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A STOCHASTIC MODEL FOR THE STEPWISE MOTION IN ACTOMYOSIN DYNAMICS

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Abstract. A jump-diffusion process is proposed to describe the displacements performed by single myosin heads along actin filaments during the rising phases. The process consists of the superposition of a Wiener and a jump process, with jumps originated by sequences of Poisson-distributed energy-supplying pulses. In a previous paper [6], the amplitude of the jumps was described by a mixture of two Gaussian distributions. To embody the effects of ATP hydrolysis [1], we now refine such a model by assuming that the jumps' amplitude is described by a mixture of three Gaussian distributions. This model has been inspired by the experimental data of T. Yanagida and his co-workers concerning observations at single molecule processes level as described in [10] and in the references therein.

1 Introduction Muscle fibers are composed by a great number of even smaller fibers, called myofibrils, arranged parallel to the muscle fiber's major axis. The myofibrils consist of two different filaments: thick filaments, composed by myosin molecules, and thin filaments, composed by actin molecules. Myosin molecules' extremity stick out from the filament as small heads. Muscle contraction occurs when myosin molecules slide along actin filaments, fuelled by the chemical energy originating from ATP hydrolysis. The traditional model explaining the mechanism of myosin movement is the so-called "lever-arm swinging model" in which the neck region of the myosin head swings to generate displacement (see Cooke [4]). The swing motion is coupled tightly to the ATP hydrolysis cycle i.e. the myosin molecule moves in a single forward step during each ATPase reaction. The size of myosin displacement is about 6nm.

Using new techniques for manipulating single actin filaments, Kitamura *et al.* [10] have obtained highly precise and reliable measurements of the displacements performed by single myosin heads along actin filaments during their rising phases. They have recorded myosin displacements of 10nm $\div$ 30nm. These values indicate that, during each biochemical cycle of ATP hydrolysis, the myosin head may interact several times with an actin filament, undergoing multiple steps. The steps occur randomly in time, mainly in a forward direction, roughly not more than 10% in the backward direction. The step-size is approximately 5.5nm, that identifies with the interval between adjacent monomers in one strand of the actin filament. These observations clearly contradict the traditional lever-arm model, suggesting that a biased Brownian ratchet mechanism could be invoked: myosin head moves along the actin filament driven by the Brownian motion and the ATP hydrolysis biases the direction of the movement.

In this paper we propose a stochastic model for the description of the displacements performed by the myosin head durig a rising phase, on account of the experimental results presented in Kitamura and Yanagida [9]. Our model is not exactly a ratchet-based model but all the relevant basic ingredients are preserved: exploitation of Brownian motion, the

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assumption that energy released by ATP hydrolysis is responsible for the myosin displacements and the intrinsic asymmetry of the actomyosin system. To achieve directional motion, in addition to thermal noise and anisotropy, we consider an energy supply, resulting from the hydrolysis of ATP (see Buonocore and Ricciardi [1]). We assume that this energy is stored by the myosin head and a part of it is released by small quanta of constant magnitudes. Usually not each energy release produces a step, but several releases are needed to generate a single step. We further assume that myosin head is embedded in a viscous fluid in thermal equilibrium and denote by β_v the viscous friction drag coefficient that in the experimental conditions is estimated as 90 pN.

Aiming to a phenomenological model to account for the available data on the displacements of the myosin head along an actin filament, we take as starting point the articles by Di Crescenzo *et al.* [6] and by Buonocore *et al.* [2], in which a stochastic process consisting of the superposition of Wiener and jump processes is discussed. Myosin head's slide along the actin filament is viewed as a Brownian motion perturbed by jumps that occurr according to a Poisson process. Their amplitude is described by a mixture of three Gaussian random variables.

The transition density of the stochastic process describing the stepwise motion and some of its moments are obtained in Section 2. In Section 3 we analyze the duration of the rising phase U and the position V of the myosin at the end of the rising phase. For both variables we obtain the density and some moments. In Section 4 the special case when the backward jumps are not allowed is considered. Our results appear to be in qualitative agreement with the available experimental observations.

