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A Dynamic Model for the Processive Motion of Dynein on Microtubules

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Abstract

We propose a dynamic mechanism for the processive motility of dynein on microtubules (MTs). The force generated for the motion of dynein is purely mechanical in origin. When a dynein monomer binds to a MT, the AAA ring of dynein might fit into one of the trenches on the outer surface of the MT, with the linker domain leaning on the ratchet-shaped protofilament. At room temperature, the dynein molecule exhibits random thermal motion on the outer surface of the MT. The collision between the asymmetric ratchet teeth and the linker exerts a reactive impulsive force on the dynein molecule. The probability of producing an impulse with a longitudinal component pointing to either end of the MT depends on the instantaneous motion of dynein, the shape of the linker, and the mass distribution of the dynein with/without a load. In the dynamic mechanism, dynein monomers can move independently and processively toward either end of the MT. Many observations of the motility of dynein can be reproduced in a simulation system.

Keywords

Dynamic Mechanism, Dynein, Processive Motility

1. Introduction

Cytoplasmic dyneins are dimeric molecular motors that transport various intramolecular cargoes toward the minus end of microtubules (MTs) [1]-[7]. Dyneins are large and structurally complex [6] [8]-[14] compared with other cytoskeletal molecular motors such as kinesin and myosin. In general, the structure of a dynein monomer mainly comprises a large AAA ring, a stalk domain connecting the AAA ring, a small MT-binding domain (MTBD), and a linker domain that arches across the AAA ring and extends to the tail domain. The long tail domain is flexible and binds with the counterpart of another dynein monomer to form a dimer [11]-[14]. The transported cargoes are attached to the tail domains.

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The mechanism of the minus end-directed processive motion of dynein along MTs is not yet clear. Time traces have revealed that dynein moves along MTs in steps [5] [7] [15] [16]. Moreover, similar to the motion of kinesin on MTs, a hand-over-hand model of walking on MTs has been proposed for dynein dimers, and the MTBDs of two dynein monomers are coordinately bound to and released from MTs [3]-[9]. However, the hand-over-hand model is difficult to account for three recent observations. First, dynein steps onto neighboring protofilaments frequently [5] [15]. Second, the stepping of two monomers is not coordinated [15]. The dynein dimer can move processively on MTs with only one active monomer. Third, dynein can slide two MTs across each other by the separate binding of monomers to two MTs [17]. These observations also suggest that the monomers can move independently on MTs.

Recent studies have demonstrated that the individual rat brain cytoplasmic dynein dimer does not move processively on MTs, but moves processively on MTs after forming a complex with dynactin and a cargo adapter [18]-[20]. Because complex formation at the distal, flexible tail domain rarely affects the internal conformational changes, the motility of dynein may not be related to the internal conformation changes, at least for rat cytoplasmic dynein. Moreover, the linker domain connects directly to the tail domain; thus, complex formation at the tail domain may impair the movement of the linker domain and may reduce the power stroke. However, complex formation enhances the motility of rat brain cytoplasmic dynein; thus, the power stroke model is questionable.

From a mechanical perspective, the MT exerts a longitudinal force on the dynein molecules that drives their motility along the MT. The internal conformation change within the dynein molecule may only shift the center of mass (CM) of dynein and the MT back and forth, with no net force acting on the CM of dynein required for the CM to move. Thus, dynein must make contact with the MT at other points where the MT can exert a longitudinal force on dynein that drives its motility on the MT. The linker domain has been suggested to be the source of the force and is the most probable point of contact with the MT.

2. The Dynamic Mechanism

Based on the aforementioned considerations, we propose a dynamic mechanism for the directional force exerted by MTs on dynein that has the structural features of both dynein and the MT. First, we propose a conformation for the dynein-MT complex that differs from the previously proposed ones. As shown in **Figure 1**, α and β tubulins stack to form a long, ratchet-shaped protofilament, and 13 protofilaments constitute a cylindrical MT [21]. Such a perception of MT is consistent with structure of MT [21], however, is different from those appeared in many previous publications [2] [4] [5] [7] [9], where the tubulins were thought to be spheres. The ratchet-shaped outer surface was found to be the key for the generation of force for the motion of kinesin on MT [22]. Owing to the cuboid shape of tubulins, trenches exist on the outer surface of the MT. The average widths of the trenches are 6.5 nm and are close to the thickness of the AAA ring of dynein. When the MTBD of the dynein monomer binds to the MT, the AAA ring of dynein might fit into one of the trenches, with the linker domain leaning on the ratchet-shaped protofilament. At room temperature, because of thermal motion, the dynein molecule moves

