TRANSPORT PROPERTIES OF RIGID BENT-ROD MACROMOLECULES AND OF SEMIFLEXIBLE BROKEN RODS IN THE RIGID-BODY TREATMENT. ANALYSIS OF THE FLEXIBILITY OF MYOSIN ROD

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ABSTRACT The translational diffusion coefficients, rotational relaxation times and intrinsic viscosities of rigid bent rods, composed by two rodlike arms joined rigidly at an angle α, have been evaluated for varying conformation using the latest advances in hydrodynamic theory. We have considered semiflexible rods in which the joint is an elastic hinge or swivel, with a potential $V(\alpha) = \frac{1}{2}Q\alpha^2$ with constant Q. Accepting the rigid-body treatment, we calculate properties of broken rods by averaging α-dependent values for rigid rods. The results are finally used to interpret literature values of the properties of myosin rod. Q is regarded as an adjustable parameter, and the value fitted is such that the average bending angle of myosin rod is ~60°.

INTRODUCTION

Several important biopolymers present a typical broken-rod conformation in which two rodlike arms are joined either rigidly or by means of a flexible hinge or swivel. A well-known example is myosin rod (Harvey and Cheung, 1982; Trybus et al., 1982), and other relevant cases include fibronectin (Odermatt et al., 1982), proteoglycan (Trimm and Jennings, 1982) and, in some regard, DNA (Hagerman, 1984). For rigid bent rods, the hydrodynamic properties can be obtained using the theory of rigid particles (Garcia de la Torre, 1981; Garcia Bernal and Garcia de la Torre, 1980; Garcia de la Torre and Bloomfield, 1978, 1981). Some results have been already presented (Garcia de la Torre and Bloomfield, 1978; Mellado and Garcia de la Torre, 1982; Wegener, 1984, 1986; Roitman, 1984). Recently, a modification that affects mainly the rotational coefficients was introduced in the theory (Garcia de la Torre and Rodes, 1983). Here, we use the most rigorous version of the theory in a systematic calculation of hydrodynamic properties of rigid bent rods.

The dynamics of semiflexible, broken rods is more complex owing to the additional degrees of freedom and the interplay between internal and frictional forces. For completely flexible rods, a formalism developed by Wegener and others is available (Wegener et al., 1980; Wegener, 1982; Harvey et al., 1983; Garcia de la Torre et al., 1985). A different approach for semiflexible rods is the so-called rigid-body treatment. In this formalism, one obtains first the properties for instantaneous conformations of the particle that are regarded as rigid structures, and the observable properties are later calculated averaging over conformations. This procedure is implicit in early studies of broken rods (Yu and Stockmayer, 1967; Wilemski, 1977), and was used in previous estimations of the flexibility of myosin rod (Garcia de la Torre and Bloomfield, 1980; Garcia Molina and Garcia de la Torre, 1984; Solvez et al., 1987). In combination with Monte Carlo averaging, the rigid-body treatment has been employed by Hagerman and Zimm (1981) in their study of rotational dynamics of weakly bending worm-like rods.

The rigid-body treatment is generally regarded in macromolecular hydrodynamics as an approximation that furnishes bounds for the transport properties (Wilenski and Tanaka, 1981; Zimm, 1982; Fixman, 1983). As kindly pointed out by a referee of this paper the rigid-body treatment may be even exact (although the conformational average is carried out *a posteriori*) if the function over which the average is done has been derived without using the rigid-body treatment. We do not address here this theoretical aspect but, from a practical point of view, we just recall that, usually, the results of this treatment differ only a few percent from the rigorous ones. Such is the case, precisely for some properties of semiflexible broken rods, as shown by Wegener (1986). The rigid-body results for a simple model, the semiflexible trimer with moderate or high stiffness are also in very good agreement with those obtained from solution of the diffusion equation (Roitman and Zimm, 1984 *a*, *b*) or from Brownian dynamics simulation (Diaz and Garcia de la Torre, 1988).

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Here we apply the rigid-body treatment to semiflexible rods, averaging the conformation dependent values obtained for rigid rods. The properties are evaluated as functions of a flexibility parameter, whose value is adjusted for myosin rod. This represents an improvement over previous studies of the flexibility of this fibrous protein.

