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The Exact Probability Distribution of a Two-Dimensional Random Walk

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A calculation is made of the exact probability distribution of the two-dimensional displacement of a particle at time t that starts at the origin, moves in straight-line paths at constant speed, and changes its direction after exponentially distributed time intervals, where the lengths of the straight-line paths and the turn angles are independent, the angles being uniformly distributed. This random walk is the simplest model for the locomotion of microorganisms on surfaces. Its weak convergence to a Wiener process is also shown.

KEY WORDS: Two-dimensional random walk; cell motion on surfaces; exact probability distribution.

1. INTRODUCTION

Several experimental studies on the motion of microorganisms on planar surfaces suggest that this motion can be approximately described as a random broken line.[1-5] After a straight-line path of random length, the microorganism appears to try to find a new direction of linear motion and then continues to move in this direction.

Nossal and Weiss[6,7] developed a model for these locomotions and a method for calculating asymptotically the mean and the covariance matrix of the displacement of these random walks. In this paper we consider the case when the lengths of the linear segments are exponentially distributed (according to the experimental results in Ref. 3), the speed is always constant, the turn angles all have a uniform distribution, and all path lengths and angles are stochastically independent. This can be considered as a model for cell motion, if no chemical stimuli are present. Under these

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assumptions the exact probability distribution of the displacement $X(t)$ of the microorganism at time t can be derived in closed form, which turns out to be astonishingly simple. The density of $X(t)$ on $\{x \in \mathbb{R}^2 \mid |x| < t\}$ is given by Eq. (1.3) (λ^{-1} is the mean length of a linear segment), which is the main result of this paper.

We thus consider the random walk of a particle in $\mathbb{R}^2$ starting at the origin and consisting of straight-line paths separated by discrete turns. The motion along any path is assumed to have constant speed 1. Let $\xi_1, \xi_2,\ldots$ be the random lengths of the straight-line paths and $\theta_1, \theta_2,\ldots$ be the random angles. We assume that $\xi_1, \theta_1, \xi_2, \theta_2,\ldots$ are independent, that $\xi_1, \xi_2,\ldots$ are exponentially distributed with mean $1/\lambda$, and that $\theta_1, \theta_2,\ldots$ have a uniform distribution on $[0, 2\pi)$. Let $Y^{(n)} = \xi_n \exp(i\theta_n)$. The particle travels in direction θ_{n+1} during the time interval $[\sum_{n=1}^{m} \xi_n, \sum_{n=1}^{m+1} \xi_n)$. If t is in this interval, say

$$t = \sum_{n=1}^{m} \xi_n + \alpha\xi_{m+1} \tag{1.1}$$

for some $\alpha \in [0, 1)$, the position of the particle at time t is given by

$$X(t) = \sum_{n=1}^{m} Y^{(n)} + \alpha Y^{(m+1)} \tag{1.2}$$

(position at time $\sum_{n=1}^{m} \xi_n$ plus α times the step in direction θ_{m+1}).

Clearly, $|X(t)| \leqslant t$, where $|\cdot|$ denotes Euclidean length. We shall show that on $\{x \in \mathbb{R}^2 \mid |x| < t\}$, $X(t)$ has the density

$$f_t(x) = \frac{\lambda}{2\pi} (t^2 - |x|^2)^{-1/2} \exp[\lambda(t^2 - |x|^2)^{1/2} - \lambda t] \tag{1.3}$$

It is then obvious that the complete probability distribution of $X(t)$ is given by

$$P(X(t) \in dx) = f_t(x)\, dx + e^{-\lambda t} \mu_t(dx) \tag{1.4}$$

where μ_t is the uniform distribution on the circle $\{x \in \mathbb{R}^2 \mid |x| = t\}$ (the second term is due to the fact that with probability $e^{-\lambda t}$ the direction does not change up to time t).

A particle using this random mechanism to rule its walk might be considered as trying to make it as difficult as possible for an observer to predict its future location. Due to the lack of memory of the exponential distribution, it is impossible to learn from experience about the remaining time of locomotion of the particle in the actually observed direction. The equidistribution of new directions independent of the past excludes any preferences that would facilitate prediction.