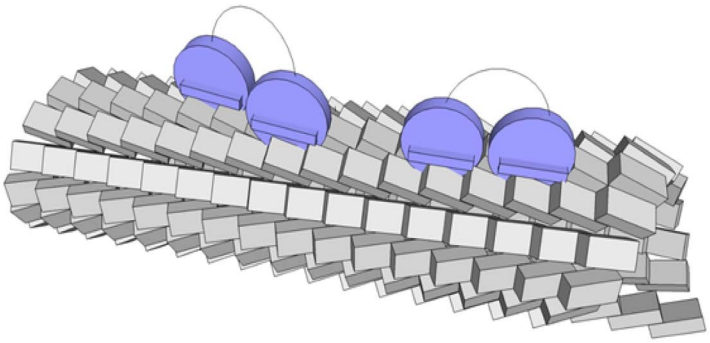


Figure 1. Schematic drawing of proposed configurations of dynein-MT complexes. The α and β tubulins stack to form a long, ratchet-shaped protofilament, and 13 protofilaments constitute a cylindrical MT. The minus end is on the left hand side of the drawing. The AAA rings are represented by cylindrical disks with a thickness that can fit in the trenches on the surface of MT. The linker domain, that can be straight or curved, leans on the ratchet teeth on MT. The wire connects the two disks represents the flexible tail domain. Dynein dimers are bound to MT through MTBD (not shown here).

randomly on the outer surface of the MT. The asymmetric ratchet teeth frequently collide with the linker, which may generate an instantaneous impulse with a longitudinal component pointing to the minus and plus ends of the MT. The probability of producing an impulse with a longitudinal component pointing to the minus end depends on the instantaneous motion of dynein, the shape of the linker, and the mass distribution of the dynein with/without a load.

If the CM of dynein molecule shifts toward the minus end of the MT, the linker is highly likely to tilt in the direction of the minus end. Consequently, the portion of the linker toward the direction of the minus end would have a high probability of colliding with the top of the teeth on the outer surface of the MT. Such a collision produces minus end-oriented impulses that drive the dynein motor to move toward the minus end of the MT. While dynein lies on the MT, the tail domain extending from the linker will further shift the CM toward the minus end. If the shift in the CM is reversed by the load material, the direction of motion may also be reversed. In our mechanism, dynein is a reversible motor, and the direction of motion depends on the position of the CM of the dynein-load complex. This mechanism may also explain the observation that binding of dynein to dynactin might enhance the processivity and might sometimes change the direction of motion of dynein [18] [19]. The dynein-dynactin complex may stabilize the binding of dynein to the MT and shift the CM of the complex owing to the flexibility of the tail domain.

The combined effects of the asymmetric teeth on the outer surface of the MT, the conformation of the linker domain, and the mass distribution of dynein may generate forces that favor motion toward the minus end. Consequently, the dynein monomers may stochastically and independently move toward the minus end of the MT [23] when the instantaneous force is larger than the longitudinal component of the binding force between the MTBD of dynein and the MT. Such a dynamic mechanism explains the motion of the dynein monomer and dimer. The dimers stay on the MT longer than the monomers do for two reasons: first, dimerization may exert the same effect as binding with dynactin; second, two monomers are less likely to fall off the tracks at the same time compared with one monomer. Even if one monomer falls off the track, it may return to the track after exhibiting diffusive motion on the MT for some time, as observed by Reck-Peterson *et al*. [5] as well as in this study.

3. The Simulation System

In this study, we demonstrate that most of the observed properties of the motility of dynein on the MT can be reproduced in a simulation model, which has all the crucial structural features of the dynein-MT complex. As shown in **Figure 2**, we simulated the outer surface of the MT [21] by using a series of ratchet arrays on a plate. The widths of the trenches were chosen so that the ratio of the width (11 mm) to the period (7 mm) of the ratchet teeth was approximately the same as that on the outer surface of the MT (6.5 nm to 4 nm). Thus, the simulation system is 1.7×10^6 times the actual MT. The direction toward the minus end of the MT is defined according to the asymmetry of the ratchet tooth. The AAA ring of dynein was modeled using an acrylic disk with a 25-mm diameter and a 9-mm thickness. The linker was simulated using a piece of acrylic attached to the side of the disk. The position of the linker was chosen so that the disk does not touch the bottom of the trench. Both straight and curved linkers were used to generate the minus end-directed force. The MTBD of the dynein monomer was si-

Figure 2. Picture of the simulation dynein-MT system. The monomers of the dynein dimer may be arranged in the same trench (in series) or in different trenches (in parallel). The binding between the simulation dynein and MT is achieved with the magnetic attraction between the iron balls (MTBD) connected to the head and the magnets under the trenches. The white spots of different sizes on the heads are used to detect the positions of the monomers from analyzing the video images taken during the experiments. The plate is vertically vibrated with an electromagnetic shaker.

mulated using magnetic balls connected to the acrylic disk. The attraction between the iron balls and the magnets arrays fixed on the plate simulated binding between actual dynein and MT. The period of the magnet array was twice that of the ratchet teeth to simulate the period of the binding of MTBD to the MT. The simulation monomer can be connected together with a thin flexible wire, which simulated the tail domain of the dynein dimer.