METHODS

The geometry of the bent rod model is presented in Fig. 1. The particle has two straight, rod-like arms of diameter b and lengths L_1 and L_2, which are modeled as strings of $N_1 = L_1/b$ and $N_2 = L_2/b$ touching beads. The total length of the particle is

$$L = L_1 + L_2 = Nb, \quad (1)$$

where $N = N_1 + N_2$. We shall use a length ratio γ defined as

$$\gamma = L_1/L = N_1/N \quad (2)$$

with $\gamma = 1/2$ for the case of equal arms. The arms are rigidly joined, making an angle α as defined in Fig. 1.

For the calculation of hydrodynamic properties we use the most rigorous form of the bead-model theory (Garcia de la Torre and Bloomfield, 1978; Garcia Bernal and Garcia de la Torre, 1980), including a volume correction for the rotational constants (Garcia de la Torre and Rodes, 1983). A brief description of the theory can be found in reviews (Garcia de la Torre and Bloomfield, 1981; Garcia de la Torre, 1981). Here we just introduce the needed quantities. The translational diffusion coefficient, D_t, is extracted from the translational diffusion tensor evaluated at the center of diffusion $D_{D,t}$

$$D_t = (1/3)\mathrm{Tr}\,(D_{D,t}). \quad (3)$$

All the information needed to study rotational dynamics is contained in the rotational diffusion tensor, D_r. The five rotational relaxation times describing the time course of properties like electric birefringence and electric dichroism (Wegener et al., 1979) and fluorescence polarization anistropy (Belford et al., 1972), reduce to three for the bent rod due to the existence of a plane of symmetry. D_r can be diagonalized to obtain three eigenvalues and the corresponding eigenvectors. One of the eigenvectors is perpendicular to the particle's plane, and its eigenvalue is denoted as D_z. The other two eigenvectors are in the particle's plane, and define the two other principal axes of rotation, indicated as x_p and y_p in Fig. 1. For convenience, x_p is taken as the axis defined by the eigenvector of the largest eigenvalue. The corresponding eigenvalues are D_x and D_y. The reciprocals of the three relaxation times are given by

$$1/\gamma_1 = 6D - 2\Delta \quad (4a)$$

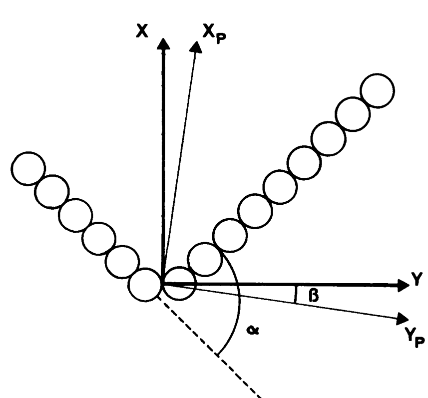

FIGURE 1 Geometry of the bent-rod model.

$$1/\gamma_2 = 3(D + D_z) \quad (4b)$$

$$1/\gamma_3 = 6D + 2\Delta, \quad (4c)$$

where

$$D = (1/3)\,(D_x + D_y + D_z) \quad (5a)$$

$$\Delta = (D_x^2 + D_y^2 + D_z^2 + D_xD_y + D_xD_z + D_yD_z)^{1/2}. \quad (5b)$$

The amplitudes of the three exponential terms in the decay of electro-optical or spectroscopic properties depend on the components of certain tensors or vectors in the system of principal axes of rotational diffusion. These are specified giving just the director cosine of x_p with respect to x ($\cos\beta$ in Fig. 1).

The intrinsic viscosity, $[\eta]$, has been calculated as described elsewhere (Garcia de la Torre and Bloomfield, 1978, 1981). The subtle coupling effects described by Wegener (1984) have not been included in our computational procedures because, as shown by him, their effects on $[\eta]$ of bent rods would be smaller than 1%.

