Dynamic instability of collective myosin II motors*

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Some kinds of muscles can oscillate spontaneously, which is related to the dynamic instability of the collective motors. Based on the two-state ratchet model and with consideration of the motor stiffness, the dynamics of collective myosin II motors are studied. It is shown that when the motor stiffness is small, the velocity of the collective motors decreases monotonically with load increasing. When the motor stiffness becomes large, dynamic instability appears in the force–velocity relationship of the collective-motor transport. For a large enough motor stiffness, the zero-velocity point lies in the unstable range of the force–velocity curve, and the motor system becomes unstable before the motion is stopped, so spontaneous oscillations can be generated if the system is elastically coupled to its environment via a spring. The oscillation frequency is related to the motor stiffness, motor binding rate, spring stiffness, and the width of the ATP excitation interval. For a medium motor stiffness, the zero-velocity point lies outside the unstable range of the force–velocity curve, and the motion will be stopped before the instability occurs.

Keywords: ratchet model, motor stiffness, dynamic instability, spontaneous oscillation

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1. Introduction

Molecular motors, or motor proteins, can convert chemical energy, typically obtained from the hydrolysis of ATP, into mechanical work and walk along filaments, which are related to many active processes in biological systems such as cargo transport, cell motility, and muscular contraction.[1–6] Some kinds of motors can walk hundreds of discrete steps along their tracks before finally dissociating, such as kinesin 1, mysion V, etc., they are called processive motors.[7–14] While other kinds of motors unbind from their tracks frequently, such as myosin II, Ncd, etc., which are called nonprocessive motors.[15–17] The nonprocessive motors cannot work alone, but evoke motion of large velocity when working with large groups, for example, the contraction of muscle is the cooperation of a large amount of myosin II motors.[15,16,18,19]

There are some interesting dynamics in the process of multi-motor cooperation.[20] The cooperation of processive motors can increase the run-length of the cargo particle significantly, but the velocity sometimes decreases with increasing motor number.[21–26] The cooperation of nonprocessive motors can generate large velocity and force (such as the macroforce of muscle is generated by a large amount of myosin II motors) and has a high mechanical efficiency.[15,16,27–30] Under certain conditions, collective myosin II motors can generate oscillations. For example, the flight muscle of some insects (e.g., bees and wasps) can generate oscillations with high frequency.[31,32] Skeletal muscle myofibrils have been shown to oscillate spontaneously, *in vitro* in the absence of any external driving.[33] Spontaneous oscillations have also been observed in a minimal actomyosin system, where the collective-myosin system is elastically coupled with its environment.[34] Some theoretical results show that dynamic instability would occur in the force–velocity relationship of the multiple-motor transport,[35–37] and that the motor system can oscillate spontaneously if it is coupled with a harmonic potential.[38,39]

For different kinds of muscles, their functions are quite different from each other. The flight muscle of some insects can oscillate with a frequency of about 100 Hz.[32] Whereas the main function of the skeletal muscle is contraction in one direction, and oscillations are seldom observed in the skeletal muscle. The function difference of different kinds of muscles may be related to their structure difference. In theory, the structure difference is usually reflected in some physical parameters which are important to the motion of the motor system. In this paper, we investigate the influence of some parameters on the dynamic instability of collective myosin II motors.

We base our model on the two-state ratchet model[35,40,41] and consider the motor stiffness, since the real myosin II motor has a long stalk (coiled coil) which is elastic.[42,43] The results show that the motor stiffness can affect the dynamic instability of the collective-nonprocessive-motor system. When the motor stiffness is large, dynamic instability appears in the force–velocity relationship of the collective-motor transport, and spontaneous oscillations can be generated if the system is elastically coupled to its environment.

2. Model

With consideration of the motor elasticity, the two-state ratchet model is shown in Fig. 1. The motor tails are tightly bound to the backbone with fixed spacing s, and the motor