The simulation system was vibrated using an electromagnetic shaker to generate random motion of simulation dynein. The shaker was set at the commonly used vibration acceleration Γ of 1.4 G, and the vibration frequency was arbitrarily set at 19.7 Hz. The rest of the experimental setup was the same as that in Jeng *et al.* [24]. To increase the probability of generating a minus end-directed force, the mass distribution was slightly shifted toward the minus end of the MT by attaching an additional small mass, which is consistent with the actual dynein-MT complex. The individual simulation monomer moved toward the minus end when the plate was vibrated. The monomers of the dynein dimer showed motility for both serial arrangement in one trench and parallel arrangement with monomers moving along different trenches.

4. Force Generation

Figure 3 shows a series of rapid side-view images of a serial dimer with a straight linker to demonstrate the fundamental mechanism for minus- and plus-end-directed motions. In these images, the thin lines represent the starting position of the dimer. The linkers are painted white to visualize the detail motion of the heads. The process of a minus-end directed jump is depicted in **Figure 3(a)**. The number 1 picture shows that both the leading and trailing monomers jump up after a previous collision with the ratchet teeth. In the number 2 picture, the leading monomer slightly tilts and collides with the top of the ratchet tooth right below and gains an impulse with a longitudinal component toward the minus end. In the number 3 and 4 pictures, the leading monomer moves ahead after bouncing up from the ratchet.

Figure 3(b) shows the similar process of a plus-end directed jump. **Figure 3(c)** and **Figure 3(d)** show the schematics of the collisions in the number 2 pictures that produce the minus-end and plus-end directed impulses respectively. Such collisions may occur at either one of the monomers. In the case of actual dynein, the trans-

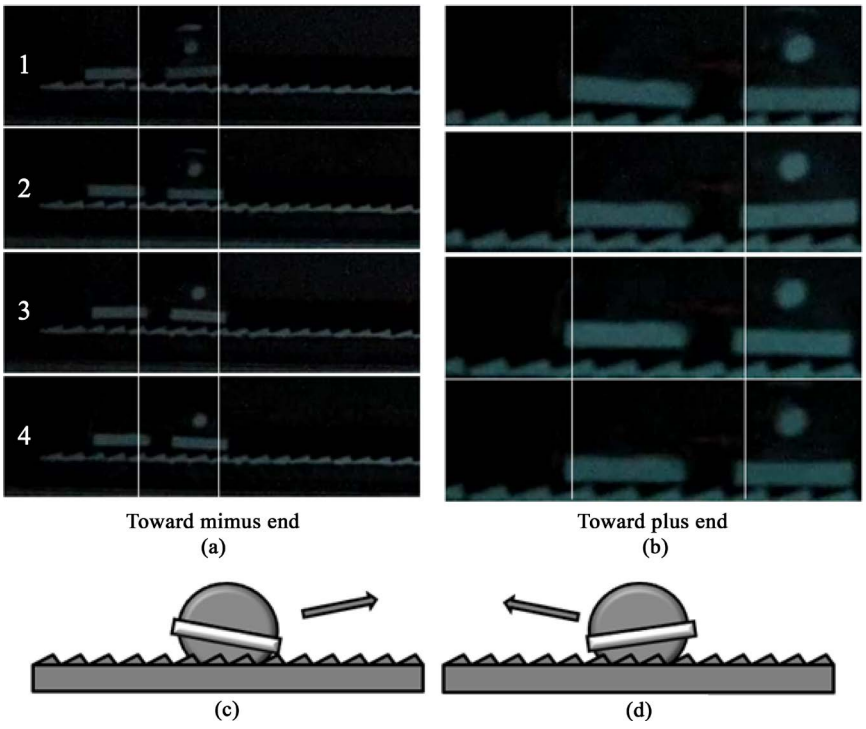


Figure 3. Mechanism for minus- and plus-end-directed motions. (a) Series of side-view images of the minus-end directed motion taken with a fast camera at a frame rate of 800 frames/sec; (b) same as in (a) for a plus-end jump; (c) and (d) collisions producing minus-end and plus-end directed impulses respectively.

verse component of the binding force exerted by the MT plays a role similar to that played by gravity in our simulation, which pulls the transversely moving AAA ring back toward the MT. The linker of the simulation model may collide with the long side of the ratchet teeth and produce plus end-directed movement, which is observed in both actual [18] [20] and simulation dynein. However, for our simulation, the probability of movement toward the plus end can be reduced by attaching an additional mass for shifting the CM of simulation dynein toward the minus direction. Such a shift in the CM may ensure that the linker slightly tilts in the direction of the minus end, and the collision process illustrated in **Figure 3(a)** is likely to occur. In actual dynein, the tail domain curves up sharply near the end of the linker on the side of the minus end, and the load may shift the CM toward the minus end through the tail domain.