For semiflexible rods we assume a potential, V, which is quadratic in α with equilibrium at $\alpha = 0$:

$$V/k_BT = Q\alpha^2. \quad (6)$$

The elastic constant Q in Eq. 6 is regarded as an adjustable flexibility parameter such that $Q = 0$ for a completely flexible rod and $Q \longrightarrow \infty$ for a very rigid rod. Then, the probability of a conformation with angle α is

$$p(\alpha) = g(\alpha)\exp(-Q\alpha^2)\Big/\int_0^{\pi} g(\alpha)\exp(-Q\alpha^2)\,d\alpha, \quad (7)$$

where $g(\alpha)$ is a weighting factor. In principle, one can distinguish (Harvey et al., 1983) between hinged and swivel-jointed rods. In the first type the bending motion takes place in the particle's plane only, and $g(\alpha)$ is a constant, while in the second one torsional motions are allowed and $g(\alpha) = \sin\alpha$. We anticipate that, in practice, the results for the two types are nearly identical if Q is high, and for low Q (high flexibility), the swivel-jointed rod seems to be more realistic. Therefore we have chosen the $\sin\alpha$ weight in our calculations.

Having assigned statistical weights to conformations corresponding to each value of α, in the rigid-body approximation one obtains the observable value of a given property, B, as the average of $B(\alpha)$ over angles:

$$B = \int_0^{\pi} d\alpha\, p(\alpha)B(\alpha). \quad (8)$$

RESULTS AND DISCUSSION

Straight Rods

The cases $\alpha = 0$ and $\gamma = 0$ correspond to a rigid, straight rod. In Table I we present results for the hydrodynamic properties of rigid rods of varying length. Actual values of the properties can be obtained from the normalized values listed in Table I and factors involving the thermal energy k_BT, the diameter of the macromolecule, b and its molecular weight, M.

For the straight rod the relaxation times are

$$1/\gamma_1^{str} = 6D_z^{str} \quad (9a)$$

$$1/\gamma_2^{str} = 5D_z^{str} + D_x^{str} \quad (9b)$$

$$1/\gamma_3^{str} = 2D_z^{str} + 4D_x^{str}. \quad (9c)$$

The values of D_z^{str} to be used in Eq. 9b and c can be

TABLE I
HYDRODYNAMICS PROPERTIES* OF A RIGID, STRAIGHT RODS, MODELED AS STRINGS OF TOUCHING BEADS

$N = L/b$	$[\eta]^{str}$	D_t^{str}	$1/\tau_1^{str}$
10	0.651	2.845	26.298
16	2.147	2.057	7.968
20	3.820	1.754	4.458
24	6.144	1.536	2.760
30	11.047	1.302	1.526
32	13.102	1.241	1.284
40	23.711	1.048	0.706
48	38.630	0.912	0.432

*The quantities actually listed are $(M/N_A b^3)[\eta]^{str}$, $(6\pi\eta_0 b/kT)D_t^{str}$) and $(6\pi\eta b^3/kT)(1/\tau_1^{str})$.

obtained from the values of $1/\gamma_1^{str}$ using Eq. 6. The rotational diffusion coefficient for rotation around the rod axis can be estimated for the rod of beads, in the context of the volume correction, from

$$D_x^{str} = k_B T/\pi\eta_0 L b^2 \tag{10}$$

For the purposes of interpolation and extrapolation of the properties for other values of N, we have obtained by least squares fitting of the results in Table I the following relationships:

$$D_t = (k_B T/3\pi\eta_0 L) \cdot (ln\,N + 0.5014 + 0.1118/N + 2.5274/N^2) \tag{11a}$$

$$1/\gamma_1^{str} = (18 k_B T/\pi\eta_0 L^3) \cdot ln\,N - 0.3325 - 0.5461/N + 3.1608/N^2) \tag{11b}$$

$$1/[\eta]^{str} = (45M/2N_A\pi L^3) \cdot (ln\,N - 0.6811 + 0.2362/N + 6.0470/N^2) \tag{11c}$$

These equations reproduce the values in Table I with an error that is smaller than 0.1% in most cases.

We must stress that the present values of properties of rigid rods modeled as straight strings of beads are to be used as references in the analysis of the properties of bent and hinged rods. Since a cylindrical model is more realistic for rodlike biopolymers than a string of beads, the results reported for cylinders (Tirado et al., 1979, 1980, 1984) should be preferred in the interpretation of experimental data of straight rods.

