilon^{-1}(1 - \cos \vartheta)}\right\}^2 \frac{d\vartheta}{\sin \vartheta} \\ &= \int_0^\pi \left\{1 - e^{-\varepsilon^{-1}(1 + \cos \vartheta)}\right\}\left\{1 - e^{-\varepsilon^{-1}(1 - \cos \vartheta)}\right\} \frac{d\vartheta}{\sin \vartheta}\end{aligned} \tag{11}$$

5. THE COMPUTATION OF THE DISTRIBUTION

Although the first-passage time provides the answer to our question, it is also of interest to obtain a solution to the basic equation (4), again in the limit of small ε. That means that the Brownian fluctuations are small and the rotation is mainly determined by (1), excepting the polar caps. Accordingly, it will be necessary to subdivide the interval $(0, \pi)$ into a main center region and two end regions to be treated separately. (In the language of singular perturbation theory: one inner region and two outer regions.)

The center region can be treated as if no fluctuations exist. Consequently one knows that, if at t_1 the value of ϑ was ϑ_1, its value at a later time t is given by the macroscopic equation (2). Hence

$$P_c(\vartheta, t \mid \vartheta_1, t_1) = \delta[\vartheta - 2\arctan(e^{t-t_1} \tan \tfrac{1}{2}\vartheta_1)]$$

The delta function may be expressed in terms of ϑ_1 as a new variable, provided that the factor $d\vartheta_1/d\vartheta$ is added,

$$P_c(\vartheta, t \mid \vartheta_1, t_1) = \delta\left[\vartheta_1 - 2\arctan\left(e^{-(t-t_1)} \tan \frac{1}{2}\vartheta\right)\right] \times e^{-(t-t_1)} \frac{\cos^2 \frac{1}{2}\vartheta_1}{\cos^2 \frac{1}{2}\vartheta} \tag{12}$$

where the subscript c refers to the center region.

6. STARTING AT THE NORTH POLE

To cover the region near the north pole we rescale:

$$\vartheta = \sqrt{\varepsilon}\,\rho$$

$$\frac{\partial P}{\partial t} = \frac{\partial^2 P}{\partial \rho^2} - \frac{\partial}{\partial \rho}\left(\frac{1}{\rho} + \rho\right) P + \mathcal{O}(\varepsilon) \tag{13}$$

One easily verifies the solution

$$P_0(\rho, t) = \frac{\rho}{e^{2t} - 1} \exp\left[-\frac{\rho^2}{2(e^{2t} - 1)}\right] \tag{14}$$

For $t \to 0$ it reduces to a delta peak on the north pole of our unit sphere and therefore refers to a bacterium that at $t = 0$ points precisely in the z-direction. This solution has to be attached to a solution in the center region obtained in the previous section.

For that purpose consider the general Chapman–Kolmogorov equation for the transition probability,

$$P(\vartheta, t \mid 0, 0) = \int P(\vartheta, t \mid \vartheta_1, t_1)\, d\vartheta_1\, P(\vartheta_1, t_1 \mid 0, 0) \tag{15}$$

Choose the intermediate time t_1 such that $e^{t_1} \sim \varepsilon^{-1/4}$. It is then possible to substitute (14) for the latter factor and (12) for the former. The integration is trivial and the result is

$$P(\vartheta, t \mid 0, 0) = \frac{e^{-(t-t_1)}}{\varepsilon(e^{2t_1}-1)} \frac{\cos^2 \frac{1}{2}\vartheta_1}{\cos^2 \frac{1}{2}\vartheta}\, \vartheta_1 \exp\left[-\frac{\vartheta_1^2}{2\varepsilon(e^{2t_1}-1)}\right]$$

in which ϑ_1 now merely serves as an abbreviation for $2\arctan(e^{-(t-t_1)}\tan\frac{1}{2}\vartheta)$. Evidently only values $\vartheta_1 \sim \varepsilon^{1/4}$ occur, so that one may put

$$\vartheta_1 = 2e^{-(t-t_1)}\tan\tfrac{1}{2}\vartheta, \qquad \cos\tfrac{1}{2}\vartheta_1 = 1$$

Also $e^{2t_1} \sim \varepsilon^{-1/2} \gg 1$, so that

$$P(\vartheta, t \mid 0, 0) = \frac{e^{-2t}}{\varepsilon} \frac{2\sin\frac{1}{2}\vartheta}{\cos^2\frac{1}{2}\vartheta} \exp\left[-\frac{2}{\varepsilon} e^{-2t}\tan^2\frac{1}{2}\vartheta\right] \tag{16}$$