5. Results

Figure 4 demonstrates the effect of the shift in CM on the velocity of simulation dynein. **Figure 4(a)** shows the time traces of the displacement of the head of simulation dynein dimer for various shifts of CM. The straight simulation linker is used in this experiment. A zero shift implies that the head and linker are symmetric about the vertical axis. Both the shift in the CM and the displacement of the simulation dynein are assigned positive values for the minus end-directed shift and motion as judged from the structure of MT. The main purpose of this

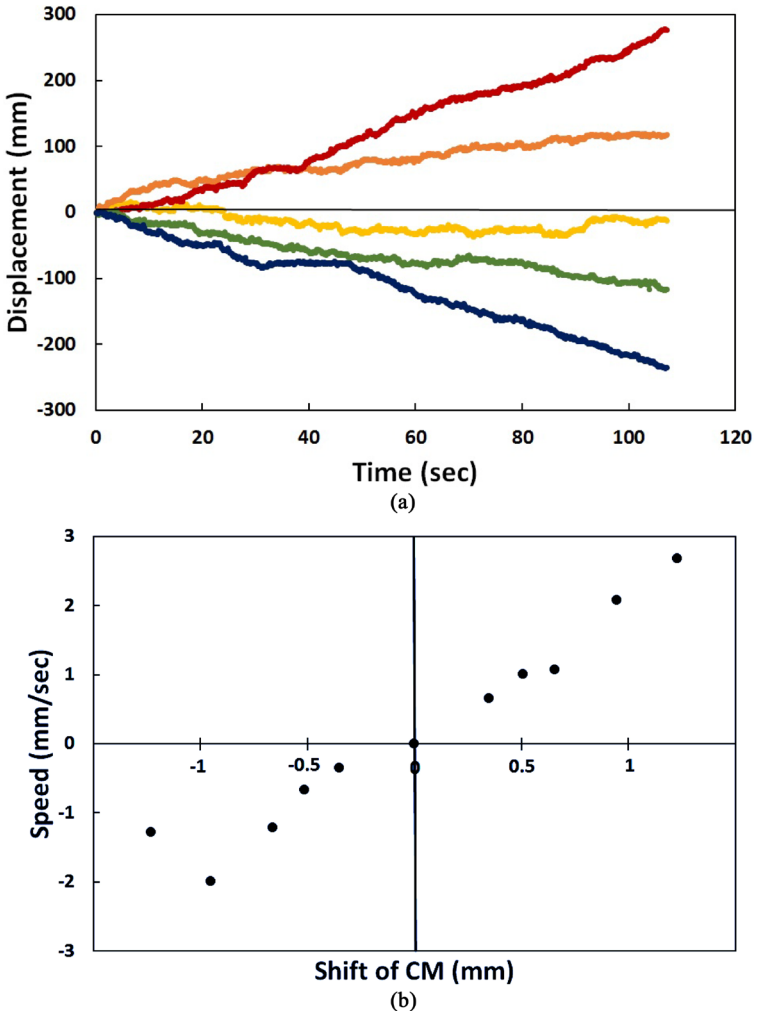


Figure 4. (a) Time traces of the simulation dynein for the different shifts in CM. Red: 1 mm, Orange: 0.5 mm, Yellow: 0 mm, Green: −0.5 mm, Blue: −1 mm. Both the shift in the CM and the displacement of the simulation dynein are assigned positive values for minus end-directed shift and motion; (b) effect of the shift of the center of mass (CM) on the speed of the dynein dimer. The direction of motion can be reversed by shifting CM of the two individual monomers.

part of experiments is to demonstrate the effects of symmetry by the shift of CM, therefore, the simulation MTBD is disconnected so that CM of the symmetric simulation dynein is on the vertical axis. **Figure 4(b)** shows the averaged velocity as a function of the shift in the CM. Symmetric dynein moves randomly around the initial position. Moreover, the directional motion becomes more obvious as an additional mass is attached to the linker of simulation dynein. Thus, the direction of the motion of dynein can be determined based on the shift in the CM (asymmetry) of dynein according to the proposed dynamic mechanism. We found that the shape of the linker is not crucial, and a curved linker may facilitate the processive motion of simulation dynein. In the remainder of this study, curved linkers were used. Furthermore, no difference was observed in motility between simulation dyneins with two heads arranged in series and parallel.

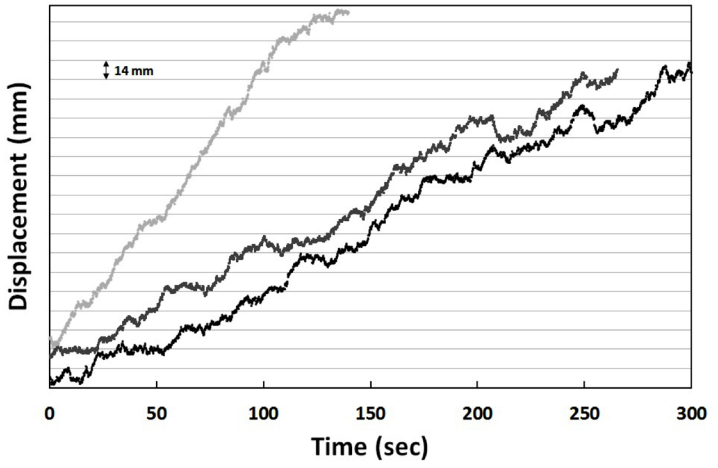
In this study, we also compared the behaviors of simulation dynein with those of cytoplasmic dynein described in the literature.