2 The model Let $\{X(t),\, t \geq 0\}$ denote the real-valued stochastic process describing the motion of the myosin head along the actin filament during the rising phase. In the absence of jumps, the myosin head is assumed to move according to a Wiener process with zero drift and infinitesimal variance $\delta^2 = 0.09\,(\mathrm{nm})^2/\mathrm{ms}$. Here use of relation $\delta^2 = 2k_BT/\beta_v$ has been made, with $\beta_v = 90\,\mathrm{pN}$ and where $k_BT \sim 4\,\mathrm{pNnm}$ is the thermal energy at absolute temperature T, $k_B = 0.01381\,\mathrm{pN}\cdot\mathrm{nm/K}$ denoting the Boltzmann constant and $T = 293\,\mathrm{K}$ the environmental temperature. According to the previous assumptions, at the occurence of the i-th event of a Poisson process $\{N(t),\, t \geq 0\}$ of intensity λ, an energy release occurs and consequently the myosin head performs a jump of random amplitude Y_i. The mean amplitude of such a jump is L, 0 and $-L$ with probabilities p, $1-p-q$ and q, respectively. The following stochastic equation thus holds:

$$X(t) = \delta\, B(t) + \sum_{i=1}^{N(t)} Y_i, \qquad t > 0, \tag{1}$$

where $\{B(t),\, t \geq 0\}$ is the standard Brownian motion, and $X(0) = 0$. (We have arbitrarily set 0 as the starting point of the motion). Note that the diffusive component of the motion has zero drift, according to the experimental evidence (see Kitamura *et al.* [10]). We suppose that processes $B(t)$, $N(t)$ and r.v.'s $Y_1, Y_2, \ldots$ are independent, where Y_i's are copies of a random variable Y characterized by distribution function $F_Y(y)$ and probability density $f_Y(y)$. The latter is assumed to be a mixture of three Gaussian densities $f_{Z_1}(y)$, $f_{Z_2}(y)$ and $f_{Z_3}(y)$ with means L, 0 and $-L$ respectively, and identical variance σ^2. Hence, for all $y \in \mathbb{R}$ we have

$$\begin{aligned} f_Y(y) &= \frac{\mathrm{d}F_Y(y)}{\mathrm{d}y} = p\, f_{Z_1}(y) + (1-p-q)\, f_{Z_2}(y) + q\, f_{Z_3}(y) \\ &= \frac{1}{\sqrt{2\pi\sigma^2 t}} \left\{ p \exp\Big(-\frac{(y-L)^2}{2\sigma^2 t}\Big) + (1-p-q) \exp\Big(-\frac{y^2}{2\sigma^2 t}\Big) + q \exp\Big(-\frac{(y+L)^2}{2\sigma^2 t}\Big) \right\}, \end{aligned} \tag{2}$$

with $\mathrm{E}(Y) = L\,(p-q)$ and $\mathrm{Var}(Y) = \sigma^2$. We set $L = 5.5\,\mathrm{nm}$ (the distance between adjacent actin monomers) and $\sigma^2 = 0.1\ (\mathrm{nm})^2/\mathrm{ms}$. Densities $f_{Z_1}(y)$, $f_{Z_2}(y)$ and $f_{Z_3}(y)$ account for the following: $f_{Z_1}(y)$ describes the size of forward steps, $f_{Z_3}(y)$ that of backward steps, whereas $f_{Z_2}(y)$ accounts for an energy release that does not produce a step.