Bent Rods

We have calculated D_t, $[\eta]$ and the three relaxation times for rigid bent rods as a function of L/b, L_1/L, and α. The results are displayed in Table II. If desired, the three eigenvalues can be extracted from Eqs. 4 and 5. We tried to present our results in the form of interpolating functions of the three variables. This can be done individually for L/b, and perhaps for γ, but not for the angle because the properties depend appreciably on α. On the other hand, an interpolating function of three variables would surely fail in some regions. Therefore, we decided to present, albeit at the cost of more space, the numerical values. Nonetheless, we have found that the following functions of N (with given α and γ) are valid for interpolation and moderate extrapolation: D_t/D_t^{str}, $a + b\,ln\,N$; γ_1^{str}/γ_1 and $[\eta]/[\eta]^{str}$, $a + b/N$; γ_1^{str}/γ_2 and γ_1^{str}/γ_3, $aN + b + c/N$. Note that the two shortest relaxation times are normalized with the longest relaxation time of the straight rod.

The $\cos\beta$ values needed to determine the orientation of the principal axes of rotational diffusion are presented separately in Table III. For the limiting case of equal arms, we illustrate in Fig. 2 the deviation of the properties from those of a straight rod as α increases. While D_t is practically insensitive to conformation, γ_3 and $[\eta]$ decrease down to ~1/5. The two largest relaxation times are very sensitive to the conformation. For α close to 0 or 180°, we have γ_3, $\gamma_2 \ll \gamma_i$, and there will be two well-separated time scales in the decay of electro-optical properties. However, for intermediate α the three relaxation times are of the same order of magnitude and the decays will be typically multiexponential. Examples of such behavior have been presented already (Mellado and Garcia de la Torre, 1982).

Semiflexible Rods

By numerical integration of the data in Table II and according to Eq. 8, the properties of semiflexible rods can be evaluated as functions of the flexibility parameter, Q. We recall that the rotational quantities that are averaged are the reciprocals of the relaxation times. In Fig. 3 we present some results for equal arms, expressed as in the case of bent rods with reference to the values for the straight rod. An example of the utility of Fig. 3 for evaluating flexibility will be presented later on.

The various properties differ with regard to their Q-dependence or, in other words, their sensitivity to flexibility. While the translational diffusion coefficient, and to a lesser extent the radius of gyration, are rather insensitive to changes in Q, the intrinsic viscosity and the longest relaxation time vary remarkably with Q. The latter property will usually be preferred since it is determinable by a variety of modern electro-optical or spectroscopic techniques that (unlike the viscosity) need very small amounts of sample.

Analysis of Solution Properties of Myosin Rod

Experimental data for the translational diffusion coefficient, rotational relaxation time, intrinsic viscosity, and radius of gyration of the myosin rod are summarized in Table IV. As recently reviewed by Cardinaud and Bernengo (1985), the total length of the rod should be close to 150 nm, with 78 and 72 nm for the two arms, light meromyosin and subfragment S2 respectively, so that $\gamma \approx$ 1/2. The hydrodynamic radius of the rod is 2 nm (Garcia de la Torre and Bloomfield, 1980). Table IV shows that the properties of the rod deviate clearly from the values

