



Is the curvature of the flagellum involved in the apparent cooperativity of the dynein arms along the “9+2” axoneme?

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SUMMARY

In a recent study [Cibert, 2008. *Journal of Theoretical Biology* 253, 74–89], by assuming that walls of microtubules are involved in cyclic compression/dilation equilibriums as a consequence of cyclic curvature of the axoneme, it was proposed that local adjustments of spatial frequencies of both dynein arms and β -tubulin monomers facing series create propagation of joint probability waves of interaction (JPI) between these two necessary partners. Modeling the occurrence of these probable interactions along the entire length of an axoneme between each outer doublet pair (without programming any cooperative dialog between molecular complexes) and the cyclic attachment of two facing partners, we show that such constituted active couples are clustered. Along a cluster the dynein arms exhibit a small phase shift with respect to the order according to which they began their cycle after being linked to a β -tubulin monomer. The number of couples included in these clusters depends on the probability of interaction between the dynein arms and the β -tubulin, on the location of the outer doublet pairs around the axonemal cylinder, and on the local bending of the axoneme; around the axonemal cylinder, the faster and the larger the sliding, the shorter the clusters. This mechanism could be involved in the apparent cooperativity of molecular motors and the β -tubulin monomers, since it is partially controlled by local curvature, and the cluster length is inversely proportional to the sliding activity of the outer doublet pairs they link.

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1. Introduction

The motile axis of the flagella and cilia of eukaryotic cells — the axoneme — is formed by nine outer doublets of microtubules constituting nine outer doublet pairs (ODPs), which surround a central apparatus organized around two central microtubules. Because of the activity of dynein arms (DAs) and existence of elastic links interconnecting the ODPs, the relative shear of the ODPs is converted into bends (Gibbons, 1981; Lindemann, 1994a). Local curvature of such bends may be associated with the twist of the axonemal cylinder around its central axis (Cibert, 2001; Gibbons, 1975).

The nature of the instantaneous regulation of this mechanism, which allows propagation of a coherent wave train along these organelles, is basically unknown in spite of the existence of clever biochemical and topologic models. Such models consider the curvature and the geometrical adjustments of the axonemal machinery to be essential for the functioning of the ensemble of

diverse mechanisms (Brokaw, 1975; Dymek and Smith, 2007; Gertsberg et al., 2004; Huang et al., 1982; Inaba, 2003; Li et al., 2006; Lindemann, 1994a, 2007; Lindemann and Mitchell, 2007; Mitchell, 2003a, 2003b; Morita et al., 2006; Morita and Shingyoji, 2004; Noguchi et al., 2000, 2005; Piperno et al., 1992; Rupp and Porter, 2003; Smith and Yang, 2004; Wilson and Lefebvre, 2004; Woolley, 2007, 1997).

In parallel to these biological models, the physical ones assume that the couples “ODPs–molecular motors” produce alternative fields of internal constraints during beating movements. One of the most interesting hypothesis is the pioneering description of these active entities as “auto-driven filaments” (Camalet et al., 1999). These models postulate that the efficient DAs are uniformly distributed along each ODP, and they produce forces along the entire length of the ODPs. However, experimental observations suggest that the DAs are active when they are associated in clusters of four elements (Spungin et al., 1987), making the DAs and their partners to become cooperative systems in essence. Here, cooperativity is defined as the necessary intermolecular dialog occurring either inside a given molecular complex or between different molecular complexes, as in the case of allosteric enzymes.

From the known range of physical characteristics (elastic constants) of microtubules and of ODPs (Fujime et al., 1972;

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Schoutens, 1994; Takano et al., 2003) one can assume that microtubules are inextensible and incompressible in the limits of normal beating cycles. However, different arguments plead in favor of their deformations during the beating cycles. This allows us to bring the hypothesis that two opposite sides of the outer doublets included in the bending plane are subjected to dilation/compression equilibrium controlled by the local balance of forces and torques (Cibert, 2008). From the above discussion and the assumption that dilation/compression sequences modulate the periodic distributions of the DAs and the β -TM along the two facing verniers during a beating cycle, the joint probability of interaction (JPI) of the facing DAs and β -TM depends on: (i) local curvature, (ii) local rate of sliding, and (iii) location of the ODPs within the axoneme, all these three factors being taken into account relative to the orientation of the bending plane (Cibert, 2008).

The JPI wave trains are created by the relative displacements of the two molecular verniers, whose shearing could be positive, negative, or nil, and whose special frequencies vary with respect to local curvature of the model. Thus, the “sampling” of one vernier by the other (and conversely), i.e. the coincidence between their facing elements, is stroboscopic in essence, and the apparent displacement of the JPI wave train could be tipward, baseward, or nil, as a function of values of the physical parameters that generate them, and not as a function of polarity of the shear only (Cibert, 2008).

In the present paper, assuming that orientation of the bending plane is constant along the entire length of the model, the distribution of couples DAs- β -TMs along the nine ODPs during a beating cycle was modeled. These distributions are highly heterogeneous around and along the axonemal cylinder. The active couples tend to form cluster series along the nine ODPs in relation to sliding speed, local bending, and cylindrical location of the ODPs.