It should be remarked that the displacement of the particle at the time of the nth turn is the sum of n independent, rotationally invariant random vectors of exponentially distributed length with mean $1/\lambda$ and therefore has the density

$$\lambda^2[2\pi\Gamma(n/2)]^{-1}(\lambda|x|/2)^{(n/2)-1} K_{(n/2)-1}(\lambda|x|), \qquad x \in \mathbb{R}^2 \qquad (1.5)$$

(1.5) can be derived as follows: In general, for a rotationally invariant, two-dimensional probability density $p(x) = \tilde{p}(r)$, $r = |x|$, with Fourier transform $\varphi(u) = \tilde{\varphi}(s)$, $s = |u|$, we have

$$\tilde{\varphi}(s) = 2\pi \int_0^\infty J_0(sr)\, r\tilde{p}(r)\, dr$$

$$\tilde{p}(r) = (2\pi)^{-1} \int_0^\infty J_0(st)\, s\tilde{\varphi}(s)\, ds$$

(see Ref. 10, p. 523; the second equation follows by Hankel inversion). In our case, each $Y^{(i)}$ has the density $(2\pi|x|)^{-1}\lambda e^{-\lambda|x|}$ and thus the characteristic function

$$\varphi(u) = \int_0^\infty J_0(|u|r)\, \lambda e^{-\lambda r}\, dr = [1 + (|u|/\lambda)^2]^{-1/2}$$

(see Ref. 11, p. 686, formula 6.565.4).

In light of (1.5), the simple formula (1.3) for $f_t(x)$ is striking. One should mention that the characteristic function ϕ_t of $X(t)$ apparently cannot be given in closed form. Tedious calculations lead to the following representation for ϕ_t:

$$\phi_t(u) = (2\pi)^{-1/2} \sum_{j=0}^{\infty} \frac{1}{4^j (j!)^2} \left[\sum_{i=0}^{j} (-1)^{i+j} \binom{j}{i} b_{2i} \right] (t|u|)^{2j} + J_0(t|u|)\, e^{-\lambda t}$$

where $b_0, b_1, b_2, \ldots$ are defined recursively by

$$b_0 = 1 - e^{-\lambda t}, \qquad b_k = 1 - (k b_{k-1}/\lambda t) \quad \text{for} \quad k \geqslant 1$$

The probability distribution (1.4) (or variants of it) apparently has not yet occured in other contexts.

Figure 1 shows the curves of $f_t(x) = h_t(|x|)$ for $t = 1$ and $\lambda = 0.1$, 0.5, 1, 2, 5. Each f_t is unbounded for $|x|$ near t (see the remark at the end of Sec-

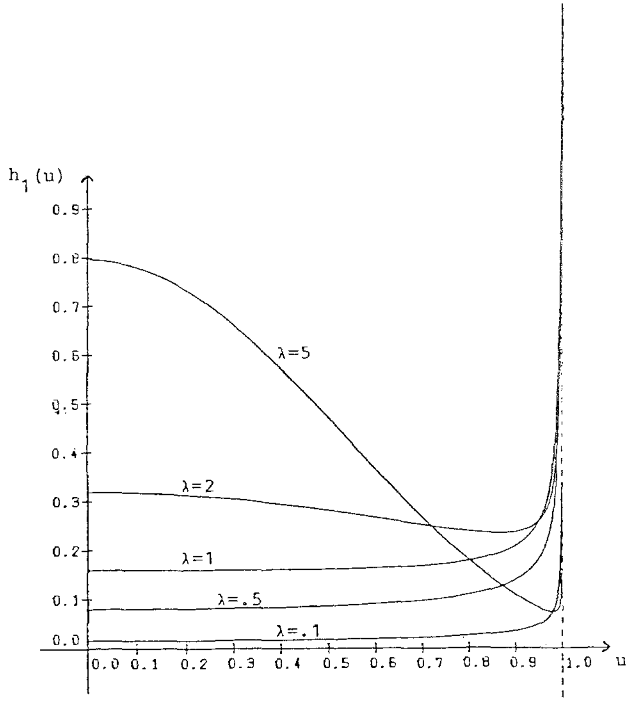

Fig. 1. Plot of $h_1(u)$ for different values of λ.

tion 2). For $\lambda t > 1$ the function h_t: $[0, t) \to (0, \infty)$ decreases in $[0, (t^2 - \lambda^{-2})^{1/2}]$ and increases in $[(t^2 - \lambda^{-2})^{1/2}, t)$ up to infinity. The minimal value is

$$h_t((t^2 - \lambda^{-2})^{1/2}) = \lambda^2/2\pi e^{\lambda t - 1}$$

If $\lambda t \leqslant 1$, h_t is monotone increasing. However, h_t' is quite small outside some neighborhood of t, so that $h_t(u)$ is nearly constant for u not close to t.