For all $x \in \mathbb{R}$ and $t \geq 0$ let us now introduce the following probability densities:

$$f(x,t) := \frac{\partial}{\partial x} \mathrm{P}\{X(t) \leq x \,|\, X(0) = 0\}, \tag{3}$$

$$f_n(x,t) := \frac{\partial}{\partial x} \mathrm{P}\{X(t) \leq x \,|\, X(0) = 0, N(t) = n\}, \qquad n = 1, 2, \dots . \tag{4}$$

One has:

$$f(x,t) = \sum_{n=0}^{\infty} f_n(x,t)\, \mathrm{P}\{N(t) = n\}, \tag{5}$$

where

$$\mathrm{P}\{N(t) = n\} = \frac{(\lambda t)^n\, \mathrm{e}^{-\lambda t}}{n!}, \qquad n = 0, 1, \dots, \tag{6}$$

is the probability distribution of a Poisson process $N(t)$ having intensity λ. The conditional density $f_n(x,t)$ can be expressed as follows:

$$f_n(x,t) = \begin{cases} f_W(x, t \,|\, x_0) & \text{if } n = 0 \\ \displaystyle\int_{-\infty}^{\infty} f_W(x-y, t \,|\, x_0)\, \mathrm{d}F_Y^{(n)}(y) & \text{if } n = 1, 2, \dots, \end{cases} \tag{7}$$

where

$$f_W(x,t) = \frac{1}{\sqrt{2\pi\delta^2 t}} \exp\left\{ -\frac{x^2}{2\delta^2 t} \right\}, \qquad x \in \mathbb{R}$$

is the transition density of a Wiener process with zero drift and infinitesimal variance δ^2, and where $F_Y^{(n)}(y)$ denotes the n-fold convolution of $F_Y(y)$ with itself. From (2), by induction we obtain:

$$\mathrm{d}F_Y^{(n)}(y) = \sum_{k=0}^{n} \binom{n}{k} (1-p-q)^{n-k} \sum_{j=0}^{k} \binom{k}{j} p^j\, q^{k-j}\, \psi_{j,k,n}(y)\, \mathrm{d}y, \tag{8}$$

where $\psi_{j,k,n}(y)$ denotes a normal density with mean $(2j-k)L$ and variance $n\sigma^2$. Hence, from (7) and (8), for $x \in \mathbb{R}$, $t > 0$ and $n = 0, 1, \dots$ we have:

$$f_n(x,t) = \frac{1}{\sqrt{2\pi(\delta^2 t + n\,\sigma^2)}} \sum_{k=0}^{n} \binom{n}{k} (1-p-q)^{n-k} \sum_{j=0}^{k} \binom{k}{j} p^j\, q^{k-j} \exp\left\{ -\frac{[x-(2j-k)\,L]^2}{2(\delta^2 t + n\,\sigma^2)} \right\}. \tag{9}$$

Recalling Eq. (5), from Eqs. (9) and (6), for all $x \in \mathbb{R}$ and $t \geq 0$ we finally obtain the probability density of $X(t)$:

$$f(x,t) = \mathrm{e}^{-\lambda t} \sum_{n=0}^{\infty} \frac{(\lambda t)^n}{n!\,\sqrt{2\pi(\delta^2 t + n\,\sigma^2)}} \sum_{k=0}^{n} \binom{n}{k} (1-p-q)^{n-k} \times \sum_{j=0}^{k} \binom{k}{j} p^j q^{k-j} \exp\left\{ -\frac{[x-(2j-k)\,L]^2}{2(\delta^2 t + n\,\sigma^2)} \right\}. \tag{10}$$

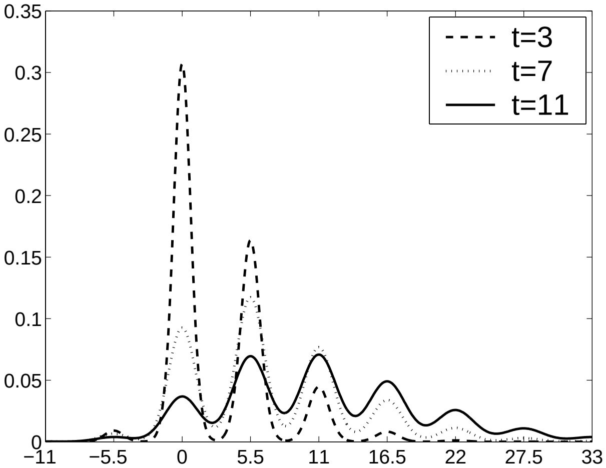

Figure 1: Plot of density (10) with $\sigma^2 = 0.1$, $p = 0.18$, $q = 0.01$ and $\lambda = 1.10$.