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heads can transit between two states 1 and 2. The tail and the head of a motor are connected with a spring of stiffness k_m. x is the position of the binding point of a given motor tail on the backbone at time t, and z is the position of the motor head in state 1 or 2. The energy of a motor head in state σ ($\sigma = 1,2$) is given by periodic potentials $W_\sigma(z) = W_\sigma(z+l)$ with period l, which reflects the regular structure of the track filament with subunits of size l. For simplicity, we set W_2 as a flat potential, and W_1 as a saw-tooth periodic potential with period $l = a+b$, where a is the width of the downhill region (i.e., region I), and b is that of the uphill region (i.e., region II). For nonprocessive motor myosin II, state 1 can be seen as the attached state, i.e., the motor head binds on the filament, and state 2 corresponds to the detached state. The detached motor can bind to the filament with a rate of $\omega_{on}(z)$, in turn, the attached motor can unbind from the filament with a rate of $\omega_{off}(z)$. Here we assume that the binding rate ω_{on} is a constant. The unbinding rate $\omega_{off}(z) = \Omega\Theta(z)$, which is related to the ATP excitations, is a piecewise constant,[35] as shown in Fig. 1, which means that the motor can detach from the filament only after a power stroke. This idea is consistent with that of the cross bridge model.[44,45] The free energy change for the ATP excitations is denoted by $\Delta G_{excitation}$.

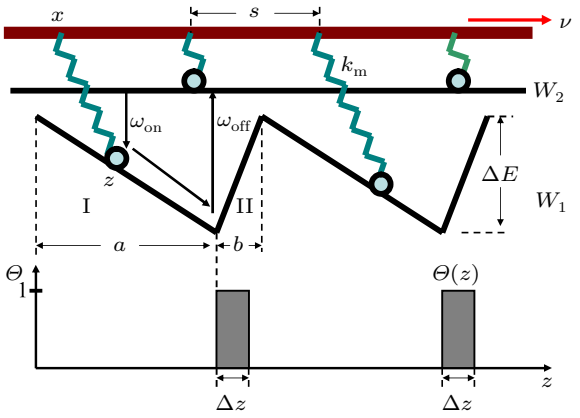


Fig. 1. (color online) Schematic diagram of a two-state multi-motor system and the rate of ATP excitations $\Omega\Theta(z)$. Motors are attached periodically with spacing s via springs to a backbone, and the motor heads can transit between two states 1 and 2, with l-periodic ($l = a+b$) potentials W_1 and W_2, respectively. x denotes the position of the binding point of a given motor tail on the backbone, and z denotes the position of the motor head at state 1 or 2. The transition rate ω_{on} is a constant. ATP excitations, $\omega_{off}(z) = \Omega\Theta(z)$, occur only within an interval of width Δz, where $\Theta(z) = 1$.

In the calculations, we adopt $\Delta E = 64$ pN·nm, because the hydrolysis of ATP in the typical *in vivo* enviroment yields a ΔG_{ATP} of about 20 k_BT,[46] and ΔE should be less than ΔG_{ATP} in this case (since $\Delta E + |\Delta G_{excitation}| = \Delta G_{ATP}$ in the typical *in vivo* enviroment[47]); and $l = 10$ nm, $b/l = 0.2$, as the muscle myosin can make a power stroke of about 5–10 nm in each dynamic cycle.[27,42,43] Here, we adopt $\Omega = 1000$ s^{-1}, i.e., $\omega_{off} = 1000$ s^{-1} within the ATP excitation region and $\omega_{off} = 0$ in the other regions (see Fig. 1), since it was reported that the muscle myosin unbinding rate from the filament can reach 1000 per second or more.[27,32] The width of the ATP excitation interval, Δz, and ω_{on} are free parameters.

We now define the probability density $p_a(x,z,t)$ for a motor with its tail at x and head at z to be attached to the filament, i.e., the motor in state 1. Likewise, the probability density for a motor to be detached, i.e., the motor in state 2, is denoted as $p_d(x,z,t)$. The probabilities $p_a(x,z,t)$ and $p_d(x,z,t)$ obey the following coupled Fokker–Planck equations:

$$\begin{aligned}\partial_t p_a &= D\partial_z[p_a(\partial_z W_1 - F_s)/k_BT + \partial_z p_a] - v\partial_x p_a \\ &\quad - \omega_{off}(z)p_a + \omega_{on}(z)p_d, \qquad (1)\\ \partial_t p_d &= D\partial_z[-p_d F_s/k_BT + \partial_z p_d] - v\partial_x p_d \\ &\quad + \omega_{off}(z)p_a - \omega_{on}(z)p_d, \qquad (2)\end{aligned}$$

where $F_s = k_m(x-z)$ is the elastic force, v is the velocity of the backbone, and D is the diffusion constant. We define the probability density

