Polarized and Depolarized Dynamic Light Scattering Study on F-Actin in Solution: Comparison with Model Calculations

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ABSTRACT: We have studied the dynamics of F-actin of different average filament lengths by polarized and depolarized dynamic light scattering. The experimental data have been compared with model calculations for rigid and semiflexible macromolecules. The polarized DLS spectra follow the predictions for semiflexible rods with a persistence length of (7.5 ± 2.5) μm. Because there is no theory available that includes flexibility in the calculation of the depolarized dynamic structure factor, to a first approximation we used the diffusion coefficients for semiflexible molecules in our rigid-rod model calculations. In the dilute solution regime, this modification provided good agreement between experimental and calculated depolarized correlation functions for F-actin with an average degree of polymerization $\langle X \rangle \leq 350$. Internal bending motions give significant contributions to the scattered intensity only for longer filaments. Concentration-dependent depolarized dynamic light scattering measurements on actin filaments revealed a slow relaxation mode in semidilute solution. A comparison with the corresponding polarized DLS measurements is presented.

Introduction

Many biological and synthetic polymers are rigid or semiflexible molecules. The stiffness and dynamic behavior determine their physical and functional properties. For example, synthetic polymers with extraordinary mechanical characteristics are of rodlike structure, and other semirigid macromolecules were developed for electrical and nonlinear optical applications.[1] The stiffness of biopolymers is often essential for their biological function and there exists a regulation mechanism to control their rigidity. To understand the macroscopic characteristics of such polymers, it is important to relate their physical properties to microscopic aspects like molecular structure and dynamic behavior.

In a previous paper,[2] we have investigated the dynamics of actin filaments whose average degree of polymerization was controlled by the actin-binding protein gelsolin. Comparison of the polarized electric field autocorrelation function from a homologous series of filament lengths with theoretical predictions for rigid and semiflexible macromolecules revealed that F-actin is a rather stiff polymer with a persistence length of 7.5 ± 2.5 μm. These polarized dynamic light scattering (DLS) results indicate that the system is well suited to test a recently developed theory[3] for the depolarized dynamic structure factor of rigid rodlike polymers in the isotropic phase.

The dynamics of rigid rodlike macromolecules are characterized by a variety of complex translational and rotational motions.[4] Besides the anisotropy in translational motion and the coupling of translational and rotational relaxation, Maeda considered concentration effects like rod–rod interaction, entanglement, and hydrodynamic drag in his theory. Evaluation of the VH depolarized dynamic structure factor followed a procedure described by Doi et al.[5] who developed expressions for the complementary polarized dynamic structure factor. The excluded-volume interaction of the rods was included explicitly by a mean-field hard-rod interaction potential. It leads to a decrease in the initial decay rate, Γ_{init}, with concentration because the repulsive rod–rod interaction slows down the orientational motion of the rigid molecules. This is in contrast to the polarized dynamic structure factor,[6] where a higher density of polymers causes an increase of Γ_{init}. The diffusion coefficients for translational and rotational motions were considered as adjustable parameters to account for hydrodynamic as well as steric interactions between the molecules. Although no explicit prediction is given, in general, the self-diffusion coefficients decrease with concentration, and hence in a depolarized dynamic light scattering experiment magnify the contribution from thermodynamic effects, while for the polarized spectra rod entanglement and hydrodynamic interactions counteract the excluded-volume effect.

In this paper we will present results from polarized and depolarized dynamic light scattering experiments on F-actin of different average filament lengths. The experimental correlation functions were compared with model calculations for rigid and semiflexible rodlike macromolecules. Our aim was to investigate the consistency of the polarized and depolarized spectra within the framework of the applied theories. For longer semirigid filaments we tried to include the effect of flexibility in the expressions for the diffusion coefficients when calculating the depolarized dynamic structure factor. We will also present preliminary concentration-dependent measurements of the depolarized component of scattered light for a given average filament length and compare the results with corresponding data from polarized DLS experiments.