TABLE II
HYDRODYNAMIC PROPERTIES OF BENT RODS NORMALIZED TO THE VALUES OF STRAIGHT RODS

α	$\gamma = 1/2$					$\gamma = 1/3$			$\gamma = 1/4$		
$N =$ $L/b =$	16	24	32	40	48	15	24	48	16	24	48
					Translational diffusion: D_t/D_t^{str}						
15	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
30	1.001	1.000	1.000	1.000	1.000	1.001	1.000	0.999	1.001	1.000	0.999
60	1.005	1.003	1.002	1.000	1.000	1.005	1.003	0.999	1.004	1.001	0.998
45	1.002	1.001	1.000	1.000	1.000	1.002	1.001	0.998	1.002	1.002	0.998
75	1.011	1.008	1.006	1.003	1.003	1.010	1.007	1.001	1.008	1.006	1.001
90	1.020	1.017	1.014	1.011	1.011	1.018	1.015	1.008	1.015	1.012	1.007
105	1.035	1.032	1.029	1.027	1.025	1.030	1.027	1.021	1.025	1.023	1.017
120	1.057	1.055	1.052	1.050	1.049	1.048	1.047	1.041	1.037	1.038	1.034
135	1.088	1.089	1.087	1.085	1.085	1.072	1.074	1.071	1.056	1.058	1.057
150	1.134	1.138	1.139	1.137	1.138	1.105	1.111	1.112	1.079	1.084	1.087
165	1.205	1.218	1.223	1.225	1.227	1.147	1.161	1.170	1.106	1.117	1.126
180	1.351	1.403	1.438	1.461	1.483	1.204	1.237	1.276	1.139	1.159	1.187
					Longest relaxation time τ_1^{str}/τ_1						
15	1.015	1.016	1.017	1.017	1.018	1.012	1.014	1.015	1.010	1.010	1.011
30	1.062	1.067	1.070	1.071	1.072	1.050	1.055	1.060	1.038	1.042	1.046
45	1.145	1.156	1.162	1.166	1.169	1.114	1.126	1.137	1.086	1.094	1.103
60	1.270	1.292	1.304	1.312	1.317	1.208	1.229	1.249	1.154	1.167	1.182
75	1.450	1.490	1.511	1.524	1.534	1.330	1.367	1.400	1.234	1.257	1.281
90	1.702	1.771	1.808	1.831	1.847	1.485	1.540	1.589	1.329	1.362	1.396
105	2.058	2.176	2.240	2.279	2.307	1.666	1.744	1.813	1.433	1.475	1.517
120	2.551	2.754	2.864	2.932	2.979	1.858	1.963	2.051	1.536	1.587	1.636
135	3.072	3.337	3.476	3.561	3.618	2.044	2.169	2.274	1.632	1.689	1.744
150	3.328	3.598	3.741	3.830	3.889	2.201	2.340	2.459	1.715	1.777	1.835
165	3.581	3.896	4.066	4.171	4.242	2.321	2.473	2.604	1.783	1.850	1.917
180	4.152	4.653	4.954	5.157	5.306	2.410	2.575	2.740	1.840	1.918	2.010
					Relaxation time τ_1^{str}/τ_2						
15	5.883	9.406	12.867	16.021	18.782	5.624	9.981	21.627	6.275	10.656	25.445
30	4.430	5.883	6.906	7.620	8.128	4.582	6.759	10.183	5.363	7.998	13.699
45	3.365	3.971	4.326	4.548	4.695	3.666	4.730	5.972	4.450	5.969	8.402
60	2.760	3.060	3.222	3.319	3.383	3.081	3.660	4.254	3.815	4.748	6.028
75	2.469	2.657	2.756	2.815	2.854	2.761	3.140	3.506	3.420	4.085	4.921
90	2.389	2.542	2.622	2.671	2.704	2.638	2.943	3.233	3.235	3.790	4.464
105	2.468	2.627	2.711	2.763	2.799	2.664	2.970	3.262	3.210	3.762	4.440
120	2.692	2.891	2.998	3.065	3.110	2.820	3.192	3.555	3.338	3.981	4.831
135	3.081	3.371	3.531	3.631	3.700	3.117	3.641	4.213	3.617	4.495	5.839
150	3.716	4.219	4.519	4.715	4.853	3.603	4.484	5.709	4.088	5.465	8.157
165	4.802	5.965	6.829	7.493	8.016	4.321	6.193	10.098	4.754	7.132	13.946
180	6.667	10.103	14.178	18.947	24.418	5.236	9.172	25.224	5.480	9.314	26.704
					Relaxation time τ_1^{str}/τ_3						
15	20.866	34.573	48.415	61.029	72.070	19.327	36.969	83.475	22.018	39.813	98.749
30	14.528	20.324	24.406	27.257	29.286	15.186	23.836	37.550	18.188	28.754	51.684
45	10.020	12.406	13.803	14.675	15.524	11.309	15.549	20.518	14.593	20.585	30.335
60	7.232	8.358	8.961	9.323	9.558	8.713	10.979	13.321	11.729	15.417	20.628
75	5.564	6.185	6.504	6.693	6.817	7.040	8.505	9.892	9.960	12.493	15.927
90	4.570	4.967	5.170	5.290	5.369	6.109	7.188	8.235	8.901	10.979	13.788
105	4.001	4.300	4.453	4.545	4.607	5.684	6.672	7.666	8.480	10.532	13.337
120	3.761	4.040	4.187	4.276	4.337	5.745	6.888	8.114	8.655	11.046	14.549
135	4.041	4.500	4.763	4.923	5.049	6.365	8.069	10.085	9.508	12.802	18.272
150	5.452	6.616	7.356	7.862	8.226	7.816	10.979	15.564	11.106	16.394	27.237
165	8.521	12.106	14.992	17.299	19.157	10.422	17.502	32.731	13.641	22.786	50.121
180	13.968	26.057	41.386	59.816	81.236	13.805	28.984	92.824	16.299	31.504	100.896
					Intrinsic viscosity $[\eta]/[\nu]^{str}$						
15	0.991	0.990	0.990	0.990	0.989	0.993	0.992	0.991	0.995	0.995	0.994
30	0.965	0.962	0.960	0.959	0.958	0.972	0.969	0.966	0.979	0.977	0.975
45	0.922	0.916	0.912	0.910	0.909	0.937	0.931	0.926	0.952	0.949	0.945
60	0.865	0.854	0.849	0.846	0.842	0.892	0.881	0.873	0.918	0.911	0.905
75	0.797	0.782	0.774	0.769	0.765	0.837	0.822	0.809	0.876	0.866	0.857

