1 Torsional turning motion of chromosomes as an accelerating force to align homolog
2 ous chromosomes during meiosis

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21 Abstract

22 Homologous sets of parental chromosomes must pair during meiosis to produce
 23 recombined sets of chromosomes for their progeny. This is accompanied by nuclear
 24 oscillatory movements. This study aimed to elucidate the significance of these
 25 movements with a model, wherein external force was applied to the oscillating nucleus
 26 and via hydrodynamic interactions within the nucleus. Simulations revealed that a major
 27 force for aligning homologous chromosomes is length-dependent sorting during
 28 chromosomal torsional turning, which occur when the nucleus reverses the direction of
 29 its movement.

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32 Meiosis is an important process for eukaryotic organisms to generate inheritable haploid
33 gametes from a diploid cell. During meiosis, homologous (paternal and maternal)
34 chromosomes recombine; these recombined chromosomes are inherited by their
35 progeny. For recombination of homologous chromosomes, side-by-side alignment of
36 homologous loci along the chromosome is necessary [1]. During this alignment of
37 homologous chromosomes, telomeres form a cluster beneath the nuclear envelope in
38 various eukaryotic organisms [2].

39 Unicellular fission yeast *Schizosaccharomyces pombe* is a useful model system for
40 studying the alignment of homologous chromosomes during meiosis [3, 4]. A meiotic
41 cell of *S. pombe* contains 3 pairs of homologous chromosomes (chromosomes 1, 2, and
42 3 of 5.6, 4.6, and 3.5 Mb, respectively) [5]. During meiotic prophase, the nucleus
43 elongates, oscillates between the cell poles, and shows drastic deformation, so-called
44 “horsetail movement” [6], during which telomeres remain clustered at the spindle pole
45 body (SPB) at the leading edge of the nuclear movement [6]. Telomere clustering and
46 nuclear movements reportedly promote the alignment of homologous chromosomes
47 [7,8,9].

48 To elucidate mechanisms underlying the alignment of homologous chromosomes,
49 computer simulation strongly facilitates the examination and prediction of biological
50 events under conditions that are never accomplished empirically. Various theoretical
51 models of the pairing of homologous loci during meiosis have been proposed on the
52 basis of telomere clustering [10, 11, 12, 13]. However, the role of the nuclear envelope,
53 which confines the chromosomes, remains unknown in these models.

54 Studies are required to consider the role of the nuclear envelope in models of the
55 meiotic nucleus of *S. pombe*, since its nucleus migrates and undergoes striking
56 deformation during meiosis. During the horsetail movements, the nuclear envelope
57 receives drag forces from the cytoplasm and from the nucleoplasm, while each
58 chromosome receives drag forces only from the nucleoplasm. Thus, models of the
59 meiotic nucleus of *S. pombe* would help describe the motion of the deformable nuclear
60 envelope, direct collisions between the nuclear envelope and chromosomes, effects of
61 the cytoplasm on the nuclear envelope, and effects of the nucleoplasm on chromosomes
62 and the nuclear envelope, in addition to telomere clustering at the SPB. This study

63 aimed to propose the first model displaying the aforementioned nuclear membrane
64 dynamics and investigate the role the horsetail nuclear movements in the alignment of
65 homologous chromosomes via simulations of the presented model..

66 **Model construction:** A model of chromosomes confined within the nuclear envelope of
67 *S. pombe* cells (Fig. 1(a)) was developed using the following methods. We described
68 each chromosome as a chain and the nuclear envelope as a one-layered shell—both
69 comprising particles with an excluded volume (Fig. 1(b)). Each chromosome was
70 assumed to consist of particles with uniform radii since they were expected as almost
71 uniformly condensed chains during meiosis. A meiotic nucleus of *S. pombe* contains 3
72 homologous pairs of chromosomes; thus, the model contains 6 chains in total confined
73 in the shell. To account for the effects of the SPB on chromosomal movement, we
74 constructed a virtual sphere around the SPB (“the SPB sphere”), penetrating a limited
75 area of the shell (nuclear envelope) extending toward the space inside the shell (Fig.
76 1(b)). To simulate telomere movement, which are clustered near the SPB during the
77 horsetail movement, we assumed that ends of the chromosome chains move along the
78 surface of the SPB sphere inside the shell.