This is the distribution after the unstable polar cap has been left behind, i.e., for $t > t_1$. The explicit mention of t_1 has disappeared from it, as it should. In addition it may be remarked that, as $e^{2t} \gg 1$, no error is made on writing

$$P(\vartheta, t \mid 0, 0) = \frac{1}{\varepsilon(e^{2t}-1)} \frac{2\sin\frac{1}{2}\vartheta}{\cos^2\frac{1}{2}\vartheta} \exp\left[-\frac{2}{\varepsilon}\frac{\tan^2\frac{1}{2}\vartheta}{e^{2t}-1}\right] \tag{17}$$

In this form the result remains true for all t down to $t=0$. For, if one inserts $e^{2t} \sim 1$, the distribution P is seen to be negligible outside a range $\vartheta \sim \sqrt{\varepsilon}$; and inside this range (17) coincides with (14), which had been derived for that region by a different expansion.

7. INITIAL DISTRIBUTION AROUND THE NORTH POLE

In this section the solution of (4) is obtained when the initial distribution is (9) rather than the unrealistic delta function at the pole. First it is necessary to find that solution of (13) that reduces at $t=0$ to $\delta(\rho-\rho_0)$. Such a solution can be found by considering the surface distribution

$p(\vartheta, \psi)$ on the unit sphere. We identify the polar cap with its tangent plane, introduce rectangular coordinates $\xi = \rho \cos \psi$, $\eta = \rho \sin \psi$, and consider the equation

$$\frac{\partial p}{\partial t} = \frac{\partial^2 p}{\partial \xi^2} + \frac{\partial^2 p}{\partial \eta^2} - \frac{\partial}{\partial \xi} \xi p - \frac{\partial}{\partial \eta} \eta p$$
$$= \frac{\partial^2 p}{\partial \rho^2} + \frac{1}{\rho} \frac{\partial p}{\partial \rho} + \frac{1}{\rho^2} \frac{\partial^2 p}{\partial \psi^2} - \rho \frac{\partial p}{\partial \rho} - 2p \tag{18}$$

Take a solution $p(\rho, t)$ that does not depend on ψ; then the function $P(\rho, t) = \rho p(\rho, t)$ obeys (13). The solution of (18) with initial delta peak at ρ_0, ψ_0 is elementary:

$$p = \frac{1}{2\pi(e^{2t} - 1)} \exp\left[-\frac{\rho^2 - 2\rho\rho_0 e^t \cos(\psi - \psi_0) + \rho_0^2 e^{2t}}{2(e^{2t} - 1)} \right]$$

Integration over ψ gives the desired solution of (13),

$$P_{\mathrm{n}}(\rho, t \mid \rho_0, 0) = \frac{\rho}{e^{2t} - 1} \exp\left[-\frac{\rho^2 + \rho_0^2 e^{2t}}{2(e^{2t} - 1)} \right] I_0\left(\frac{\rho\rho_0 e^t}{e^{2t} - 1} \right) \tag{19}$$

where I_0 denotes the Bessel function with imaginary argument and the subscript n refers to the north polar cap. Incidentally, the normalization requires the identity

$$\int_0^\infty e^{-ax^2/2} I_0(bx) x \, dx = \frac{1}{a} e^{b^2/2a} \tag{20}$$

To find the evolution of the distribution once it enters the central region, use again (15), but this time with (19) for the latter factor, and perform the trivial integration. The result is

$$P(\vartheta, t \mid \vartheta_0, 0) = \frac{e^{-2t}}{\varepsilon} \frac{2 \sin \frac{1}{2}\vartheta}{\cos^3 \frac{1}{2}\vartheta} \exp\left[-\frac{2}{\varepsilon} e^{-2t} \tan^2 \tfrac{1}{2}\vartheta \right]$$
$$\times e^{-\vartheta_0^2/2\varepsilon} I_0\left(\frac{2}{\varepsilon} \vartheta_0 e^{-t} \tan \frac{1}{2} \vartheta \right) \tag{21}$$

This is valid for $t > t_1$. No error is made on writing

$$P(\vartheta, t \mid \vartheta_0, 0) = \frac{1}{\varepsilon(e^{2t} - 1)} \frac{2 \sin \frac{1}{2}\vartheta}{\cos^3 \frac{1}{2}\vartheta} \exp\left[-\frac{2 \tan^2 \frac{1}{2}\vartheta}{\varepsilon(e^{2t} - 1)} \right]$$
$$\times \exp\left[-\frac{\vartheta_0^2 e^{2t}}{2\varepsilon(e^{2t} - 1)} \right] I_0\left(\frac{2\vartheta_0 e^t \tan \frac{1}{2}\vartheta}{\varepsilon(e^{2t} - 1)} \right) \tag{22}$$

and in this form it remains valid all the way down to $t = 0$.