Note that, as shown in Di Crescenzo *et al.* [6], this is the solution of the following integro-differential equation:

$$\frac{\partial f}{\partial t} = -\lambda f + \frac{\delta^2}{2}\frac{\partial^2 f}{\partial x^2} + \lambda \int_{-\infty}^{\infty} f(x-y,t)\, \mathrm{d}F_Y(y),$$

with initial condition $\lim_{t\downarrow 0} f(x,t) = \delta(x)$. Density (10) is multimodal, with peaks located at multiples of L (see the example plotted in Figure 1). If $p > q$, at each point $x = kL$ (k integer) where a peak exists, this peak is higher than the symmetric peak located at $-kL$, a manifestation of the prevalence of forward with respect to backward displacements.

Let us now obtain some moments of $X(t)$. From (1) we have:

$$\mathrm{E}[X(t)] := m(t) = L(p-q)\,\lambda t, \tag{11}$$

$$\mathrm{Var}[X(t)] := v^2(t) = \{[L^2(p+q)+\sigma^2]\,\lambda + \delta^2\}\,t, \tag{12}$$

$$\mathrm{E}\{[X(t)-m(t)]^3\} = L(p-q)(L^2+3\sigma^2)\,\lambda t. \tag{13}$$

Hence, from (11) and (12) the coefficient of variation follows:

$$\mathrm{CV}[X(t)] := \frac{v(t)}{m(t)} = \frac{\sqrt{[L^2(p+q)+\sigma^2]\,\lambda+\delta^2}\;\sqrt{t}}{L(p-q)\lambda\, t}. \tag{14}$$

Let us denote by $\mu(t) = X(t)/t$ the velocity of the myosin head displacement. Making use of Eqs. (11) and (12) we obtain the mean and the variance of $\mu(t)$:

$$\begin{aligned} \mathrm{E}[\mu(t)] &= L(p-q)\lambda, \\ \mathrm{Var}[\mu(t)] &= \frac{[L^2(p+q)+\sigma^2]\,\lambda+\delta^2}{t}. \end{aligned} \tag{15}$$

Finally, Eqs. (12) and (13) yield the skewness:

$$\frac{\mathrm{E}[X(t)-m(t)]^3}{v^3(t)} = \frac{\lambda(p+q)L(p-q)(L^2+3\sigma^2)}{\{[L^2(p+q)+\sigma^2]\lambda+\delta^2\}^{3/2}\ \sqrt{t}}. \tag{16}$$

The skewness goes to zero as $t \to +\infty$, it is positive (negative) as $p > q$ ($p < q$), whereas it vanishes when $p = q$. Under the assumption $p > q$, which is of interest in the context of myosin head's motion, we have the following monotonicity properties of the skewness:

(i) as a function of $\lambda \in (0, +\infty)$, it is increasing for $\lambda < \overline{\lambda} \equiv 2\delta^2/[L^2(p+q)+\sigma^2]$, decreasing for $\lambda > \overline{\lambda}$, and goes to 0 as $\lambda \to +\infty$;

(ii) as a function of $\sigma^2 \in (0, +\infty)$, it is increasing if $\sigma^2 < \overline{\sigma}^2 \equiv L^2[2\,(p+q)-1]+2\delta^2/\lambda$, decreasing for $\sigma^2 > \overline{\sigma}^2$, and tends to 0 when $\sigma^2 \to +\infty$.