Note that λt is the mean number of turns in the time interval $[0, t)$. If $\lambda t \leqslant 1$, $P(X(t) \in dx)$ is an increasing function of $|x|$, so that the probability that $X(t)$ takes a value x with $|x|$ close to t is higher than the corresponding probability for any other value with smaller distance to the origin. A similar situation occurs for the so-called arcsine distribution with density $[r(1-r)]^{-1/2}$, $r \in (0, 1)$ (see, e.g., Ref. 9, Chapter III). If $\lambda t > 1$, both extreme values 0 and t of the range of $|X(t)|$ are maxima of h_t; however, h_t is unbounded only near t. It is astonishing that the phenomenon that $P(X(t) \in dx)$ remains maximal in the neighborhood of $|x| = t$ does not disappear for large λt.

If $t \to \infty$ and $\lambda \to \infty$ in such a way that t/λ converges, say $t/\lambda \to \beta > 0$, the density f_t satisfies

$$f_t(x) = (2\pi)^{-1}[(t/\lambda)^2 - (|x|/\lambda)^2]^{-1/2} \exp(-|x|^2 \lambda/2\theta)$$

where $(t^2 - |x|^2)^{1/2} \leqslant \theta \leqslant t$. Therefore,

$$f_t(x) \to (2\pi\beta)^{-1} \exp(-|x|^2/2\beta)$$

Thus, the asymptotic distribution of $X(t)$ is symmetric bivariate normal. In Section 3 we sharpen this result and show that the motion of the particle can be approximately described by a two-dimensional Wiener process.

For random vectors U and V, the quantities $L(U)$, $L(U \mid V)$, and $L(U \mid V = v)$ denote the distribution of U, the conditional distribution of U, given V, and the conditional distribution of U, given $V = v$, respectively. For any set A we set $1_A(x) = 1$ if $x \in A$ and $= 0$ if $x \notin A$.

2. DERIVATION OF THE DENSITY

Let

$$\tau(t) := \sup \left\{ n \geqslant 0 \,\middle|\, \sum_{j=1}^{n} \xi_j \leqslant t \right\}$$

$\tau(t)$ is the number of turns up to time t and obviously has a Poisson distribution with parameter λt. Let μ_t be the equidistribution on $\{x \in \mathbb{R}^2 \mid |x| = t\}$. Then $L(X(t) \mid \tau(t) = 0) = \mu_t$. We shall prove by induction that for $n \geqslant 1$, $L(X(t) \mid \tau(t) = n)$ has a density $f_t(x \mid n)$ given by

$$f_t(x \mid n) = (n/2\pi t^2)[1 - (|x|/t)^2]^{(n-2)/2} 1_{[0,t)}(x), \qquad n \geqslant 1 \tag{2.1}$$

It follows by the formula of total probability that

$$\begin{aligned} L(X(t)) &= \sum_{n=0}^{\infty} P(\tau(t) = n)\, L(X(t) \mid \tau(t) = n) \\ &= e^{-\lambda t} \left[\mu_t + \sum_{n=1}^{\infty} \frac{(\lambda t)^n}{n!} L(X(t) \mid \tau(t) = n) \right] \end{aligned} \tag{2.2}$$

By (2.2), the density of $X(t)$ on $\{x \in \mathbb{R}^2 \mid |x| < t\}$ is thus given by

$$\begin{aligned} f_t(x) &= \exp(-\lambda t)(2\pi t^2)^{-1} \sum_{n=1}^{\infty} \frac{n(\lambda t)^n}{n!} \left[1 - \left(\frac{|x|}{t} \right)^2 \right]^{(n-2)/2} \\ &= \frac{\lambda}{2\pi} (t^2 - |x|^2)^{-1/2} \exp[\lambda (t^2 - |x|^2)^{1/2} - \lambda t] \end{aligned} \tag{2.3}$$

Hence it suffices to derive (2.1). Before proceeding, it is interesting to note that $f_t(x\mid n)$ is also the density of the first two coordinates of a random vector with uniform distribution on the sphere $\{y\in\mathbb{R}^{n+2}\mid |y|=t\}$.