79 To simulate the horsetail movements, we assumed that the SPB sphere oscillates
80 periodically in the cell. Here, the drag force from the cytoplasm is exerted exclusively
81 on the nuclear envelope. Since the cytoplasm can be considered a static intracellular
82 fluid, we assumed that this drag force is proportional to the velocity of the nuclear
83 envelope. However, the drag forces from the nucleoplasm to the nuclear envelope and
84 chromosomes depend on the intranuclear velocity profile of the nucleoplasm, which is
85 primarily determined on the basis of velocity profiles of chromosomes and the nuclear
86 envelope. Thus, drag forces from the nucleoplasm could be described by the
87 hydrodynamic interaction among particles in the chains and the shell. Furthermore, we
88 assumed the volume of the nucleus tend to be sustained since the in and out flow of
89 nucleoplasm through the nuclear envelope were considered to be little during meiosis.

90 These methods allowed for the generation of an appropriate model involving the effects
91 indispensable for simulating the *S. pombe* meiotic nucleus.

92 **Model implementation:** We assumed that chromosomes 1, 2, and 3 consist of N_n
 93 particles ($n = 1, 2$, or 3) and the nuclear envelope consists of M particles with radii $= r$.
 94 The motion of the i -th particle is given as

$$95 \quad m\ddot{\vec{x}}_i = -\gamma_i\dot{\vec{x}}_i - \nabla_i U(\{\vec{x}_i\}) + \sum_j \vec{F}_{ij} \quad (1)$$

96 where $\vec{x}_i = (x_i, y_i, z_i)$ and m are the position and mass of the i -th particle,
 97 respectively. γ_i indicates the coefficient of a drag force from the cytoplasm where
 98 $\gamma_i = 6\pi r\eta$ if the i -th particle is on the nuclear envelope and $\gamma_i = 0$ if the i -th particle
 99 is on the chromosome. Here, η was assumed as the viscosity of cytoplasm.

100 In the second term of equation (1), the potential of the system $U(\{\vec{x}_i\})$ is given as
 101 follows:

$$102 \quad U(\{\vec{x}_i\}) = U_{cs} + U_{ms} + U_e \quad (2)$$

103 where U_{cs} is the contribution from the chain, U_{ms} is the contribution from the nuclear
 104 envelope, and U_e is the potential of the excluded volume effects.

105 The potential contribution from the chromosome chain U_{cs} is given as follows:

$$106 \quad U_{cs} = \sum_{i < j} \frac{k_c}{2} (|\vec{x}_i - \vec{x}_j| - 2r)^2 + \sum_{i=telo} \frac{k'_c}{2} (|\vec{x}_i - \vec{X}_{SPB}| - (R_s + r))^2 \quad (3)$$

107 where the i -th particle is a part of chromosomes, r indicates the radii of particles, and
 108 $\vec{X}_{SPB}$ and R_s indicate the position of the center and the radius of the SPB sphere. We
 109 assumed each chromosome is a chain of particles connected in a line. Σ in the 1st term
 110 indicates the sum for the i -th and j -th particles ($i < j$) that are adjacent and bonded along
 111 the chromosome, and Σ in the 2nd term indicates the sum for the i -th particle at the
 112 ends of chromosomes corresponding to the telomeres.

113 The potential contribution from the nuclear envelope U_{ms} is given as follows:

$$\begin{aligned}
 U_{ms} = & \sum_{i < j, L_{i,j} < 3r} \frac{k_m}{2} (|\vec{x}_i - \vec{x}_j| - L_{i,j})^4 + \sum_{L_{i,SPB} < R_s} \frac{k'_m}{2} (|\vec{x}_i - \vec{X}_{SPB}| - L_{i,SPB})^2 \\
 & + \frac{k_v}{2} \left(\sum_i \frac{\pi r^2}{3} |\vec{x}_i - \vec{x}_{CM}| - V \right)^2 \\
 & + \sum_i \theta(\sqrt{x_i^2 + y_i^2} - (R_c - r)) \frac{k_w}{2} (\sqrt{x_i^2 + y_i^2} - (R_c - r))^2
 \end{aligned}$$

114 (4)