Theoretical Background

For a monodisperse system of short rodlike molecules in dilute solution the depolarized correlation function consists of a single exponential[7]

$$I_{\mathrm{VH}}(q,t) = N\beta^2 \exp[-(q^2D + 6\Theta)] \qquad (1)$$

where D and Θ are the translational and rotational diffusion coefficients, respectively. For longer rods, such as the actin filaments studied here, the friction coefficient for sidewise motion is much larger than for lengthwise diffusion. The resulting coupling of rotational and translational motion has been considered by Zero and Pecora.[8] In semidilute solution, rod–rod interactions due to excluded-volume effects, topologic constraints, and hydrodynamic interactions will affect the dynamics of the polymers. Doi et al.[5] have included all these effects to derive a theory for the polarized structure factor of rigid rodlike molecules. Maeda[3] applied the formalism to derive expressions for the complementary depolarized dynamic structure factor.

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For the apparent diffusion coefficient, $D_{\mathrm{app}} = \Gamma_{\mathrm{init}}/q^2$, with $\Gamma_{\mathrm{init}} \equiv -\lim_{t\to 0} [(\mathrm{d}/\mathrm{d}t)\, g(q,t)/g(q,0)]$, he obtained

$$D^{\mathrm{VH}} = [D_\perp + \Theta_\perp f_1{}^*(qL,\theta) + (D_\parallel - D_\perp) f_2{}^*(qL,\theta)]\, A^*(qL,\theta,c) \quad (2)$$

which is similar to the corresponding expression for the polarized dynamic structure factor[6]

$$D^{\mathrm{VV}} = [D_0 + (L^2/12)\Theta_\perp f_1(qL) - (D_\parallel - D_\perp)[{}^1/_3 - f_2(qL)]]\, A^*(qL,\theta,c) \quad (3)$$

The first term in eqs 2 and 3 considers the translational motion of the macromolecule. While in the VV experiment the lengthwise and sidewise translational motion of the molecules contribute equally to the scattering intensity, in case of the VH component, only $D_\perp$ appears in eq 2. The second term results from rotational reorientation, where Θ is the rotational diffusion coefficient and L the length of the rod. The third expression describes the coupling of translational and rotational motion, and in both equations, results in a decrease of the apparent diffusion coefficient. The weight factors f_1 and f_2 are known functions of q and the values for $q \to 0$ and $q \to \infty$ are $f_1(0) = 0$, $f_1(\infty) = 1$ and $f_2(0) = {}^1/_3$, $f_2(\infty) = 0$, respectively. Therefore, from a VV light scattering experiment we obtain the translational diffusion coefficient, D_0, from measurements at low scattering vector and for not too long molecules. On the other hand, in the limit of $qL \to 0$ the initial decay rate is given by $\Gamma_{\mathrm{init}}/f_1{}^* = \Theta$, and the depolarized correlation function provides knowledge about the rotational motion of the molecules. Thus, studying both components of scattered light gives complementary information about the dynamics of rodlike molecules in solution.

The excluded-volume effect on the rod–rod interaction was considered using the mean-field approximation. In general, $A(qL,c)$ increases with the number concentration c, while $A^*(qL,\theta,c)$ is a decreasing function of polymer concentration. Because of the topologic constraints and hydrodynamic interactions, the self-diffusion coefficients of a rodlike molecule decrease with concentration. In a polarized light scattering experiment the change in the self-diffusion coefficients with concentration is opposite to $A(qL,c)$ and, hence, makes the polarized spectra less sensitive to concentration effects than the depolarized, where all contributions intensify. The interaction parameters were also considered to be q dependent with the most significant contribution in the forward scattering direction.[6]

Most rodlike macromolecules exhibit some dynamic flexibility. These internal bending motions become evident at high scattering angles in the polarized DLS experiment in such a way that the apparent diffusion coefficient is larger than expected for a stiff molecule. To our knowledge, there is no theory for rodlike molecules available that includes the effect of flexibility in the expression for the depolarized dynamic structure factor over the entire range of scattering vector. Because our polarized DLS experiments have shown that longer actin filaments exhibit semirigid behavior, we modified Maeda's rigid-rod theory by using the correction factors for the transport coefficients of semiflexible macromolecules,[9,10] $\Theta^{\mathrm{sfr}} = \Theta^{\mathrm{rr}} g(\gamma,L,d)$ and $D^{\mathrm{sfr}} = D^{\mathrm{rr}} f(\gamma,L,d)$, as well as an approximate relation[11] for $(D_\perp{}^{\mathrm{sfr}} - D_\parallel{}^{\mathrm{sfr}})/D_0{}^{\mathrm{sfr}}$, to partly account for the flexibility, γ, of the filaments.