It is now possible to average (22) over the initial distribution (9),

$$\overline{P(\vartheta, t)} = C\int_0^\pi e^{\varepsilon^{-1}\cos\vartheta_0} \sin\vartheta_0 \, d\vartheta_0 \, P(\vartheta, t \mid \vartheta_0, 0)$$

$$= \frac{1}{\varepsilon(2e^{2t}-1)} \frac{2\sin\frac{1}{2}\vartheta}{\cos^3\frac{1}{2}\vartheta} \exp\left[-\frac{2\tan^2\frac{1}{2}\vartheta}{\varepsilon(2e^{2t}-1)}\right] \tag{23}$$

This is the probability distribution of the ensemble of bacteria that had reached equilibrium around the north pole before the field was reversed. The south polar cap, however, is not covered by (22) owing to the use of the approximation (12), which diverges at the south pole. This restriction will now be overcome by attaching (22) to an expansion around the south pole, $\vartheta = \pi$.

8. THE SOUTH POLE

To cover the region about the south pole we set $\vartheta = \pi - \sqrt{\varepsilon}\rho$,

$$\frac{\partial P}{\partial t} = \frac{\partial^2 P}{\partial \rho^2} - \frac{\partial}{\partial \rho}\left(\frac{1}{\rho} - \rho\right) P$$

In the same way as in Section 7 one may construct a solution with initial condition $\delta(\rho - \rho_0)$:

$$P_s(\rho, t \mid \rho_0, 0) = \frac{\rho}{1-e^{-2t}} \exp\left[-\frac{\rho^2 + \rho_0^2 e^{-2t}}{2(1-e^{-2t})}\right] I_0\left(\frac{\rho\rho_0 e^{-t}}{1-e^{-2t}}\right) \tag{24}$$

As a preliminary step we attach this solution to a particular solution in the center region, namely (12), which is the solution that starts at t_1 as a delta function at ϑ_1. Since ϑ traverses the center region in a time of order unity, we choose t_2 such that $e^{t_2 - t_1} \sim \varepsilon^{-1/4}$ to make sure that at t_2 the peak has reached the south polar cap. Accordingly, we write the Chapman–Kolmogorov equation with intermediate time t_2,

$$P(\vartheta, t \mid \vartheta_1, t_1) = \int P_s(\vartheta, t \mid \vartheta', t_2) \, d\vartheta' \, P_c(\vartheta', t_2 \mid \vartheta_1, t_1)$$

$$= P_s(\vartheta, t \mid \vartheta_2, t_2) \tag{25}$$

in which $\vartheta_2 = 2\arctan(e^{t_1-t_2}\tan\frac{1}{2}\vartheta_1)$. Setting $\vartheta_2 = \pi - \sqrt{\varepsilon}\rho_2$, one has

$$\rho_2 = \frac{2}{\sqrt{\varepsilon}}\left\{\frac{\pi}{2} - \arctan\left(e^{t_2-t_1}\tan\frac{1}{2}\vartheta_1\right)\right\}$$

$$= \frac{2}{\sqrt{\varepsilon}}\operatorname{arccot} e^{t_2-t_1}\tan\frac{1}{2}\vartheta_1$$

$$= \frac{2}{\sqrt{\varepsilon}}e^{-(t_2-t_1)}\cot\frac{1}{2}\vartheta_1$$

Hence we find for (25)

$$P(\vartheta, t \mid \vartheta_1, t_1) = \frac{\rho}{\sqrt{\varepsilon}}e^{-\rho^2/2}\exp\left[-\frac{2}{\varepsilon}e^{-2(t-t_1)}\cot^2\frac{1}{2}\vartheta_1\right]$$
$$\times I_0\left(\frac{2}{\sqrt{\varepsilon}}\rho e^{-(t-t_1)}\cot\frac{1}{2}\vartheta_1\right)$$

This is how the distribution that started as a delta peak in the center region develops on arrival in the south polar cap.

Our final task is to average ϑ_1 over the distribution (23) of bacteria emerging from the the north polar cap. We use $e^{2t_1} \gg 1$, transform the integration variable ϑ_1 to $\sigma = e^{-t_1}\tan\frac{1}{2}\vartheta_1$, and find

$$\int P(\vartheta, t \mid \vartheta_1, t_1)\,\overline{P(\vartheta_1, t_1)}\,d\vartheta_1$$

$$= 2e^{-3/2}\rho e^{-\rho^2/2}\int \sigma\,d\sigma\exp\left[-\frac{2}{\varepsilon}\frac{e^{-2t}}{\sigma^2} - \frac{1}{\varepsilon}\sigma^2\right] I_0\left(\frac{2}{\sqrt{\varepsilon}}\rho\frac{e^{-t}}{\sigma}\right)$$

It is true that the precise value of t_1 has disappeared, but unfortunately I have not found a more elegant form of this result.

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