Steps have been observed during the processive motion of dynein along MTs [5] [7] [15] [16]. The distribution of the step size is wide, with a maximum size of 8 nm, which is twice the period of the ratchet structure on the outer surface of MTs. In our proposed dynamic mechanism, the force for the motion of dynein is generated by the random collision between the linker domain and the ratchet structure on the MT. Moreover, the steps are a result of the temporary stopping of dynein by binding between the MTBD of dynein and MT. When the random impulsive force overcomes the attraction (binding) force, the dynein monomer advances in the direction of the random force. In the simulation of the motion of dynein on the MT, binding between MTBD and the MT is simulated as the magnetic attraction between iron balls connected to the head domain with a bead chain and small magnets embedded in the trenches between two arrays of ratchet structures with a period of 14 mm, which is twice the period of the ratchet structure used in this study.

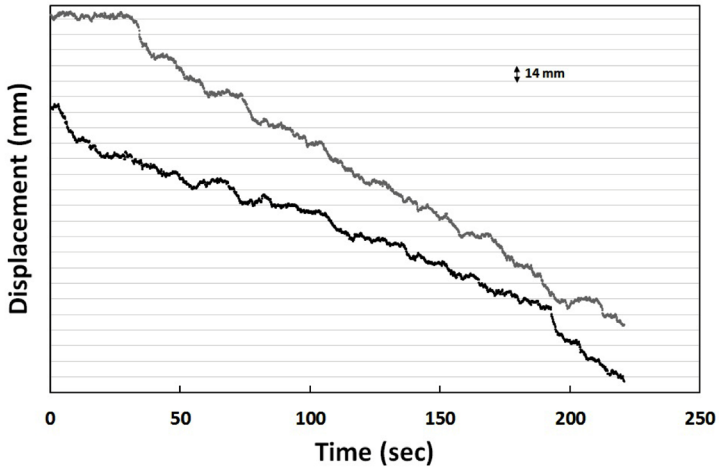
Figure 5 shows the time traces of simulation dynein with head-labeled monomers in series. The loading force (F) is applied with a hanging weight on the wire (tail domain) connecting the two monomers. The vibration acceleration of the shaker was set at 1.4 G. Without the application of the loading force, the dynein dimer moves toward the minus end, judging from the shape of the ratchet teeth, with a very high speed (**Figure 5(a)**, light gray curve); hence, the steps are not discernible. The position and speed are assigned positive values for minus end-directed motion and negative values for plus end-directed motion. Examples of the time traces with observable steps are shown in the gray and black curves for a loading force of 110 mg in **Figure 5(a)**. Occasional back steps are also observed. As the loading force is increased, the speed of simulation dynein decreases. The direction of motion changes toward the plus end when the applied load exceeds the stall force. Examples of the time traces of the force-induced plus end-directed motion are shown in **Figure 5(b)** for a loading force of 390 mg. Similar to the observations for cytoplasmic dynein, steps can be seen in the motion of dynein in both directions. The velocity-force (V-F) relation [7], which is a demonstration of the ability to output power of a motor, is shown in **Figure 5(c)**.

Statistical analysis revealed that the distribution of the dwell time and the size of the steps are similar to those of cytoplasmic dynein [5]. **Figure 6(a)** shows the histogram of the dwell times of the experiments for a leading force of 110 mg, which is consistent with a stochastic distribution. **Figure 6(b)** shows the histogram of the step size for the same experiment. The distribution of the step size peaks at 14 mm (equivalent to a step size of 8 nm for cytoplasmic dynein) for motion in both directions. Large steps are also observed.

Unlike kinesin, cytoplasmic dynein occasionally jumps to neighboring protofilaments, exhibits diffusive motion for some time, and then moves forward again, although it might not return to the previous protofilament [5]. Such behaviors are consistent with the dynamic mechanism proposed in this study. The conditions for dynein monomers to move along the protofilament are (a) the monomer is bound to the MT through MTBD, (b) the head domain fits into one trench on the outer surface of the MT, and (c) the random collisions between the linker and the ratchet on the MT generate the force required for the motion of dynein. The dimer can move forward even if the monomers are not in the same trench. However, if the reactive force resulting from the collision between the linker and the ratchet tooth is too large, then the head domain, even the whole monomer, may detach from the trench. The detached monomer can only exhibit diffusive motion on the surface of the MT. Once the randomly moving head fits into any one of the trenches, the monomer moves forward again. During the period in which one monomer detaches from the trench, if the other monomer stays in the trench, then when the detached one fits into a trench again, the dimer moves in a straight line. In some cases, both monomers detach from the trenches; the resulting off-axis movement may be very large, as observed by Reck-Peterson *et al*. [5]. Such detach-and-reattach events are observed in the simulation experiments (see supplementary material S1 for