Materials and Methods

Purification of the proteins actin and gelsolin and sample preparation for the dynamic light scattering experiments were described in detail in the preceding paper.[2]

Dynamic Light Scattering Measurements and Analysis. The depolarized dynamic light scattering experiments were performed with the same standard light scattering apparatus as the polarized measurements. The only modification we made was that we used an additional polarizer with an extinction coefficient > 10^7 to select the vertically polarized component of the incident beam. Both polarizers, for the incident and scattered light, were fine-tuned to optimize the intensity of the depolarized component of scattered light.

Due to the weak VH scattering intensity, we generally measured correlation functions for short periods of time (5–20 min). Single spectra with a baseline difference <1% were accumulated up to 50 000 to 1×10^6 counts in the baseline channels. Data acquisition for a VH correlation function took between 30 min and 8 h, depending on the scattering angle and sample concentration. Because we usually performed a number of angular or concentration-dependent measurements on the same sample, longer accumulation times were not feasible due to the limited stability of the actin/gelsolin system. For longer average filament lengths we used the multi-τ option of the correlator to cover the broad relaxation range of the depolarized spectra.

Simulation of the VV- and VH-Correlation Function. For calculating the depolarized dynamic light scattering spectra we modified a program kindly provided by T. Maeda. This program computes the depolarized correlation function for rigid rodlike macromolecules at delay times of $\tau = 1\ \mu$s to 0.5 s in steps of 1, 2, and 5, starting at $\tau_0 = 0\ \mu$s for given scattering angles.

To account for the polydispersity of the system, we used a similar procedure as for our simulations of polarized DLS spectra. We computed $g_{\mathrm{VH}}(L_n,\tau_i)$ for n = 105–120 different rod lengths with $L_n = L_0 c^n$. The size of n increased with scattering vector, and in comparison to the polarized dynamic structure factor, we calculated a much larger number of points, because the depolarized correlation functions have a broader relaxation profile and change more rapidly with filament length, and therefore we needed more points for accurate interpolation. The constant c was chosen to be $c = 1.1$ and $L_0 = 11$ nm. For the dimensions of the actin helix we assumed an increase in length by 2.77 nm per monomer unit and a diameter of 10 nm.[2] The depolarized dynamic structure factors for 19 delay times τ_i and four different scattering angles (θ = 20°, 35°, 60°, and 90°) were computed on a mainframe computer (Convex C240) and stored for further calculations on a workstation (HP 9000-300). Assuming that the optical anisotropy ($\Delta\alpha \equiv \alpha_\parallel - \alpha_\perp$) is proportional to $L - d$, where d is the diameter of the rod, the unnormalized dynamic structure factor was obtained by averaging over the different degrees of polymerization, X, according to

$$g_{\mathrm{VH}}(\tau_i) = \frac{\sum_{X=X_{\min}}^{X_{\max}} Y_X (L_X - d)^2\, g_{\mathrm{VH}}(L_X,\tau_i)}{\sum_{X=X_{\min}}^{X_{\max}} Y_X (L_X - d)^2} \quad (4)$$

For an exponential distribution of filament length, $X_{\max}$ was chosen to be $10\langle X\rangle$. Finally, the normalized electric field autocorrelation function $g_1(\tau)$ was obtained by cubic-spline interpolation of $\ln[g_{\mathrm{VH}}(\tau_i)/g_{\mathrm{VH}}(0)]$ versus τ_i for 136 delay times, chosen according to the experimental conditions.

Because there is no corresponding model for semiflexible molecules available, we tried to account for the flexibility of longer actin filaments by considering the diffusion coefficients for semiflexible rodlike molecules, instead of the rigid rod values from Tirado and García de la Torre.[12]

Results and Discussion

In the preceding paper,[2] we presented a detailed polarized dynamic light scattering study to elucidate the flexibility of actin filaments in solution. In this work we provide corresponding depolarized and, if necessary to complete the picture, additional polarized DLS experiments on F-actin of different average length. In the following, we will compare the results we obtained from polarized and depolarized DLS spectra with theoretical