Let $g_t(x\mid s,\alpha,n)$ be the conditional density of $X(t)$ given that $\tau(t)=n$ and $Y^{(1)}=y=se^{i\alpha}$. Let $h(s,\alpha\mid n)$ be the joint conditional density of the polar coordinates (s,α) of $Y^{(1)}$ given that $\tau(t)=n$. For $\alpha\in[0,2\pi)$ and $0<s<t$ we have

$$\begin{aligned} h_t(s,\alpha\mid n) &= \frac{P(\tau(t)=n\mid Y^{(1)}=se^{i\alpha})(2\pi)^{-1}\lambda e^{-\lambda s}}{P(\tau(t)=n)} \\ &= \frac{\lambda}{2\pi}e^{-\lambda s}\frac{P(\tau(t-s)=n-1)}{P(\tau(t)=n)} \\ &= \frac{\lambda}{2\pi}e^{-\lambda s}\frac{e^{-\lambda(t-s)}(\lambda(t-s))^{n-1}/(n-1)!}{e^{-\lambda t}(\lambda t)^n/n!} \\ &= \frac{n}{2\pi t}\left(1-\frac{s}{t}\right)^{n-1} \end{aligned} \tag{2.4}$$

and

$$g_t(x\mid s,\alpha,n)=f_{t-s}(x-se^{i\alpha}\mid n-1) \tag{2.5}$$

In (2.4) we have used Bayes' formula and the relation

$$\begin{aligned} P(\tau(t)=n\mid Y^{(1)}=se^{i\alpha}) &= P(\tau(t)-\tau(s)=n-1\mid Y^{(1)}=se^{i\alpha}) \\ &= P(\tau(t-s)=n-1) \end{aligned} \tag{2.6}$$

Relation (2.5) follows from the equation

$$\begin{aligned} &P(X(t)\in B\mid Y^{(1)}=se^{i\alpha},\tau(t)=n) \\ &\quad = P(X(t-s)\in B-se^{i\alpha}\mid \tau(t-s)=n-1) \end{aligned} \tag{2.7}$$

where, of course, $B-se^{i\alpha}=\{b-se^{i\alpha}\mid b\in B\}$ and B is a Borel set in $\mathbb{R}^2$. To see (2.7), note that $Y^{(1)}=se^{i\alpha}$ implies that the first turn occurs at time s so that in the time interval $(s,t]$ the direction changes $n-1$ times, because $\tau(t)=n$. Further, one has to use the fact that the conditional distribution of $X(t)-X(s)$, given $Y^{(1)}=se^{i\alpha}$, is equal to $L(X(t-s))$ and that $X(t)-X(s)$ is conditionally independent of $\{X(t')\mid 0\leqslant t'<s\}$, given that $Y^{(1)}=se^{i\alpha}$.

Our induction proof of (2.1) is based on the identity

$$\begin{aligned} f_t(x\mid n) &= \int_0^t\int_0^{2\pi} g_t(x\mid s,\alpha,n)\,h_t(s,\alpha\mid n)\,d\alpha\,ds \\ &= \frac{n}{2\pi t}\int_0^t\int_0^{2\pi} f_{t-s}(x-se^{i\alpha}\mid n-1)\left(1-\frac{s}{t}\right)^{n-1}d\alpha\,ds \end{aligned} \tag{2.8}$$

[the second equation follows from (2.4) and (2.5)]. Suppose that (2.1) holds for $f_t(x \mid n-1)$ for some $n \geqslant 2$. To prove (2.1) for $f_t(x \mid n)$, we insert the expression for $f_t(x \mid n-1)$ into (2.8) and obtain

$$\begin{aligned}
f_t(x \mid n) &= \frac{n(n-1)}{4\pi^2 t} \int_0^t \left\{ \int_0^{2\pi} \left(1 - \frac{|x - se^{i\alpha}|^2}{(t-s)^2} \right)^{(n-3)/2} (t-s)^{-2} \right. \\
&\quad \left. \times \left(1 - \frac{s}{t} \right)^{n-1} 1_{[0, t-s)}(|x - e^{i\alpha}|) \, d\alpha \right\} ds \\
&= \frac{n(n-1)}{4\pi^2 t^2} \int_0^1 \left\{ \int_0^{2\pi} \left[1 - \frac{|x/t|^2 + u^2 - 2u\langle x/t, e^{i\alpha} \rangle}{(1-u)^2} \right]^{(n-3)/2} \right. \\
&\quad \left. \times (1-u)^{n-3} 1_{[0,1)} \left(\frac{(|x|/t)^2 + u^2 - 2u\langle x/t, e^{i\alpha} \rangle}{(1-u)^2} \right) d\alpha \right\} du \\
&= \frac{n(n-1)}{4\pi^2 t^2} \int_0^1 \left\{ \int_0^{2\pi} \left[(1-u)^2 - \left(\frac{|x|}{t} \right)^2 - u^2 \right. \right. \\
&\quad \left. + 2u \frac{|x|}{t} \cos(\alpha + \arg x) \right]^{(n-3)/2} \\
&\quad \left. \times 1_{[0,1)} \left(\frac{|x/t|^2 + u^2 - 2u(|x|/t) \cos(\alpha + \arg x)}{(1-u)^2} \right) d\alpha \right\} du \\
&= \frac{n(n-1)}{4\pi^2 t^2} \int_0^1 \left\{ \int_{\arg x}^{2\pi + \arg x} \left(1 - 2u - \left| \frac{x}{t} \right|^2 + 2u \frac{|x|}{t} \cos \beta \right)^{(n-3)/2} \right. \\
&\quad \left. \times 1_{[0,1)} \left(\frac{|x/t|^2 + u^2 - 2u(|x|/t) \cos \beta}{(1-u)^2} \right) d\beta \right\} du \qquad (2.9)
\end{aligned}$$