(a)



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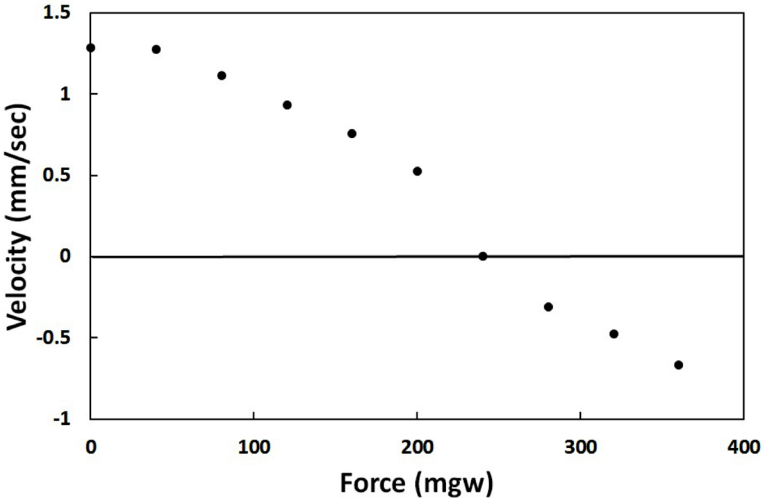
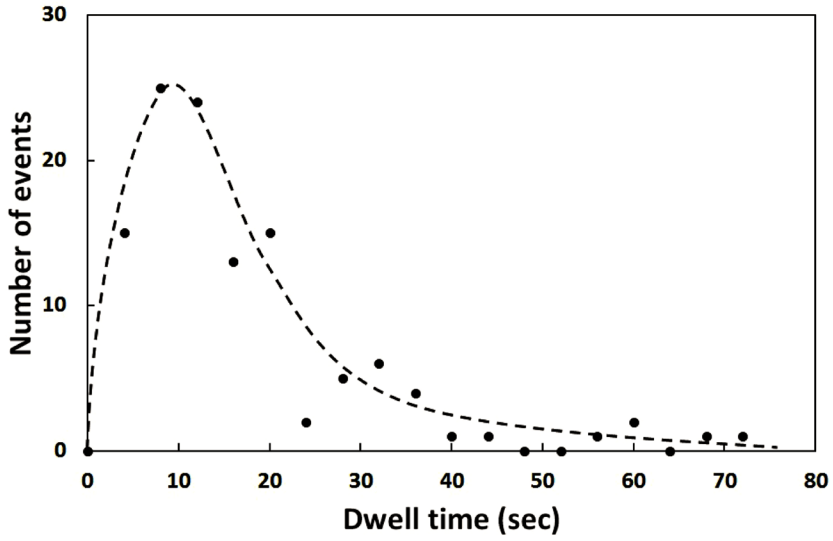
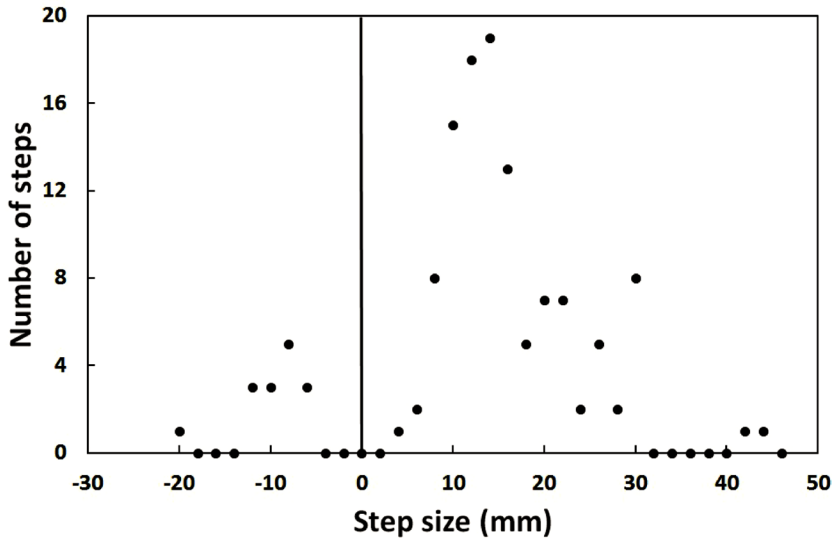


(c)

Figure 5. Force induced bidirectional motion. (a) The light gray curve is the time trace of the free simulation dynein. The gray and black curves are the time traces of the simulation dynein with a loading force 110 mgw (1 mgw = 0.98 dynes) pointed to the plus end. Steps are discernable. The thin horizontal lines separated by 14 mm are drawn to guide the eyes; (b) two examples of the time traces with the loading force of 390 mgw. Curves in (a) and (b) are shifted by multiples of 14 mm for clarity; (c) the force-velocity relation of the simulation dynein.