$$p(x,t) \equiv \int_{-\infty}^{\infty}[p_a(x,z,t) + p_d(x,z,t)]dz, \qquad (3)$$

which gives the probability to find a motor with its tail at position x at time t. In the limit of large motor number N, p approaches a constant, $p(x,t) = 1/l$, if the structures of the motors and the track filament are incommensurate, i.e., the ratio l/s is irrational.[35,48] Then we define a function $G(x,t) \equiv \int_{-\infty}^{\infty} p_d(x,z,t)dz$ which gives the probability to find a detached motor with its tail at position x at time t. In the limit of large N,

$$G(x,t) = \frac{1}{l} - \int_{-\infty}^{\infty} p_a(x,z,t)dz. \qquad (4)$$

If the rate of linker relaxation for a detaching motor is fast compared to the rate of attachment, the head position distribution of the detached motor approximately satisfies the Boltzmann distribution[49]

$$p_d(x,z,t) \approx G(x,t)C_0 \exp\left[-\frac{k_m(z-x)^2}{2k_BT}\right], \qquad (5)$$

where $C_0 = \sqrt{k_m/(2\pi k_BT)}$.

The average force exerted by a single motor on the backbone is given by

$$F_{motor} = \int_0^l dx \int_{-\infty}^{\infty} k_m(z-x)p_a(x,z,t)dz. \qquad (6)$$

The average externally applied force per motor is given by

$$F_{ext} = \lambda_0 v - F_{motor}, \qquad (7)$$

where $-\lambda_0 v$ is the friction force of the backbone per motor, and λ_0 is the damping coefficient. The friction force is usually a few orders of magnitude smaller than F_{motor},[46] so the first term in Eq. (7) can be ignored, and $F_{ext} \approx -F_{motor}$.

3. Results and discussion

3.1. Dynamic instability in the force–velocity relationship

We are interested in the steady-state solution of Eqs. (1) and (2). By submitting Eqs. (4) and (5) into Eq. (1), p_d can be canceled from Eq. (1), and we can obtain the probability distribution p_a numerically. For large time t, p_a can get to a steady state. Then using Eqs. (6) and (7), we can obtain the relationship between F_{ext} and the velocity of the backbone in the steady state. The force–velocity relation is shown in Fig. 2(a). When the motors are strongly coupled, i.e., with large motor stiffness k_m, the motor system can carry a very large load force exceeding 5 pN per motor. Whereas, when the motors are weakly coupled (for small stiffness), the force carried by the motor system is usually less than 1 pN per motor. It is not difficult to understand this result. When the motor stiffness is large, the heads of the attached motors mostly lie in the downhill region, i.e., the region I shown in Fig. 1, and they can hardly slide down to the bottom of W_1 due to the large stiffness of the motors, especially in the case of small backbone velocity, so these motors can generate a large force to the backbone. While the motor stiffness is small, the motors can easily go down to the bottom of the potential W_1, and then transit to state 2 (i.e., detach from the filament), so the number of attached motors is small in this case; on the other hand, each attached motor can just generate a small force to the backbone due to the small motor stiffness, so the force generated by the motor system is small.

In the calculation, we ignore the friction of the backbone. If the friction is considered, when the velocity is greater than zero, the externally applied force F_{ext} would increase; when the velocity is less than zero, F_{ext} would decrease, especially for a large $|v|$. But this change can be ignored if $|v|$ is not too large, as mentioned in Section 2, the friction force is usually a few orders of magnitude smaller than F_{motor}.

It is interesting that when the motor stiffness k_m is large, dynamic instability appears in the force–velocity relationship of the collective motor transport (in the range with $\partial F_{ext}/\partial v < 0$), which can be explained as follows. If a load is applied ($F_{ext} < 0$), v decreases. The maximal load force that the motor system can carry is the extreme value of $|F_{ext}(v)|$. If this load is exceeded, the system then changes the direction of motion discontinuously.[35] In the case of small motor stiffness, the velocity of the motor system decreases monotonously with increasing load force, and there is no instability in the force–velocity relationship, as shown in Fig. 2(a). It means that the motor stiffness k_m can affect the dynamic instability of the motor system. The dynamic instabilities are also found in other isothermal rectifying processes,[40] and some processes exhibit the absolute negative mobility (ANM) behavior,[50] in which the Brownian particles always move in a direction opposite to the external force. Although different approaches may differ in the details of the rectification process, they share in common the main features.[40] In our model, the rectification is obtained from the localized ATP excitations.