115 where the i -th particle is a part of the nuclear envelope. θ is Heaviside step function
 116 and $L_{i,j}$ indicates the initial distance between the centers of the i -th and j -th particles
 117 constructing the nuclear envelope ($L_{i,SPB}$, the initial distance between the centers of the
 118 i -th particle and the SPB sphere). Here, the initial structure of the nuclear envelope is
 119 indicated as a spherical shell with a thickness of one particle layer constructed by the
 120 rings along with y-axis with various radii consisting of particles (Fig. 1(c)), and initial
 121 position of the center of the SPB sphere is denoted as $\vec{X}_{SPB}(0) = (R_c, 0, 0)$ (R_c is the
 122 radius of the cell as described below). Σ in the 1st term of U_{ms} indicates the sum for
 123 the i -th and j -th particles ($i < j$) that are adjacent and bonded obeying $L_{i,j} < 3r$; Σ in
 124 the 2nd term indicates the sum for the i -th particle obeying $L_{i,SPB} < R_s$; Σ in other
 125 terms indicate sum for all particles constructing the nuclear envelope. Notably, we
 126 assumed that the nuclear envelope can deform easily since it consists of lipids that can
 127 exhibit the elasticity as well as the fluidity. Thus, we used an unharmonic potential in
 128 the 1st term of U_{ms} which provides weaker tension for local small changes in relative
 129 positions among particles in the nuclear envelope than the harmonic potential, inducing
 130 larger global deformation of nuclear envelope.

131 The 2nd term of U_{ms} indicates the binding of the SPB to the nuclear envelope,
 132 where particles constituting the nuclear envelope and confined in the SPB sphere were
 133 connected tightly to the center of the SPB sphere. The 3rd term of U_{ms} provides the
 134 force to sustain the volume of the cell nucleus where $\vec{x}_{CM}$ and V indicate the position
 135 of the center of mass and the volume of the nucleus, respectively. Here, V is denoted by

136 $\sum_i \frac{\pi r^2}{3} |\vec{x}_i - \vec{x}_{CM}|$ with initial values of $\vec{x}_i$. The 4th term of U_{ms} indicates the

137 excluded volume effect of the cell wall, where the cellular shape was assumed to be a
138 parallel cylinder along the z -axis, with a radius R_C . Here, the central axis of this cylinder
139 is denoted as $(0,0,z)$, and θ indicates the Heaviside function.

140 U_e denotes the potential of the excluded volume effects among particles and the SPB
141 sphere as follows:

$$U_e = \sum_{i < j} \theta(2r - |\vec{x}_i - \vec{x}_j|) \frac{k_e}{2} (|\vec{x}_i - \vec{x}_j| - 2r)^2 \\ + \sum_i \theta((R_S + r) - |\vec{x}_i - \vec{X}_{SPB}|) \frac{k'_e}{2} (|\vec{x}_i - \vec{X}_{SPB}| - (R_S + r))^2$$

142 (5).

143 In the third term of equation (1), $\vec{F}_{ij}$ indicates the force of hydrodynamic effects
144 from the j -th particle to the i -th particle, providing a drag force to each particle from the
145 nucleoplasm. Herein, we employ the lubrication approximation [14, 15] because it can
146 describe hydrodynamic effects among polymers modeled by particle chains in the
147 simulation of the polymers suspension in shear flow suitably [15], which is denoted as
148 follows:

$$149 \quad \vec{F}_{ij} = \begin{cases} \frac{3}{2} r^2 \pi \eta \frac{(\vec{x}_j - \vec{x}_i) \cdot \vec{n}_{ij}}{|\vec{x}_j - \vec{x}_i| - 2r} \vec{n}_{ij} & (\text{if } |\vec{x}_j - \vec{x}_i| > 2.001r) \\ \frac{3}{2} r^2 \pi \eta \frac{(\vec{x}_j - \vec{x}_i) \cdot \vec{n}_{ij}}{0.001r} \vec{n}_{ij} & (\text{if } |\vec{x}_j - \vec{x}_i| \leq 2.001r) \end{cases} \quad (6)$$

150 where r and $\vec{n}_{ij}$ denoted the radius of the particle and a relative unit vector from the
151 j -th particle to the i -th particle $\vec{n}_{ij} = \frac{\vec{x}_i - \vec{x}_j}{|\vec{x}_i - \vec{x}_j|}$, respectively. Nucleoplasm viscosity was
152 assumed the same as the cytoplasm viscosity η in this model.