Let us denote by M the r.v. describing the number of energy quanta releases required to produce one step, that corresponds to a jump of mean amplitude $-L$ or L. On the ground of our assumptions, M is a geometric r.v. with parameter $p+q$. Denoting by D the r.v. describing the dwell time, i.e. the time between consecutive myosin jumps, we have

$$D = T_1 + \cdots + T_M, \tag{17}$$

where T_i is the duration of the effect of the i-th energy quantum release. Being $N(t)$ a Poisson process with intensity λ, we have that $T_1, T_2, \ldots$ are i.i.d. exponential r.v.'s with mean λ^{-1}. This is in agreement with Kitamura and Yanagida [9], whose dwell-time histograms are well fitted by exponential curves. From (17) we obtain

$$\mathrm{E}(\mathrm{e}^{Ds}) = \sum_{k=1}^{+\infty} \mathrm{E}(\mathrm{e}^{s(T_1+\cdots+T_k)})\,\mathrm{P}(M=k) = \frac{\lambda(p+q)}{\lambda(p+q)-s}, \qquad s < \lambda(p+q),$$

so that the dwell time D is exponentially distributed with mean

$$\mathrm{E}(D) = \frac{1}{\lambda(p+q)}. \tag{18}$$

From (15) and (18) we have

$$\mathrm{E}[\mu(t)] = \frac{p-q}{p+q}\,\frac{L}{\mathrm{E}(D)},$$

so that the mean velocity $\mathrm{E}[\mu(t)]$ can be seen as the mean net displacement in one step divided by the mean time needed to have one step.

3 Rising phase Some histograms of the number of steps per displacement have been shown in Kitamura and Yanagida [9] and Kitamura *et al.* [10]. There are 66 observed displacements under a near-zero load and 77 displacements for a load between 0 and 0.5 pN. The number of net steps in each displacement ranges from 1 to 5 under a near-zero load and from 1 to 4 for a load between 0 and 0.5 pN. Moreover, the distribution of the total number of net steps observed in a rising phase minus 1 is well-fitted by a Poisson random variable. Hence, in order to include such features in our model we introduce a random variable U that describes the duration of the myosin head rising phase. Let $\{N_+(t),\, t \geq 0\}$ and $\{N_-(t),\, t \geq 0\}$ be two independent Poisson processes characterized by intensities λp and λq, that describe the numbers of forward and backward steps performed by the myosin head during a rising phase, respectively. We assume that U is the first-passage time of the number of net steps, given by $R(t) := N_+(t) - N_-(t)$, through a Poisson-distributed random threshold S, with

$$\mathrm{P}(S = k) = \frac{\mathrm{e}^{-\rho}\,\rho^{k-1}}{(k-1)!}, \qquad k = 1, 2, \ldots, \tag{19}$$

where $\rho > 0$ (note that this assumption refines a previous model considered in Buonocore *et al.* [2]). The mean number of net steps during the rising phase is thus given by

$$\mathrm{E}(S) = \rho + 1. \tag{20}$$

We note that $R(t)$ is a randomized random walk, whose transition probability for positive λ, p and q is given by (see, for instance, Conolly [3])

$$p_k(t) = \mathrm{P}\{R(t) = k \,|\, R(0) = 0\} = \left(\frac{p}{q}\right)^{k/2} e^{-\lambda(p+q)t}\, I_k(2\lambda t\sqrt{pq}), \qquad t > 0,$$

where $I_k(x) = \sum_{n=0}^{+\infty} (x/2)^{2n+k}/[n!(n+k)!]$ is the modified Bessel function. For all $t > 0$, the p.d.f of U can be expressed as follows:

$$f_U(t) = \sum_{k=1}^{+\infty} f_{U|S}(t \,|\, k)\, \mathrm{P}(S = k), \tag{21}$$

where $\mathrm{P}(S = k)$ is given in (19) and $f_{U|S}(u \,|\, k)$ is the first-passage-time density of $R(t)$ through k. The latter is given by

$$f_{U|S}(t \,|\, k) = \frac{k}{t}\, p_k(t) = \frac{k}{t}\left(\frac{p}{q}\right)^{k/2} e^{-\lambda(p+q)t}\, I_k(2\lambda t\sqrt{pq}). \qquad t > 0. \tag{22}$$