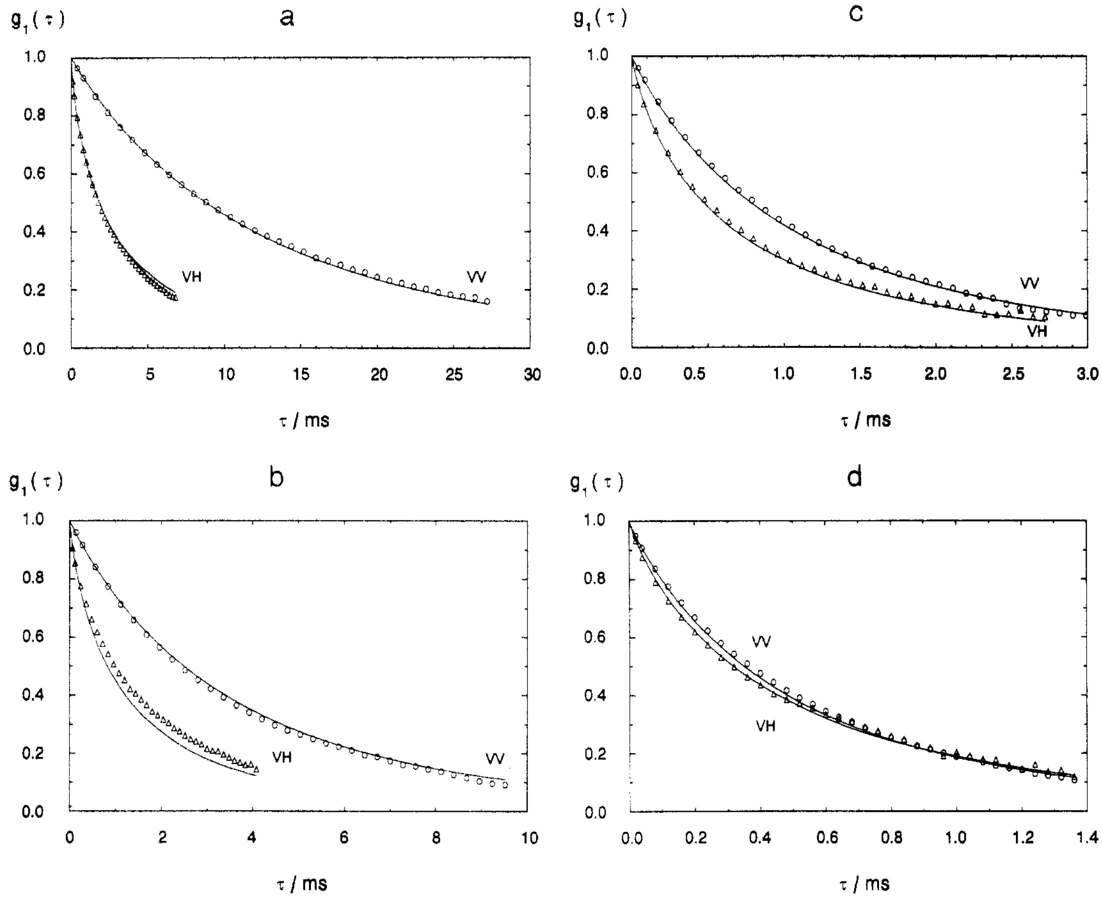

Figure 1. Comparison of polarized and depolarized first-order correlation function ($\langle X \rangle$ = 141, [A] = 15 μM) at different scattering angles: (a) θ = 20°, (b) θ = 35°, (c) θ = 60°, (d) θ = 90°. The solid lines represent model calculations for semiflexible rods. For computing the depolarized dynamic structure factor only the flexibility effect on the transport coefficients has been included. The contribution from internal motions was not considered. Details on the model calculations are given in the text.

correlation functions of rigid and semiflexible rodlike macromolecules.

Angular Dependence of the Polarized and Depolarized Correlation Functions. Figure 1 shows experimental VV and VH correlation functions for microfilaments with an average degree of polymerization of $\langle X \rangle$ = 141. The actual molar ration of active actin and gelsolin was determined by comparison of the initial decay rate of the polarized spectra with calculated data for semiflexible rods with a Kuhn length of γ^{-1} = 15 μm. A detailed description of this procedure was given in the preceding paper.[2] The actin concentration was 15 μM to obtain reasonable depolarized scattering intensities, and spectra were measured at four different scattering angles from 20° to 90°. Figure 1 clearly reveals, that at a low scattering vector the depolarized correlation function decays much faster than the VV spectra. The difference decreases, going to higher scattering vectors, and at θ = 90°, the decay profile of the VV and VH spectra are almost identical. According to eq 2, at low q ($q\langle L \rangle^3$ = 2.35) the rotational diffusion of the rodlike molecules gives the major contribution to the depolarized correlation function while the vertically polarized scattered light is caused mainly by translational motion of the filaments. At θ = 90°, the value of $q\langle L \rangle^3$ increases to 9.6 and the q dependent terms in eqs 2 and 3 become more important. Figure 1d indicates that now both relaxation modes, rotational and translational motion, and probably the coupling term give similar contributions to the polarized and depolarized spectra.