153 **Parameters for simulations:** In the simulations, we assumed a particle radius
154 $r = 0.084 \times 10^{-6} (m)$, where each particle models a local region of chromatin of ~ 100
155 kb. Here, chromosomes 1, 2, and 3 (5.6 Mb, 4.6 Mb, and 3.5 Mb, respectively) were
156 described by the chains consisting of 56, 46, and 34 particles ($N_1 = 56$, $N_2 = 46$, and N_3
157 $= 34$; we considered N_3 as an even number for convenience of analysis). The nuclear

158 envelope was constructed by using 994 particles ($M=994$) where we assumed their radii
159 were the same as those of chromosome particles ($r = 0.084 \times 10^{-6}(m)$) because of the
160 convenience to simulate the hydrodynamic effects using Eq. (6). Here, the inner
161 diameter of the initial spherical structure of the nuclear envelope was assumed to be
162 $2.7 \times 10^{-6}(m)$, the initial distance between the center of the SPB sphere and that of the
163 nucleus was assumed to be $2.0 \times 10^{-6}(m)$, and the radius of the SPB sphere was
164 assumed $R_s = 10r$ (Fig. 1(b)). In this case, the diameter of the cross-section where
165 nucleus and the SPB sphere intersect was $\sim 1.0 \times 10^{-6}(m)$. The initial configurations
166 of the chromosomes were randomized in this spherical shell.

167 The viscosity of nucleoplasm and cytoplasm η was $\sim 0.64 (kg\ m^{-1}s^{-1})$ [12].
168 The elastic constants were assumed as appropriate large values for the excluded volume
169 effects of all particles and the connections among particles in chromosomes, among
170 particles in chromosomes and the SPB sphere, and among particles in the nuclear
171 envelope and SPB sphere, as $k_c = k_w = k_e = k'_e = 2.77 \times 10^8 (kg\ s^{-2})$, $k'_c =$
172 $6.22 \times 10^8 (kg\ s^{-2})$, and $k'_m = 8.12 \times 10^8 (kg\ s^{-2})$. We also assumed the elastic
173 constant to keep the connection of particles in the nuclear envelope and the nuclear
174 volume as appropriate values as $k_m = 4.77 \times 10^{20} (kg\ s^{-2}\ m^{-2})$ and $k_v = \frac{150}{\pi} k_m$
175 with which the present model reproduced a similar shape variation of the nuclear
176 envelope via horsetail movements. The inertia term of Eq. (1) cannot be eliminated in
177 order to employ the lubrication approximation although the equation of motion of such
178 microscopic system should obey the equation with overdamp limit. However, we
179 assumed m as $\sim m/6\pi r\eta \sim 10^{-3} sec$ ($m = 8.3 \times 10^{-10}(kg)$ was assumed in this

180 paper) that indicates the relaxation times of the particle velocities were negligibly
181 smaller than the period of horsetail movement $\sim 10^2 sec$. Therefore, we could neglect
182 the effects of inertia to simulate our focused phenomena. We confirmed that the
183 following results were qualitatively unaffected by small changes in these parameters
184 when k_m was chosen appropriate to exhibit sufficient shape variation of the nuclear
185 envelope where chromosomes can elongate. Thus, we consider these parameters
186 appropriate to simulate intracellular environment.

187

188 **Results:** To evaluate the effects of the horsetail movement, we simulated the following
 189 four cases of motions of the SPB sphere in the cylinder (cell) with radius $R_c = 2 \times$
 190 $10^{-6} (m)$ as shown in Fig. 2: (a) 3-d 8-shaped oscillatory motions as $\overrightarrow{X_{SPB}} = (R_c -$
 191 $B(1 - \cos 4\pi wt), C \sin 4\pi wt, A \cos 2\pi wt)$, (b) 3-d O-shaped oscillatory motions as
 192 $\overrightarrow{X_{SPB}} = (R_c - B(1 - \cos 4\pi wt), C \sin 2\pi wt, A \cos 2\pi wt)$, (c) 1-d motions as
 193 $\overrightarrow{X_{SPB}} = (R_c, 0, A \cos 2\pi wt)$, and (d) 1-d constant velocity linear motion as $\overrightarrow{X_{SPB}} =$
 194 $(R_c, 0, \pi w A t)$. Herein, $A = 7.3 \times 10^{-6} (m)$ and $w = \frac{1}{3} \times 10^{-2} (s^{-1}) (= 12 (h^{-1}))$
 195 since the SPB completes 30 oscillations in 2 ~3 h from end to end in spheroid-shaped *S.*
 196 *pombe* cells [9]. Furthermore, we assumed $B = 0.208 \times 10^{-6} (m)$, and $C = 0.67 \times$
 197 $10^{-6} (m)$. The results were qualitatively independent of the detail values of B and C .