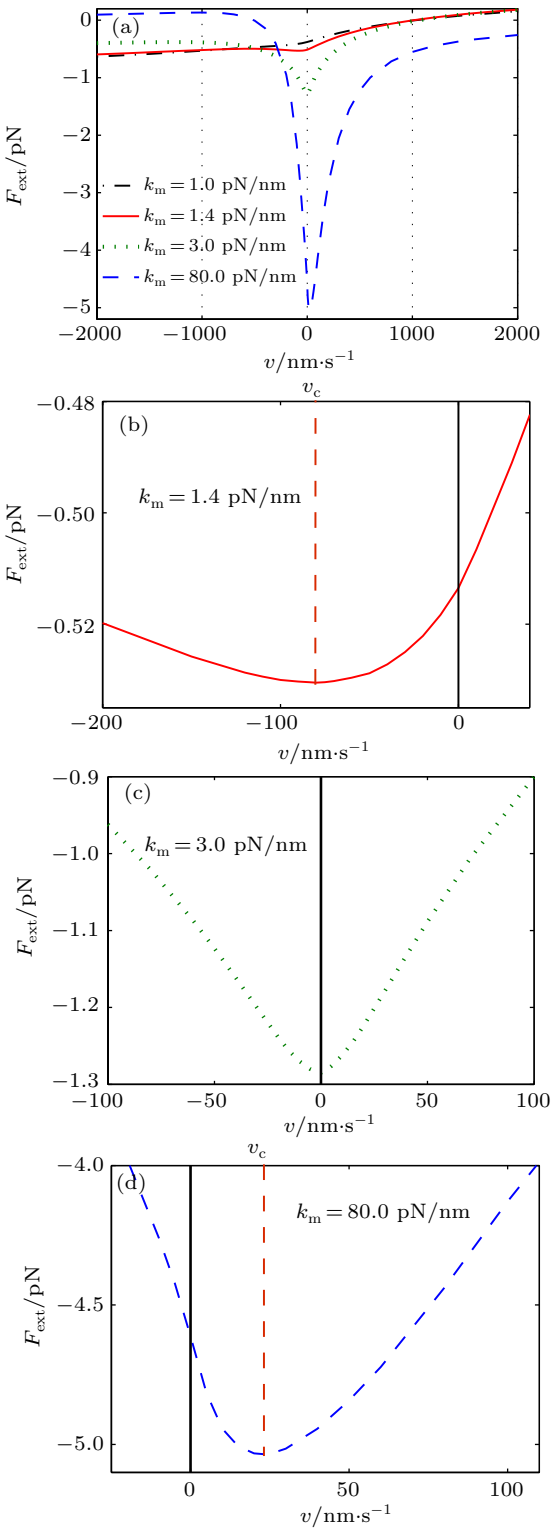


Fig. 2. (color online) (a) The relationship between externally applied force per motor F_{ext} and the velocity of the backbone for different motor stiffness with $\Delta E = 64$ pN·nm, $l = 10$ nm, $b/l = 0.2$, $\Delta z/b = 0.5$, $\omega_{on} = 40$ s^{-1}, $\Omega = 1000$ s^{-1}, and $D = 10^6$ nm^2/s. (b)–(d) The motor stiffness can affect the sign of v_c, which denotes the velocity corresponding to the extreme value of $F_{ext}(v)$: (b) $k_m = 1.4$ pN/nm, $v_c < 0$; (c) $k_m = 3.0$ pN/nm, $v_c = 0$; (d) $k_m = 80.0$ pN/nm, $v_c > 0$.

We now define the velocity that corresponds to the extreme value of $F_{\rm ext}(v)$ as $v_{\rm c}$. We find that $v_{\rm c}$ can be positive (for large $k_{\rm m}$, see Fig. 2(d)) or negative (for relatively small $k_{\rm m}$, see Fig. 2(b)), and that for a special value of $k_{\rm m}$, $v_{\rm c}$ can be equal to zero (see Fig. 2(c)). The sign of $v_{\rm c}$ is related to the spontaneous oscillations of the elastically coupled motor system (see Subsection 3.2). The relationship between $v_{\rm c}$ and $k_{\rm m}$ for different ratio $R=\Delta z/b$ is plotted in Fig. 3(a). It shows that the sign of $v_{\rm c}$ is mainly affected by the motor stiffness $k_{\rm m}$. For large $k_{\rm m}$, $v_{\rm c}$ is usually positive, while for medium $k_{\rm m}$, $v_{\rm c}$ is usually negative. In the range of 3 pN/nm $< k_{\rm m} <$5 pN/nm, $v_{\rm c}$ is equal to zero or very small. When $k_{\rm m}$ is small (usually less than 1 pN/nm), the velocity decreases monotonously with load increasing, and there is no $v_{\rm c}$. These results hint that the instability of the collective motor system is resulted from the strong coupling between motors (i.e., with large motor stiffness).