Here $\langle , \rangle$ denotes the usual scalar product, and $\arg x \in [0, 2\pi)$ is the angle between the vector x and the x_1 axis. For the third equation note that

$$\langle x/t, e^{i\alpha} \rangle = (|x|/t) \cos(\alpha + \arg x)$$

In the fourth equation the substitution $\beta = \alpha + \arg x$ is carried out in the inner integral.

Next we change the order of integration; note that the integrand does not vanish only if

$$0 < u < [1 - (|x|/t)^2]/2[1 - (|x|/t) \cos \beta] \qquad (2.10)$$

We denote the right-hand side of (2.10) by $b(x, t, \beta)$. Then, using the relation

$$\int_0^{b(x,t,\beta)} \left(1 - \frac{u}{b(x,t,\beta)} \right)^{(n-3)/2} du = \frac{2b(x,t,\beta)}{n-1}$$

we obtain

$$f_t(x\,|\,n)=\frac{n(n-1)}{4\pi^2t^2}\int_0^{2\pi}\left\{\int_0^{b(x,t,\beta)}\left[1-\frac{|x|^2}{t^2}-2u\left(1-\frac{|x|}{t}\cos\beta\right)\right]^{(n-3)/2}du\right\}d\beta$$
$$=\frac{n}{4\pi^2t^2}\left[1-\left(\frac{|x|}{t}\right)^2\right]^{(n-1)/2}\int_0^{2\pi}\left(1-\frac{|x|}{t}\cos\beta\right)^{-1}d\beta$$
$$=\frac{n}{2\pi t^2}\left[1-\left(\frac{|x|}{t}\right)^2\right]^{(n-2)/2} \tag{2.11}$$

Finally, we have to show that (2.1) also holds for $n=1$. Under the condition $\tau(t)=1$ we have

$$X(t)=Y^{(1)}+(t-|Y^{(1)}|)\,e^{i\theta_2} \tag{2.12}$$

It follows that

$$|X(t)|^2=2\,|Y^{(1)}|\,(t-|Y^{(1)}|)(\cos\eta-1)+t^2 \tag{2.13}$$

where η is independent of $Y^{(1)}$ and uniformly distributed on $[0, 2\pi)$. Conditionally on $\tau(t)=1$, $|Y^{(1)}|$ is uniform on $[0, t]$. Since $\cos\eta$ has the density $\pi^{-1}(1-u^2)^{-1/2}$, $-1<u<1$, a straightforward calculation shows that $|X(t)|$ has the density $g_t(u)=(u/t^2)(1-u^2t^{-2})^{-1/2}$, $0<u<t$. By rotational symmetry,

$$f_t(x\,|\,1)=(2\pi\,|x|)^{-1}\,g_t(|x|)$$

Now (2.1) follows for $n=1$.

We finally mention that the unboundedness of $f_t(x)$ as $|x|\uparrow t$ is caused by the contribution of $f_t(x\,|\,1)$. For $n\geqslant 2$ the density $f_t(x\,|\,n)$ is bounded on $|x|<t$. Given that the direction changes n times up to t, the probability that $\alpha<|X(t)|<\alpha+\varepsilon$ is monotone increasing with respect to $\alpha\in(0, t-\varepsilon)$ if $n=1$ and monotone decreasing if $n>1$.