(a)



(b)

Figure 6. (a) The distribution of the dwell time of the observed steps. The dashed curve is drawn to guide the eyes; (b) the distribution of the step sizes. The major peak locates at 14 mm as expected. The negative value of the step size indicates the occasional backward steps.

a video demonstration). In the simulation system, the frequency of the detach-and-reattach events decrease with the vibrational acceleration. In the dynamic mechanism, the vibrational acceleration plays the same role as the concentration of ATP as the energy supplier of the random motion of dynein. Therefore, one can infer that, for the real dynein, the frequency of the detach-and-reattach events would decrease with the concentration of ATP.

In the dynamic mechanism, the monomers move independently along two different trenches on MTs as long as the long and flexible tail domain is stretched [16] [17] [23]. Thus, the dynamic mechanism appropriately explains the findings of DeWitt *et al*. [16] that the stepping of the two monomers of cytoplasmic dynein are uncoordinated, and that the dimer can move processively with one active monomer only. The monomers interact with each other through the tension in the tail domain. When the tension is low, that is, the separation between the two monomers is low, and the tail domain is not stretched, the two monomers move forward independently, and the steps are uncoordinated. If the separation between the monomers is high, then the slow moving monomer may be dragged by the rapidly moving monomer, and the stepping of the monomers is coordinated. In the

simulation experiments, we first showed that the individual monomer of simulation dynein moves independently along two well-separated trenches (see supplementary material S2 for a video demonstration). The two monomers are connected with a long (10 cm) and thin (0.1 mm) flexible wire. The wire simulates the long and flexible tail domain of the dynein dimer. Moreover, the labeling markers are attached close to the simulation MTBD of the individual monomers to clearly detect the steps. **Figure 7** shows the time traces of the two monomers placed in the next-nearest neighboring trenches. **Figure 7** shows the time traces of the two individual monomers of a dimer. In **Figure 7**, no clear coordination was observed between the stepping of the two monomers. When the separation between the two monomers is high, the trailing monomer is dragged by the leading monomer through the tension in the wire; the stepping patterns seem to be coordinated.

Tanenbaum *et al*. [17] reported that the dynein dimer can bind two antiparallel MTs and can drive the two MTs to slide across each other. This result is consistent with the dynamic mechanism. In the dynamic mechanism, the monomers of a dimer can not only operate independently on one MT but also operate on two different MTs if their individual MTBDs bind to two different MTs. The monomers can move on the respective MTs. Consequently, the dynein molecule is always at the intersection of the two MTs sliding across each other. In the simulation experiments, we demonstrated that two protofilaments slide owing to the limited space. We made two parallel tracks with one unbound section of our simulation protofilament and a monomer of simulation dynein fitting into each track. The two monomers are connected with a thin flexible wire. The linker of a simulation dynein monomer sits on the ratchet structure of the simulation protofilament. As shown in supplementary material S3, when the setup is vibrated, the two protofilaments move antiparallel to each other. Moreover, the dynein dimer only jumps around slightly. This simulation experiment proves that the dynein dimer can drive two MTs to slide across each other, with each monomer binding to and moving one MT, as long as the monomers can independently move processively on MTs.

Ross *et al*. [18] reported that the direction of motion of the dynein-dynactin complex can change when the complex moves processively on MTs. They also observed that the process of changing the direction of motion is gradual and spontaneous [18]. Considering that dynactin itself is not a molecular motor and that only the tail domain of dynein is involved in the interaction with dynactin (*i.e.*, the motor domain remains the same in the complex), we inferred that the direction of motion of dynein is affected by factors external to the dynein molecule. In the dynamic mechanism, the factor that determines the direction of motion is the position of the CM of the complex. As shown in **Figure 4**, the direction of motion of simulation dynein can be changed by shifting the CM of dynein through the attachment of an additional mass to the simulation model. Therefore, the change in the direction of motion during the processive motion of the complex can be explained in the framework of the dynamic mechanism; because of the high flexibility of the tail domain, the relative position of dynactin to dyne-