198 Chromosomal behavior in the migrating nucleus was simulated under the
 199 aforementioned 4 conditions. Simulations were repeated with eight initial states for each
 200 condition (Figs. 3, 4, and Supplementary movies 1 and 2). Figure 3 shows typical
 201 snapshots for $t = 75, 3375$, and $7950 (s)$ in an example of 8-shaped 3-d oscillatory
 202 motion. Elongation of the nuclear envelope (Supplementary movie 1) and switching of
 203 relative positions among chromosomes (Fig. 3, Supplementary movie 2) were observed
 204 during oscillatory motions of the SPB. The present results indicate the validity of our
 205 simulations.

206 To obtain a pictorial view of chromosomal movements, we plotted positions of the
 207 chromosomes as probability distributions along the x-y plane (Fig. 4). The plots were
 208 obtained from the 34 ($= N_3$) nearest particles from the SPB sphere ($N_3 / 2 = 17$ nearest
 209 particles from each end) along each of the 6 chromosomes (Fig. 4a). Figure 4b shows
 210 typical snapshots of the probability distributions of particles for $t = 75, 3375$, and 7950
 211 (s) in the 3-d 8-shaped oscillatory motion. When $t = 75$, the probability distributions of
 212 particles of chromosome 1 and 3 exhibited two separated hills respectively, that
 213 indicated homologous pairs of chromosomes 1 and 3 were separated far away. On the
 214 other hand, the probability distributions of particles of all chromosomes exhibited only
 215 one hill respectively at different area when $t = 7950$. These facts indicated each
 216 homologous chromosome pair gathered temporally and non-homologous chromosomes

217 were separated from each other, that is, alignment of homologous chromosomes
218 occurred.

219 Figure 4 (c) – (e) show typical snapshots of the probability distributions of particles
220 at $t = 7950$ (s) when the SPB sphere exhibits a 3-d O-shaped oscillatory motion, a 1-d
221 oscillatory motion, and a linear motion. As shown in Fig. 4 (b) and (c), each
222 homologous pair of chromosomes gathered temporally and non-homologous
223 chromosomes were separated from each other when the SPB sphere exhibits 3-d
224 oscillatory motion involving 3D reversal (torsional turning) motion of chromosomes.

225 However, when the SPB sphere exhibits 1-d oscillatory motion involving no
226 torsional motion of chromosomes, some homologous chromosome pairs often stay
227 separated from each other (Fig. 4 (d); alignment of homologous chromosomes was
228 observed exceptionally only in one out of eight simulations). Furthermore, the assembly
229 of homologous chromosomes did not occur when the SPB sphere exhibits a linear
230 motion involving no chromosomal turning (Fig. 4 (e)). These results suggest that
231 chromosomal torsional turning motion is crucial for shuffling of chromosomes for
232 appropriate alignment of homologous chromosomes.

233 By the simulations of following virtual situations where chromosomes 1 and 2
234 became shorter as (i) 4.6 Mb and 4.0 Mb ($N_1 = 46$, $N_2 = 40$, and $N_3 = 34$), and (ii) 3.8
235 Mb and 3.6 Mb ($N_1 = 38$, $N_2 = 36$, and $N_3 = 34$), we found that the frequency of the
236 separation of non-homologous chromosomes decreased with the decrease in their
237 difference in chain lengths: the separation of non-homologous chromosomes was
238 observed in three out of eight simulations in both situations even when the SPB sphere
239 exhibits a 3-d 8-shaped oscillatory motion. We also found the separation of
240 non-homologous chromosomes occurred little if the elastic constant k_m among
241 particles in nuclear envelope was given so large as that the shape variation of the
242 nuclear envelope was not sufficient for the elongation of chromosomes via the SPB
243 movements. By these facts, non-homologous chromosomes are considered to separate
244 owing to differences in chain lengths among non-homologous chromosomes.

245 During the horsetail movement, the SPB movement reverses its direction
246 periodically. Chromosomes receive drag forces from the nucleoplasm at every turn of

the SPB, while no drag force is exerted on chromosomes and the nuclear envelope if SPB migrates linearly with a constant velocity. During reversal of SPB, the region distal from the SPB in longer chromosomes tends to be dragged by the slow (nearly stopped) motion of the rear region of the bent nucleus, while that in the shorter one tends to follow the SPB motion (Fig. 5). Thus, the relative positions of longer and shorter chromosomes tend to separate gradually from each other owing to reversal of the iterative direction of the SPB movement, resulting in the separation of non-homologous chromosomes. Owing to this separation, homologous chromosomes are aligned and stabilized during the periodic reciprocation of the SPB.