TABLE II
(Continued)

α N = L/b =	γ = ½					γ = ⅓			γ = ¼		
	16	24	32	40	48	15	24	48	16	24	48
90	0.721	0.701	0.691	0.684	0.679	0.775	0.755	0.738	0.828	0.815	0.803
105	0.641	0.617	0.603	0.595	0.590	0.710	0.685	0.664	0.778	0.761	0.746
120	0.561	0.532	0.517	0.508	0.501	0.645	0.615	0.590	0.728	0.707	0.688
135	0.483	0.451	0.435	0.425	0.418	0.582	0.549	0.521	0.679	0.656	0.634
150	0.411	0.377	0.360	0.350	0.343	0.525	0.490	0.461	0.634	0.609	0.586
165	0.344	0.310	0.294	0.284	0.277	0.477	0.441	0.412	0.596	0.570	0.544
180	0.269	0.235	0.218	0.207	0.200	0.440	0.406	0.375	0.566	0.538	0.508

calculated from Eq. 11 for a straight rod having L = 150 nm, b = 2 nm, and N = 75. In all cases the deviation is in the direction of a less extended conformation. Using these straight-rod values, the straight-to-flexible ratios can be evaluated for each property, and interpolating these ratios in plots like those in Fig. 3, values of the adjustable flexibility parameter can be obtained. For such purpose we constructed plots (not shown) for N = 75 by extrapolation of N-dependent results. The curves obtained were very close to those displayed in Fig. 3, thus confirming the weak dependence of the ratios on N.

In Table IV we present the results for Q. In the case of D_t, the experimental datum is out of the range of the theoretical results and therefore it cannot be used to estimate Q. Due to the insensivity of D_t to conformation, this coefficient is found to be almost useless in the analysis of flexibility. This circumstance was already detected by Garcia de la Torre and Bloomfield (1980). On the other hand, the other properties, R_G, $[\eta]$ and γ_1 can be well described in terms of partial flexibility. The interpolated Q values are in good agreement. A more illustrative measure of flexibility is the average bending angle, $\langle\alpha\rangle$, which is obtained as in Eq. 8 with $B \equiv \alpha$. The $\langle\alpha\rangle$ values corresponding to the three values of Q are given in Table IV. The agreement is excellent; the three values are very similar, and close to 60°, which would be, according to our analysis, the average bending angle of myosin rod in solution.