3. ASYMPTOTIC BEHAVIOR

In Section 1 it was proved that the relations $t\to\infty$, $\lambda\to\infty$, and $t/\lambda\to\beta>0$ imply the convergence of $X(t)$ to a bivariate normal distribution. Now let us fix $\lambda>0$ and consider the *rescaled process*

$$X_\nu(t)=\nu^{-1/2}X(\nu t),\qquad r\geqslant 0,\quad \nu>0 \tag{3.1}$$

We shall show that for all $T>0$ the process $X_\nu=(X_\nu(t))_{0\leqslant t\leqslant T}$ converges weakly to the two-dimensional Wiener process $W=(W(t))_{0\leqslant t\leqslant T}$ as $\nu\to\infty$, where $W(t) = (W_1(t), W_2(t))$ and $W_1(t)$, $W_2(t)$ are independent one-dimensional Wiener processes with drift 0 and $E(W_i(t)^2) = t/2\lambda$. Thus, for any continuous functional F: $C[0, T] \to \mathbb{R}$ we have $F(X_\nu) \to F(W)$ in distribution. If the mean step length tends to zero and the time t is large, the motion of the particle can be approximately described by a Wiener process.

In order to prove

$$X_\nu \to W \text{ weakly,} \qquad \text{as} \quad \nu \to \infty \tag{3.2}$$

note that $X_\nu(t)$ can be written as

$$X_\nu(t) = \nu^{-1/2} \left(\sum_{j=1}^{\tau(\nu t)} Y^{(j)} + \alpha Y^{(\tau(\nu t)+1)} \right) \tag{3.3}$$

where $\alpha \in [0, 1)$. We define the auxiliary process $Y_\nu = (Y_\nu(t))_{0 \leqslant t \leqslant T}$ by

$$Y_\nu(t) = (\lambda/\nu)^{1/2} \sum_{j=1}^{[\nu t]} Y^{(j)}, \qquad 0 \leqslant t \leqslant T \tag{3.4}$$

where $[\nu t]$ denotes the largest integer $\leqslant \nu t$. Then the two-dimensional version of Donsker's invariance principle[12] yields $Y_\nu \to W$ weakly in the space $D[0, T]$ of right-continuous functions on $[0, T]$ with left-hand limits. The results of Billingsley (Ref. 12, pp. 143–148) on random changes of time say that for arbitrary positive-integer-valued random variables N_ν for which there are constants $a_\nu \in \mathbb{R}$ such that $N_\nu/a_\nu \to^P 1$ $(\nu \to \infty)$ the process

$$\tilde{Y}_\nu = (Y_{N_\nu}(t))_{0 \leqslant t \leqslant T}$$

tends to W in $D[0, T]$. The strong law of large numbers gives $\tau(\nu t)/\lambda \nu t \to 1$ almost surely. The proof in Ref. 12 can be easily imitated to yield

$$\left\{ [\tau(\nu t)/t]^{-1/2} \sum_{j=1}^{\tau(\nu t)} Y^{(j)} \right\}_{0 \leqslant t \leqslant T} \to W \text{ weakly} \tag{3.5}$$

From (3.5) it will follow that $X_\nu \to W$ in $D[0, T]$ if we can prove that

$$P(\nu^{-1/2} \sup_{0 \leqslant t \leqslant T} |Y^{(\tau(\nu t)+1)}| > \varepsilon) \to 0 \qquad (\nu \to \infty) \tag{3.6}$$

for all $\varepsilon > 0$. By the strong law of large numbers, for all $\delta > 0$ there is a $\nu_0 > 0$ such that

$$P(\tau(\nu T) \leqslant \lambda \nu T(1 + \varepsilon) \text{ for all } \nu \geqslant \nu_0) > 1 - \delta$$

Hence for $v \geqslant v_0$ we obtain

$$P(v^{-1/2} \sup_{0 \leqslant t \leqslant T} |Y^{(\tau(vt)+1)}| > \varepsilon)$$
$$\leqslant \delta + P(v^{-1/2} \max_{1 \leqslant j \leqslant [\lambda v T(1+\varepsilon)]+1} |Y^{(j)}| > \varepsilon)$$
$$= \delta + 1 - P(\xi_j \leqslant \varepsilon v^{1/2} \text{ for } j = 1,..., [\lambda v T(1+\varepsilon)] + 1)$$
$$= \delta + 1 - [1 - \exp(-\lambda \varepsilon v^{1/2})]^{[\lambda v T(1+\varepsilon)]+1}$$
$$\to \delta \quad \text{as} \quad v \to \infty$$

Since $\delta > 0$ is arbitrary, (3.6) is proved.

Since X_v and W are $C[0, T]$-valued, convergence in $D[0, T]$ implies that in $C[0, T]$. Therefore, (3.2) is proved.

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