Discussion: Homologous chromosome pairing has received increasing attention in studies in physics, and several models have been proposed to describe its underlying mechanisms [10, 11, 12, 13, 16]. In the present simulations, separation of non-homologous chromosomes was achieved when the SPB sphere shows 3-d oscillations in the cell, but not when the SPB sphere exhibits only a linear motion. This result is further substantiated by previous experimental evidence regarding *S. pombe*: the efficiency of homologous recombination decreases drastically when the nucleus does not exhibit the horsetail movement but just elongates [17]; the iterative reversals of the direction of the SPB movement during the horsetail movement are essential for the alignment of homologous chromosomes via separating non-homologous chromosomes [7, 9]. Our simulation reveals that a major force for the alignment and sorting of homologous/non-homologous chromosomes is the nucleoplasmic flow generated owing to SPB reversal and deformation of the nuclear envelope, involving direct collision and indirect hydrodynamic interactions between chromosomes and the nuclear envelope, which were previously unclear. The present model is the first, to our knowledge, to consider both direct collisions and indirect hydrodynamic interactions as essential mechanisms for the alignment of homologous chromosomes.

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Figure legends

FIG. 1. (a) Illustration of the meiotic nucleus of *Schizosaccharomyces pombe* containing 3 homologous pairs of chromosomes (Chr. 1, 2, and 3), the nuclear envelope (NE), the spindle pole body (SPB), and microtubules (MT). (b) Illustration of the model composed of particle populations. (c) Illustration of the model of an intracellular region described as a cylindrical space, and the initial structure of the nuclear envelope constructed by combining particle rings (along dashed circles) along the vertical y-axis with various radii.

FIG. 2. Illustration of trajectories of the spindle pole body (SPB) sphere motions in the cell (cylindrical space). (a) 3-d 8-shaped oscillatory motions, (b) 3-d O-shaped oscillatory motions, (c) 1-d oscillatory motions, and (d) 1-d constant velocity linear motion. Yellow particle indicates the SPB sphere; red and blue arrows indicate the trajectory of downward and upward motion, respectively.

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330 FIG. 3. Typical time course of chromosome dynamics in the case that the spindle pole
 331 body (SPB) sphere exhibits 3-d 8-shaped oscillation. Snapshots of chromosome
 332 configurations in the nucleus from two points of view (projected on y - z and x - z plane)
 333 at time $t = 75$ s (after 0 oscillations), 3375 s (after 10 oscillations), and 7950 s (after 26
 334 oscillations). The large sphere indicates the SPB sphere; red, black, and blue particle
 335 chains indicate Chr. 1, Chr. 2, and Chr. 3, respectively. Blue arrows indicate the moving
 336 directions of SPB.

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339 FIG. 4. Probability distributions of particles in each of the chromosome chains near the
 340 spindle pole body (SPB) sphere along the x - y plane. (a) The 34 ($= N_3$) nearest particles
 341 from the SPB sphere along each of the 6 chromosomes (filled particles) were used to
 342 estimate probability distributions. (b) Probability distributions of the 34 ($= N_3$) nearest
 343 particles on each chromosome indicated as filled particles in (a). Curves represent
 344 contour lines of probability distributions of particles in the 3-d 8-shaped oscillation of

the SPB sphere at $t = 75, 3375, \text{ and } 7950 \text{ s}$; red, black, and blue curves indicate Chr. 1, Chr. 2, and Chr. 3, respectively. The intensity of the contour lines represents the probability values of 0.3, 0.5, and 0.75 in an increasing order of darkness. (c) – (e) Probability distributions at $t = 7950 \text{ s}$ in (c) 3-d O-shaped oscillation, (d) 1-d oscillations, and (e) constant velocity linear motion of the SPB sphere. Colors of the contour lines represent probability distributions of each chain as in (b).

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FIG. 5. Illustration of velocities of the spindle pole body (SPB; white arrow), long and short chromosomes (red and blue arrows, respectively), the nuclear envelope (yellow arrows), and the nucleoplasmic flow (black arrows). When the SPB exhibits a constant linear velocity motion, all regions of the nuclear envelope, the nucleoplasm, and chromosomes relax to the same velocity as the SPB (Left). During the turn of the SPB, the regions of the nuclear envelope, the nucleoplasm, and chromosomes at the nuclear front end (near the SPB) follow the motion of the SPB, while those at the nuclear rear end are almost stopped (Right). In the latter case, longer chromosomes tend to be dragged by the slow motion of the nuclear rear region, while shorter chromosomes tend to follow the motion of the SPB.