From (19), (21) and (22) we have

$$f_U(t) = \frac{e^{-\lambda(p+q)t}}{t}\mathrm{e}^{-\rho} \sum_{k=1}^{+\infty} \frac{k}{(k-1)!}\left(\frac{p}{q}\right)^{k/2} \rho^{k-1} I_k(2\lambda t\sqrt{pq}), \qquad t > 0. \tag{23}$$

Making use of Eq. (23) and of Eqs. 4.16.1 and 4.16.2 of Erdélyi *et al.* [7], for $p > q$ we obtain:

$$\begin{aligned} \mathrm{E}(U) &= \frac{\rho + 1}{\lambda\,(p - q)}, \\ \mathrm{Var}(U) &= \frac{(2\rho + 1)p + q}{\lambda^2\,(p - q)^3}, \\ \mathrm{CV}(U) &= \frac{1}{\rho + 1}\sqrt{\frac{(2\rho + 1)p + q}{p - q}}. \end{aligned} \tag{24}$$

Note that $\mathrm{E}(U) = \mathrm{E}(S)/\mathrm{E}[R(t)/t]$, so that the mean duration of the rising phase equals the mean number of net steps times the net steps rate. Two plots of density (23) are shown in Figure 2. Parameters p and q are chosen according to the experimental results concerning myosin number of steps along the actin filament for different load values that are given in Kitamura and Yanagida [9], where the ratio between the number of forward steps and backward steps is 18 under a near-zero load, and is 6 for a load between 0 and 0.5 pN. Moreover, recalling from (18) that the mean dwell-time is $[\lambda(p + q)]^{-1}$, λ is obtained from

$$[\lambda(p + q)]^{-1} = \begin{cases} 4.8\,\mathrm{ms} & \text{under a near-zero load} \\ 12.2\,\mathrm{ms} & \text{for a load between 0 and 0.5 pN} \end{cases}$$

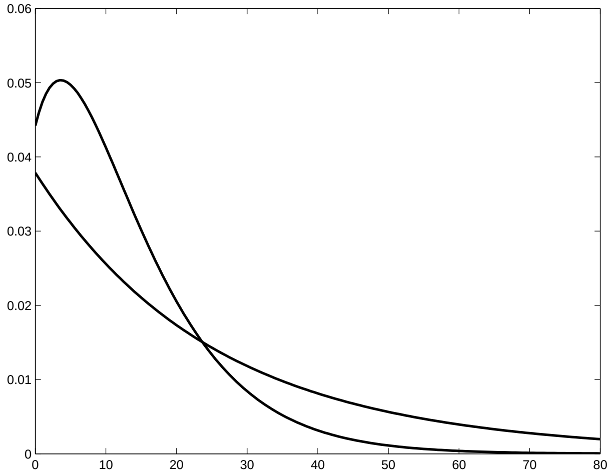

Figure 2: Plots of density (23) in the following cases: (i) $\rho = 1.5$, $[\lambda(p+q)]^{-1} = 4.8\,\mathrm{ms}$ and $p/q = 18$, where $\mathrm{E}(U) = 13.37\,\mathrm{ms}$ and $\mathrm{Var}(U) = 122.80\,\mathrm{ms}^2$, and (ii) $\rho = 0.6$, $[\lambda(p+q)]^{-1} = 12.2\,\mathrm{ms}$ and $p/q = 6$, where $\mathrm{E}(U) = 27.83\,\mathrm{ms}$ and $\mathrm{Var}(U) = 858.98\,\mathrm{ms}^2$.

where the rates of dwell times, appearing on the right-hand sides, are experimentally evaluated in the presence of 1 μM ATP and at 20 C (see Kitamura *et al.* [10] and Kitamura and Yanagida [9]). Moreover, due to (20), the value of ρ is chosen according to the following experimental mean numbers of steps observed during rising phases (see Kitamura and Yanagida [9]):

$$\rho + 1 = \begin{cases} 2.5 & \text{under a near-zero load} \\ 1.6 & \text{with a load between 0 and } 0.5\,\mathrm{pN}. \end{cases}$$

Hence, in case (i) of Figure 2, where $f_U(t)$ exhibits a positive mode, it is $p/q = 18$, $\lambda(p+q) = (4.8)^{-1}$ and $\rho = 1.5$; in case (ii), where $f_U(t)$ is strictly decreasing, we have $p/q = 6$, $\lambda(p+q) = (12.2)^{-1}$ and $\rho = 0.6$.