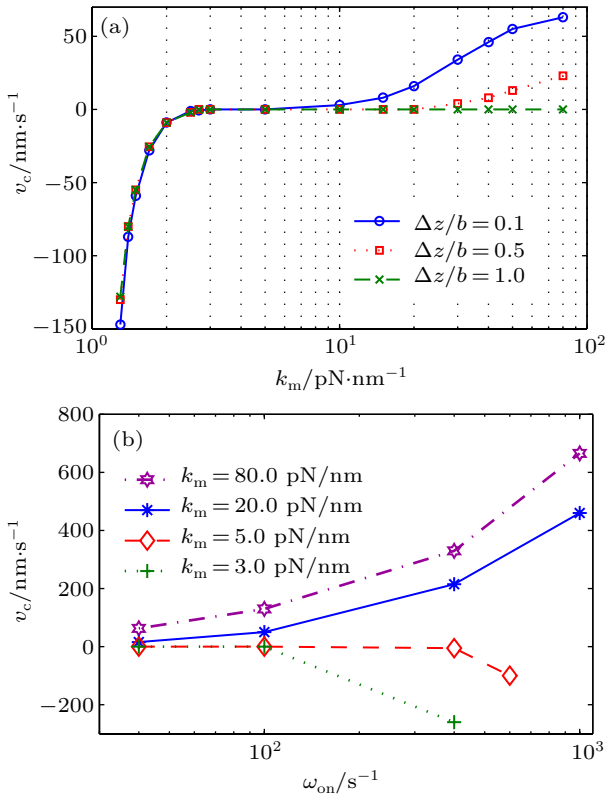


Fig. 3. (color online) (a) $v_{\rm c}$ as a function of motor stiffness $k_{\rm m}$ for different ratio $R=\Delta z/b$ when $\omega_{\rm on}=40$ s^{-1}, where Δz is the width of the nonzero range of $\omega_{\rm off}$, and b is the width of the uphill region of the sawtooth potential W_1 (see Fig. 1). (b) $v_{\rm c}$ as a function of $\omega_{\rm on}$ for different motor stiffness $k_{\rm m}$ when $R=0.1$. The other parameters are the same as those in Fig. 2.

The ratio R almost cannot affect the sign of $v_{\rm c}$, but it can affect the value of $v_{\rm c}$ (see Fig. 3(a)). Especially in the case of large motor stiffness, $v_{\rm c}$ decreases obviously with increasing R. When $R=1$, $v_{\rm c}$ always remains zero even for very large motor stiffness, which can be explained as follows. In the case of $R=1$, rigid motor, and $v=0$, the attached motor density in region I (downhill region) is greater than that of region II (uphill region) because of the nonzero transition rate $\omega_{\rm off}$ in region II. Now let the backbone go right with a small velocity, then the attached motor number in region I decreases, and the motor number in region II increases, so the force exerted to the backbone decreases. Similarly, the force also decreases when the motors go left with a small velocity. So there is a peak value of $F_{\rm motor}$ at $v=0$, i.e., $v_{\rm c}=0$, in this case. The motor binding rate $\omega_{\rm on}$ can also affect the value of $v_{\rm c}$ (see Fig. 3(b)). When the motor stiffness $k_{\rm m}$ is large, $v_{\rm c}$ increases with $\omega_{\rm on}$. However, when $k_{\rm m}$ is small, $v_{\rm c}$ decreases with $\omega_{\rm on}$.

3.2. Spontaneous oscillations of elastically coupled motor system

We now consider a collective of myosin II motors being elastically coupled with its environment as shown in Fig. 4(a). The stiffness of the spring is $K_{\rm s}=Nk_{\rm s}$, where N is the number of motors. For this elastically coupled motor system, $F_{\rm ext}=-k_{\rm s}X$ (X is the elongation of the spring) per motor, so equation (7) can be written as

$$F_{\rm motor}-k_{\rm s}X=\lambda_0 v. \tag{8}$$

Here we set $\lambda_0=0.005$ pN·s/μm. The velocity of the backbone is $v=\partial_t X$. The position of the backbone, X, can be calculated by numerically integrating Eqs. (1), (2), (6), and (8), as shown in Fig. 4(b). When $v_{\rm c}\le 0$ (for relatively small motor stiffness $k_{\rm m}$), the backbone will finally be stopped. When $v_{\rm c}>0$ (for large motor stiffness $k_{\rm m}$), the elastically coupled motor system can oscillate spontaneously.