These results confirm two things: first, that geometry could be one of the major elements involved in the definition of the apparent cooperativity existing between DAs and β -TMs during the axonemal beating, and second, that this cooperativity must be considered as adaptive because it depends on local curvature and on location of the outer doublet pairs around the axonemal cylinder.

2. Material, calculations, and assumptions

The program was written under ImageJ (1.37v) running on a MacBook Pro (Intel) OS-X platform (www.rsbweb.nih.gov/ij/download.html).

According to Gray (1955, 1958) and Gray and Hancock (1955), traces of flagellum of a sea urchin spermatozoon (chosen as a model) were calculated as products of an exponential envelope and a periodic function (Cibert, 2008), whose equations are $y_1 = a_0(1 - \exp(-a_1x))$ and $y_2 = \sin(w(kt - x/v) + \varphi)$, respectively, where: $a_0 = 100$, $a_1 = 2$, $w = 0.8$, $v = 0.31$, $k = 8r/160$, $\varphi = -23\pi/80 + \varphi_0$, x is the abscissa containing 200 points of sampling of traces that range in the interval $[0, 3]$, r the rank of the trace in the beating cycle (Fig. 1), and 160 is the number of traces that constitute a complete beating cycle. The abscissa x is calculated as $x = 3i/200$, where i is the rank of the sampling point ranging in the interval $[0, 200]$. In a periodic function the quantities k and x/v are related to displacement of the wave train along the longitudinal direction, as a function of time, and describe shape of the wave train for a given moment of time, respectively. Values of the other parameters are chosen to mimic the beating of sea urchin spermatozoon. The length of each trace equals $40 \mu\text{m}$. If the beating frequency of the model is 50 Hz the

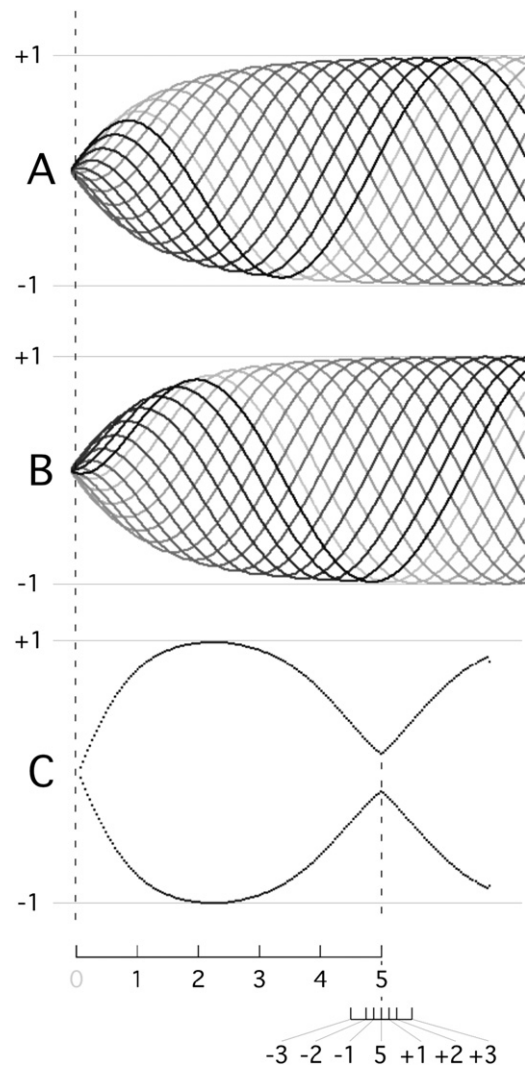


Fig. 1. The modeled wave train. (A) and (B) show 160 calculated flagellar traces where the difference between phases of the periodic functions equal 0 and $\pi/2$, respectively; one trace in 10 is represented. (C) Local extrema of the sum of the local shear along the 160 traces is clearly fish-shaped (Cibert, 2002). The five abscissas numbered 1–5 are the sites where conformations of the dynein arms were calculated; the abscissas defined as -1 , -2 , -3 , $+1$, $+2$, and $+3$ refer to abscissa #5 and were used to describe the relation between local sliding speed and local sum of the curvature through the fixed P0 point/segment. In (A)–(C) the ordinates are represented according to an arbitrary unit ranging between -1 and $+1$.

interval between two images of the bending series becomes $(1/8000)\text{s}$. One image out of ten is displayed along the series in Fig. 1A and B, where φ_0 equals 0 and $\pi/2$, respectively (higher ranks are identified by darker traces).

The range of local shear calculated along each of the 160 traces is characterized by a fish-shaped envelope, in agreement with earlier descriptions (Fig. 1C; Cibert, 2002). This plot characterizes the P0 points as curvilinear abscissas, where relative shear of the ODPs tends to a minimum, because of synchronous (Brokaw, 1996, 1993; Goldstein, 1976) and cumulative (Cibert, 2001, 2002, 2003) sliding of the ODPs. Consequently, the wave train moving along the axoneme delineates a series of P0–P0 modules along the model (Cibert, 2002), and shearing of the ODPs along the entire length of the axoneme occurs irrespective of local curvature (Cibert, 2002, 2008).

Fig. 2 shows the cross-section of the axoneme that we have used in this study, and the magnitude of compression and dilation

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