Let us now denote by V the random variable denoting the position attained by the myosin head at the end of the rising phase. Its density is given by:

$$f_V(x) := \int_0^{+\infty} f(x,t)\, f_U(t)\, \mathrm{d}t, \qquad x \in \mathbb{R} \tag{25}$$

with $f(x,t)$ expressed in (10) and $f_U(t)$ given in (23). In order to provide a qualitative insight of its behaviour, in Figures 3 and 4 we show two instances of probability density (25). For $p > q$, making use of Eq. (25), we have:

$$\mathrm{E}(V) = (\rho+1)\,L, \tag{26}$$

$$\mathrm{Var}(V) = \frac{\lambda L^2\,[(2\rho+1)\,p+q] + (\rho+1)\{\lambda[L^2(p+q)+\sigma^2]+\delta^2\}}{\lambda(p-q)}, \tag{27}$$

$$\mathrm{CV}(V) = \frac{\sqrt{\lambda L^2\,[(2\rho+1)\,p+q] + (\rho+1)\{\lambda[L^2(p+q)+\sigma^2]+\delta^2\}}}{(\rho+1)L\sqrt{\lambda(p-q)}}.$$

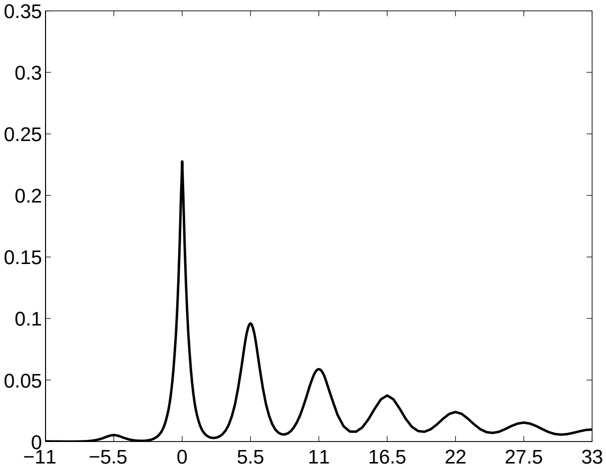

Figure 3: Plot of density (25) with $\rho = 1.5$, $\sigma^2 = 0.1$, $p = 0.72$, $q = 0.04$ and $\lambda = 0.27$.

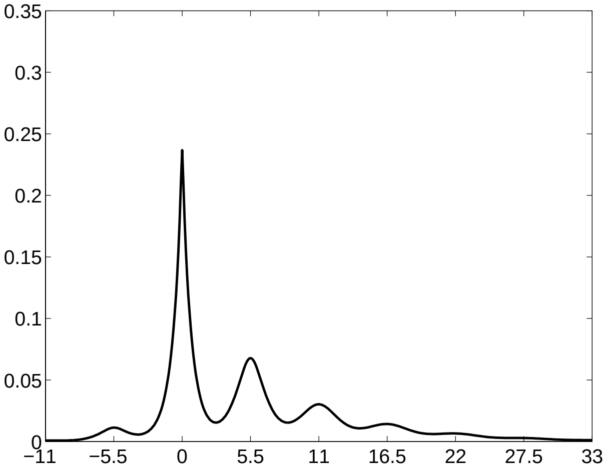

Figure 4: Plot of density (25) with $\rho = 0.6$, $\sigma^2 = 0.1$, $p = 0.18$, $q = 0.03$, $\lambda = 0.39$.