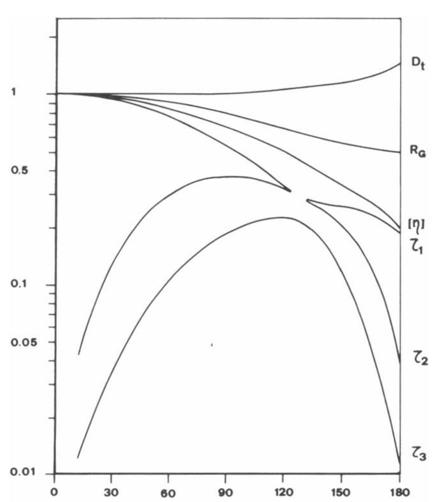

FIGURE 2 Variation of properties of rigid bent rods with equal arms, normalized to those of the straight rod, with the angle. The results correspond to L/b = 48 but are rather insensitive to this ratio.

TABLE III
COS β FOR BENT RODS OF UNEQUAL ARMS

α N = L/b =	γ = ⅓			γ = ¼		
	15	24	48	16	24	48
0	1.000	1.000	1.000	1.000	1.000	1.000
15	0.998	0.998	0.998	0.996	0.996	0.996
30	0.993	0.992	0.992	0.985	0.985	0.984
45	0.982	0.982	0.981	0.964	0.964	0.963
60	0.965	0.964	0.963	0.933	0.932	0.930
75	0.937	0.935	0.933	0.887	0.885	0.882
90	0.892	0.887	0.884	0.823	0.819	0.815
105	0.819	0.810	0.803	0.738	0.731	0.724
120	0.707	0.692	0.679	0.629	0.619	0.609
135	0.556	0.534	0.517	0.499	0.486	0.474
150	0.387	0.362	0.343	0.356	0.340	0.325
165	0.223	0.197	0.177	0.207	0.189	0.172
180	0.070	0.044	0.022	0.057	0.038	0.019

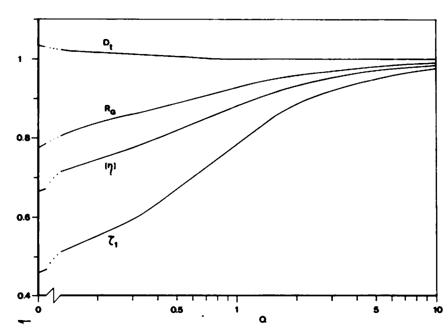

FIGURE 3 Variation of properties of semiflexible rods with the dimensionless flexibility parameter Q. The results correspond to L/b = 48 although, for the three properties shown here, they change very slowly with this ratio. Previous results for the root mean squared radius of gyration, R_G, are also displayed.

TABLE IV
EXPERIMENTAL VALUES OF SOLUTION PROPERTIES AND FLEXIBILITY PARAMETERS OF MYOSIN ROD

Property	Experimental	Reference	Straight rod (Theoretical)	Q	$\langle\alpha\rangle$
D_t, $cm^2 s^{-1}$	1.24×10^{-7}	*	1.38×10^{-7}	—	—
τ_1, μs	26	‡	37	0.65	55
$[\eta]$, $cm^3 g^{-1}$	265	§	311	0.70	53
Rg, nm	38	**	43	0.42	63
				Mean:	57

*Lowey et al. (1969).
‡Average of several literature values in the range 24–28 μs (Highsmith et al., 1977, 1982; Hvidt et al., 1982, 1984). A 17 μs value reported by Cardinaud and Berengo (1985) is not considered.
§Burke and Harrington (1972). We take a molecular weight of 250,000 (Highsmith et al., 1977).
**Hvidt et al. (1982).

The present analysis of the myosin rod flexibility improves the previous one by Garcia de la Torre and Bloomfield (1980) in several respects and provides numerical values for quantities as Q or $\langle\alpha\rangle$. Qualitatively, our conclusions confirm those from several other workers that myosin rod has an appreciable yet limited flexibility.

This work was supported by grant 561/84 from the Comisión Asesora de Investigación Científica y Técnica to J. Garcia de la Torre.

Received for publication 18 November 1987 and in final form 14 March 1988.

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