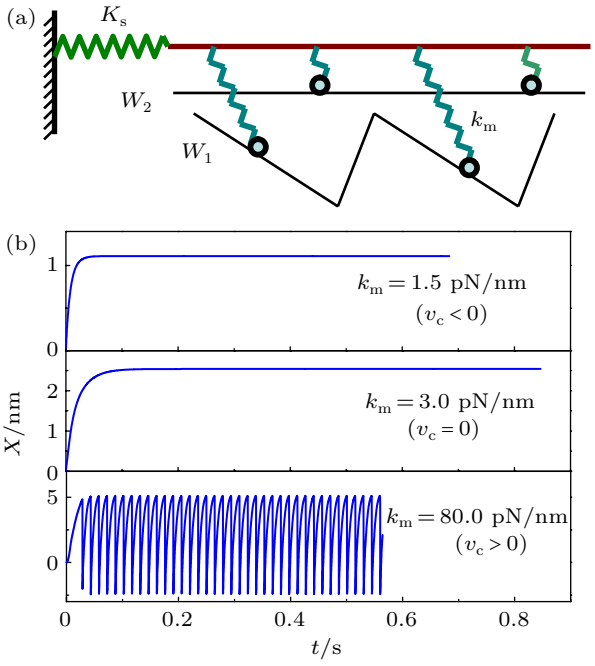


Fig. 4. (color online) (a) The motor system is connected with its environment via a spring $K_{\rm s}$. (b) Position X versus time t for different motor systems with $k_{\rm m}=1.5$ pN/nm ($v_{\rm c}<0$), $k_{\rm m}=3.0$ pN/nm ($v_{\rm c}=0$), and $k_{\rm m}=80$ pN/nm ($v_{\rm c}>0$), respectively, where $\Delta z/b=0.1$ and $k_{\rm s}=0.5$ pN/nm. The other parameters are the same as those in Fig. 2.

The spontaneous oscillation of the elastically coupled motor system is related to the dynamic instability of the motor system in Fig. 1. Although the movement of the elastically coupled motor system is not a steady-state process, it can still be treated as a quasi-steady state process. In this case, one can approximately use the steady-state force–velocity curve such as in Fig. 2 to describe the instantaneous state of the system. Let us consider an elastically coupled motor system with large motor stiffness k_m and $v_c > 0$ (for example $k_m = 80$ pN/nm in Fig. 2). Starting with a small load force and a positive velocity, the motors go forward (the states should approximately evolve along the force–velocity curve in Fig. 2), and the spring K_s is stretched more and more, and the load force increases until the system reaches the lowest point of Fig. 2(d), i.e., the point corresponding to v_c. At this point, the motor system has a positive velocity of v_c, and the spring K_s would be stretched more, then the velocity changes sign discontinuously and the spring shrinks back. This continues until the upper unstable point is reached and the velocity is again reversed discontinuously.[40] Therefore, spontaneous oscillations are generated. It can be analyzed similarly that when $v_c \leq 0$, the motion will finally be stopped, and no spontaneous oscillation occurs.

The oscillation frequency of the motor system is related to some parameters as shown in Fig. 5. Figures 5(a) and 5(b) show that the oscillation frequency increases with motor stiffness k_m and motor binding rate ω_{on}, respectively. Figure 5(c) shows that the frequency increases with the decrease of $\Delta z/b$. We believe that the major reason for the frequency increasing here is the increase of v_c. In the process of oscillations, the state of the motor system approximately evolves along the force–velocity curve of the steady state process except in the unstable range. When v_c is large, the motor system can reach the point corresponding to the extreme value of $F_{ext}(v)$ (such as the lowest point of the force–velocity curve in Fig. 2(d)) quickly, and then change the direction of motion discontinuously. Therefore, large v_c can accelerate the oscillations. As shown in Fig. 3, v_c increases with motor stiffness k_m and motor binding rate ω_{on} in the case of large k_m, and v_c also increases with the decrease of $\Delta z/b$. In Ref. [38], it was also shown that the oscillation frequency increases with ω_{on}.