Table 1: See text for explanation

p	q	λ	$\mathrm{E}(V)-2\sqrt{\mathrm{Var}(V)}$	$\mathrm{E}(V)+2\sqrt{\mathrm{Var}(V)}$
0.09	0.005	2.19	-15.82	43.32
0.18	0.01	1.10	-15.72	43.22
0.36	0.02	0.55	-15.67	43.17
0.72	0.04	0.27	-15.65	43.15

Comparing Eq. (26) with (24) and (15) we have $\mathrm{E}(V)=\mathrm{E}(U)\cdot\mathrm{E}[\mu(t)]$, so that the mean position at the end of the rising phase equals the mean duration of the rising phase times the constant mean velocity of the myosin head. In Tables 1 and 2 the values of $\mathrm{E}(V)\pm 2\sqrt{\mathrm{Var}(V)}$ are indicated. These are obtained via Eqs. (26) and (27) for some choices of p, q and λ under the conditions $p/q=18$, $\rho=1.5$ and $E(V)=13.75$ (Table 1) and $p/q=6$, $\rho=0.6$ and $E(V)=8.8$ (Table 2).

Table 2: See text for explanation

p	q	λ	$\mathrm{E}(V)-2\sqrt{\mathrm{Var}(V)}$	$\mathrm{E}(V)+2\sqrt{\mathrm{Var}(V)}$
0.03	0.005	2.34	-16.70	34.30
0.06	0.01	1.17	-16.45	34.05
0.12	0.02	0.59	-16.32	33.92
0.24	0.04	0.29	-16.26	33.86

4 Rising phase in the absence of backward steps The experimental results of Kitamura and Yanagida [9] and Kitamura *et al.* [10] show that backward steps during a rising phase are rare with respect to forward steps. Hence, it is challenging to analyse the results given in the previous section when backward steps are not allowed, i.e. by assuming $q=0$. In this section we thus assume that $R(t)$ identifies with $N_+(t)$, which is a Poisson process with intensity $\lambda\, p$. Hence, the random duration U of the rising phase in the absence of backward steps is the first-passage time of $N_+(t)$ through the random threshold S. Recalling Eq. (18), in this case the dwell time is exponentially distributed with mean value $(\lambda p)^{-1}$, so that $f_{U|S}(t\,|\,k)$ is an Erlang density with parameters k and $(\lambda p)^{-1}$:

$$f_{U|S}(t\,|\,k)=\lambda p\,\mathrm{e}^{-\lambda pt}\,\frac{(\lambda pt)^{k-1}}{(k-1)!},\qquad t>0. \tag{28}$$

From Eqs. (19), (21) and (28), we obtain the probability density of the rising phase duration in the absence of backward steps:

$$f_U(t)=\mathrm{e}^{-\rho}\,\lambda p\,\mathrm{e}^{-\lambda pt}I_0\Big(2\sqrt{\rho\,\lambda p\,t}\Big),\qquad t>0. \tag{29}$$

From (29) we have that $f_U(0)=\mathrm{e}^{-\rho}\lambda p>0$, and that $f_U(t)$ is a Polya frequency of order 2 density (PF$_2$), i.e. a logconcave density (see Marshall and Olkin [11]). This means that $[U-t\,|\,U>t]\geq_{\mathrm{lr}}[U-\tau\,|\,U>\tau]$ whenever $0<t\leq\tau$ (see Theorem 1.C.22 of Shaked and Shantikumar [12]). In other words, as time goes on, the residual time of rising phase decreases in the likelihood ratio order sense. Moreover, from (29) we obtain

$$\frac{\mathrm{d}\,f_U(t)}{\mathrm{d}t}=\mathrm{e}^{-\rho}\,(\lambda p)^2\,\mathrm{e}^{-\lambda pt}\left[(\rho-1)I_0\Big(2\sqrt{\rho\,\lambda p\,t}\Big)-\rho\,I_2\Big(2\sqrt{\rho\,\lambda p\,t}\Big)\right],\qquad t>0.$$

From this expression it is possible to show that density $f_U(t)$ is decreasing for all $t > 0$ if $\rho \leq 1$, whereas density (29) is unimodal with a positive mode if $\rho > 1$.

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