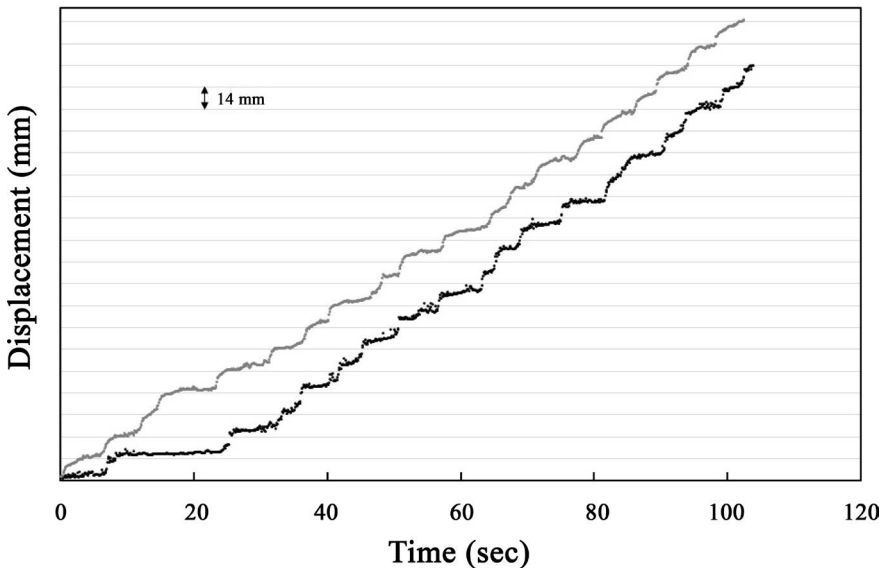


Figure 7. Time traces of the two monomers. The horizontal lines separated by 14 mm are drawn to guide the eyes. The stepping behaviors of the two monomers are clearly uncoordinated.

in might be changed by the interactions with materials near the MT. The interactions might cause slow changes in the CM, such as the drifting of dynactin, or rapid changes in the CM, such as a collision with other large molecules. In supplementary material S4, we show that the direction of motion of a simulation monomer can be changed by a shift in the position of a mesh of copper wire attached to the monomer, which simulates the dynein-dynactin complex. In this experiment, only the CM of the complex was changed.

6. Discussion

In this study, we proposed a dynamic mechanism for the processive motility of dynein on MTs. The force generated for the motion of dynein is purely mechanical in origin. When the MTBD of the dynein monomer binds to a MT, the AAA ring of dynein might fit into one of the trenches on the outer surface of the MT, with the linker domain leaning on the ratchet-shaped protofilament. At room temperature, the dynein molecule exhibits random thermal motion on the outer surface of MT. The collision between the asymmetric ratchet teeth and the linker exerts a reactive impulsive force on the dynein molecule. The probability of producing an impulse with a longitudinal component pointing to the minus end depends on the instantaneous motion of dynein, the shape of the linker, and the mass distribution of the dynein with/without a load. If the linker tilts in the direction of the minus end, the portion of the linker in the direction of the minus end would have a high probability of colliding with the top of the teeth on the outer surface of the MT. Such collisions produce minus end-oriented impulses that drive the dynein motor to move toward the minus end of the MT. Similarly, if the linker tilts in the plus end direction and collides frequently with the long side of the ratchet teeth, a plus end-oriented force is generated. Therefore, in the dynamic mechanism, the dynein monomer can move in either direction. We performed simulation experiments for the dynein motility according to the dynamic mechanism; we also stimulated the structures of the dynein molecule and MT. Similar dynamic properties, such as the steps in motion, the statistical distribution of the dwell time and the step size, and the force-velocity relation, were reproduced in the simulation system.

The shift in the CM of dynein in one direction effected by attaching a load or forming a complex with other molecules will enhance the probability of producing impulsive forces in that direction. Hence, the shift in the CM may determine the direction of the motion of the dynein complex. The aforementioned argument may explain the bidirectional motion of the dynein-dynactin complex, accounting for the flexible tail domain. In the dynamic mechanism, the monomers of the dynein dimer can move independently on the MT. If the two monomers bind to one MT, then such independent motion may lead to uncoordinated stepping of the two monomers, as observed by DeWitt *et al*. [16]. If the two monomers bind separately to two MTs, then the two MTs may slide antiparallel to each other, as observed by Tanenbaum *et al*. [17].

The notion that the random motion and collision with the asymmetric structures in the surrounding can generate unidirectional motion has been proven to be workable for many biological motors with their respective simulation counterparts, for example, the portal motor of DNA packaging in bacteriophages [24], the processive motion of kinesin on MT [22], and the rotation of the γ-subunit of ATPase [25].

Acknowledgements

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Supplementary Materials

Supplementary material S1: Detach-and-reattach events of the simulation dynein dimer. Detaching and reattaching events occur stochastically. For the event that one monomer detaches, the motion of the other monomer may or may not be affected.
https://sites.google.com/site/molecularmotor214s1/

Supplementary material S2: The individual monomer of simulation dynein moves independently along two well-separated trenches. Comparing with the dimers, the monomers are easier to fall off the track. In the other words, dimerization or complexing with other large molecules may stabilize the motion of monomers.
https://sites.google.com/site/molecularmotor214s21/

Supplementary material S3: Two protofilaments can be driven to slide in an anti-parallel fashion by one simulation dynein dimer. One white rectangle is painted on each protofilament to facilitate the visualization the motion of the protofilament.
https://sites.google.com/site/molecularmotor214s3/

Supplementary material S4: The direction of motion of a simulation dynein monomer can be reversed by a mesh of copper wire attaching at different positions. The effect of the attached copper wire is to change the position of the center of mass and the direction of motion of the complex (S5 and S61).
https://sites.google.com/site/molecularmotor214s41/
https://sites.google.com/site/molecularmotor214s5/
https://sites.google.com/site/molecularmotor214s61/

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