Figure 5(d) shows that the oscillation frequency increases with spring stiffness k_s, which is consistent with the result in Ref. [38]. It is not difficult to understand this result. When k_s is large, F_{ext} increases quickly as the motor system goes forward, and reaches the extreme value of $F_{ext}(v)$ in a short time, then the direction of motion changes discontinuously. Therefore, large k_s can result in a large oscillation frequency of the elastically coupled motor system, and vise versa.

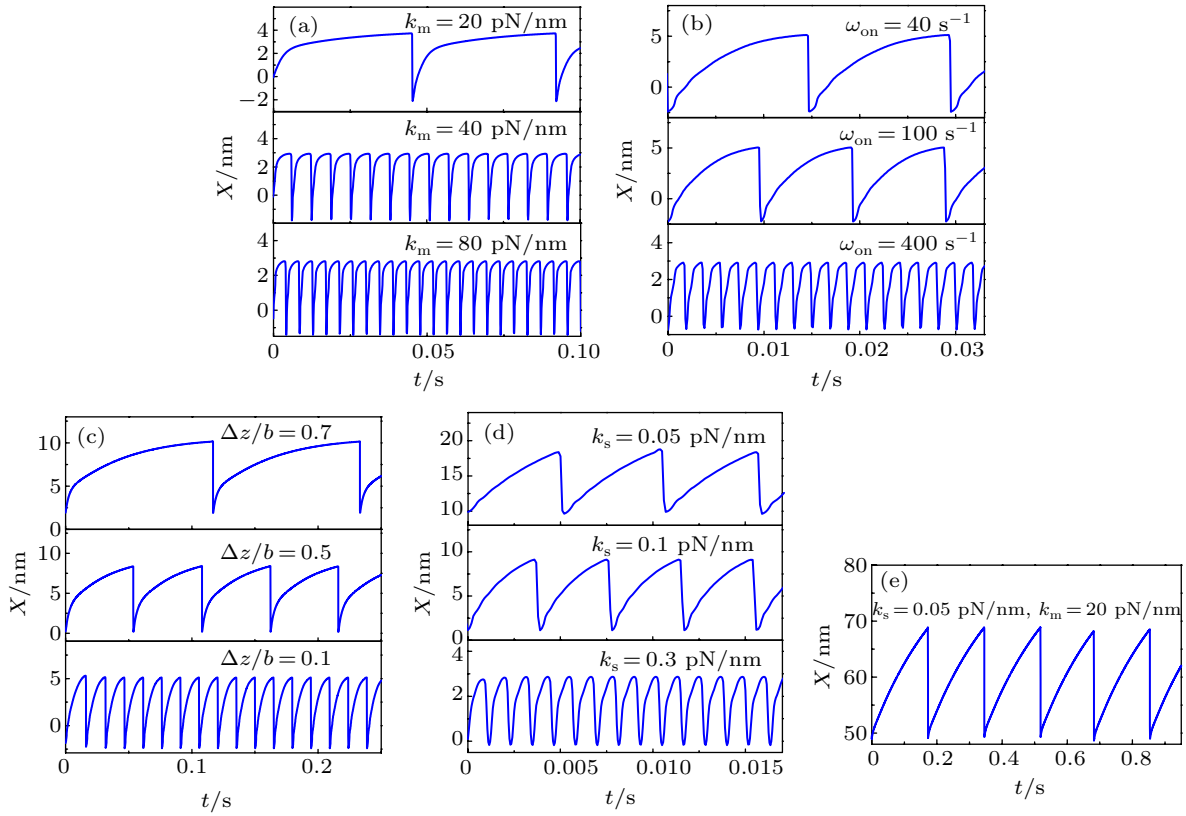


Fig. 5. (color online) The oscillation frequency is related to some parameters. (a) The oscillation frequency increases with motor stiffness k_m, where $k_s = 1.0$ pN/nm per motor, $\omega_{on} = 40$ s^{-1}, and $\Delta z/b = 0.1$. (b) The oscillation frequency increases with motor binding rate ω_{on}, where $k_s = 0.5$ pN/nm per motor, $k_m = 80$ pN/nm, and $\Delta z/b = 0.1$. (c) The oscillation frequency increases with the decrease of $\Delta z/b$, where $k_s = 0.5$ pN/nm per motor, $k_m = 80$ pN/nm, and $\omega_{on} = 40$ s^{-1}. (d) The oscillation frequency increases with spring stiffness k_s, where $k_m = 80$ pN/nm, $\omega_{on} = 1000$ s^{-1}, and $\Delta z/b = 0.1$. (e) The oscillation frequency is a few Hz when $k_s = 0.05$ pN/nm per motor, $k_m = 20$ pN/nm, $\omega_{on} = 40$ s^{-1}, and $\Delta z/b = 0.1$. The other parameters are the same as those in Fig. 2.

Interestingly, some kinds of muscles can oscillate regularly with high frequency, such as the insect flight muscle (with a frequency of about 100 Hz). Spontaneous oscillations have also been observed in the skeletal muscle myosin system *in vitro*, with a frequency of about 0.5 or a few Hz.[33,34] It is believed that the spontaneous oscillations of the muscle might result from the elasticity coupling between the motor system and its environment. The titin molecules in the muscle can play the role of elastic elements.[18,47] The frequency of the oscillations can be affected by $k_{\rm m}$, $\omega_{\rm on}$, $\Delta z/b$, and $k_{\rm s}$, as mentioned above. Our result shows that the oscillation frequency can range from a few Hz to nearly 1000 Hz with different parameters, see Figs. 5(a)–5(e). The frequency difference between the insect flight muscle and the skeletal muscle may result from their different parameters. The value of $k_{\rm s}$ should be on the order of magnitude of 0.01 pN/nm (corresponding to a few pN/nm of $K_{\rm s}$, since each half-sarcomere has 200–300 motors), so the high frequency oscillation of about 100 Hz should be related to a $k_{\rm m}$ of tens pN/nm and an $\omega_{\rm on}$ of hundreds to thousands s^{-1} according to our result. However, the stiffness of the muscle myosin obtained experimentally is just a few pN/nm.[27,43,51,52] This apparent discrepancy may be due to the following reasons. (i) We just choose a simple saw-tooth potential of W_1 in our model, while the real situation must be much more complicated. (ii) The special structure of the insect flight muscle[53] might influence the property of the muscle dynamics. These should be further studied.

4. Conclusion

We studied the dynamics of collective myosin II motors based on the two-state ratchet model,[35,40,41] considering the motor stiffness. The results show that dynamic instability can appear in the force–velocity relationship of the collective-motor transport, and that the motor stiffness affects the dynamic instability of the collective motors.

We defined $v_{\rm c}$ as the velocity which corresponds to the extreme value of externally applied force $F_{\rm ext}(v)$. The sign of $v_{\rm c}$ depends on the motor stiffness $k_{\rm m}$. (i) For large $k_{\rm m}$, $v_{\rm c}$ is usually positive, and the zero-velocity point lies in the unstable range of the force–velocity curve, so the motor system becomes unstable before the motion is stopped, and spontaneous oscillations can be generated if the system is elastically coupled to its environment. (ii) For medium $k_{\rm m}$, $v_{\rm c}$ is usually negative, and the zero-velocity point lies outside the unstable range of the force–velocity curve, and the motion will be stopped before the instability occurs, so there is no spontaneous oscillation. (iii) When $k_{\rm m}$ is small, the velocity decreases monotonously with load increasing, so no instability occurs.

When $v_{\rm c} > 0$, the elastically coupled motor system oscillates spontaneously. The oscillation frequency is related to motor stiffness $k_{\rm m}$, motor binding rate $\omega_{\rm on}$, spring stiffness $k_{\rm s}$, and $\Delta z/b$. The frequency ranges from a few Hz (or even smaller, e.g., for smaller $k_{\rm s}$) to about 1000 Hz (or even more) with different parameters. Interestingly, the previous experiments *in vitro* have observed spontaneous oscillations of myosin systems with a frequency of about 0.5 or a few Hz.[33,34] It is also believed that the oscillations of the insect flight muscle (with a frequency of about 100 Hz) may be related to the spontaneous oscillations of their motor system.[40,47] Our result shows that the motor system can oscillate when $k_{\rm m} > 10$ pN/nm, but the stiffness of the muscle myosin obtianed experimentally is just a few pN/nm.[27,43,51,52] It must be noted that we just investigate a motor system of a half-sarcomere and just choose a simple saw-tooth potential of W_1 in our model. If one considers a more complicated and more realistic model, one may observe the high-frequency spontaneous oscillation of the muscle system even when $k_{\rm m}$ is just a few pN/nm. This needs to be further studied in the near future.

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