For comparison with the experimental data, we calculated the dynamic structure factors for both scattering geometries. Figure 1 reveals that for all scattering angles studied, the polarized correlation functions are in good agreement with model calculations of semiflexible rods with a Kuhn length of 15 μm. Unfortunately, there is no equivalent theory available that predicts the depolarized dynamic structure factor for flexible rodlike macromolecules. But we have shown that for the low molar ratios of actin/gelsolin (short filaments) the contribution of internal modes to the polarized spectra is negligible, i.e. rigid-rod calculations are equivalent. Assuming that this also holds for the depolarized spectra, we computed the correlation functions for rigid filaments. The rather good agreement with experimental data indicates that the model calculations indeed do reflect the angular dependence of the depolarized DLS spectra. Contributions from internal bending motions to the intensity fluctuations of the VH component of scattered light are most probably negligible for filaments this length.

The complementary information we obtained from analyzing the horizontal and vertical component of scattered light at low scattering angles becomes evident in Figure 2. Shown is the distribution of relaxation rates as obtained from CONTIN[13] for the VV and VH correlation function at $q\langle L \rangle^3$ = 2.35 and 9.6 (θ = 20° and 90°). At low scattering vector, we observed only a small overlap of the distribution of relaxation rates, indicating the contribution of different relaxation modes, predominantly from translational motion in the polarized and from reorietation of the molecules in the depolarized correlation functions. For θ = 90°, the main peaks from the CONTIN analysis moved together. It seems that now with $q\langle L \rangle^3$ = 9.6, the internal modes, rotational motion of the filaments included, contribute almost equally to the horizontal and vertical component of scattered light. The distribution of relaxation rates from the depolarized spectra is rather

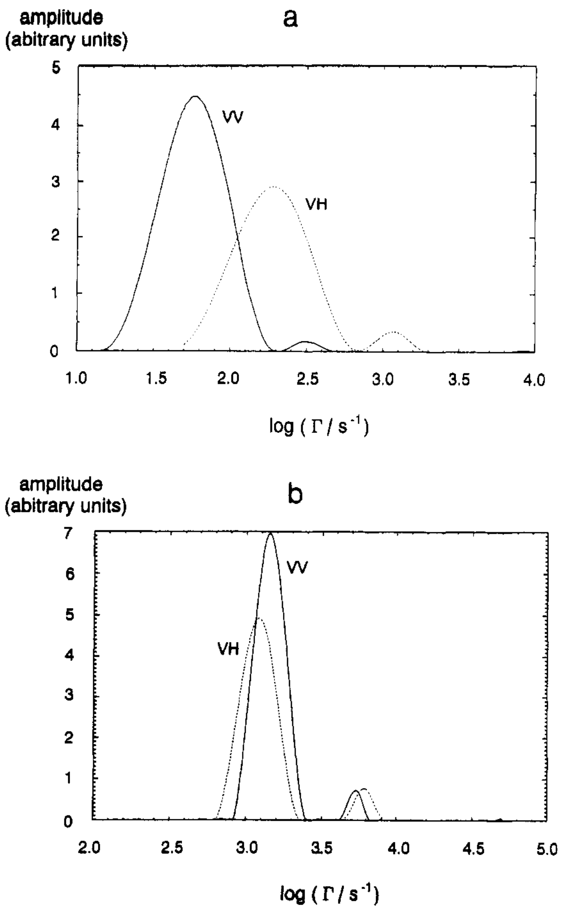

Figure 2. Distribution of relaxation rates as obtained from a CONTIN analysis. Comparison of results from polarized and depolarized correlation functions for two different scattering angles: (a) $\theta = 20°$, (b) $\theta = 90°$. ($\langle X \rangle = 141$; [A] = 15 μM.)

shifted to lower frequencies compared to the VV result. This is probably due to the fact that, neglecting the translation–rotation coupling, the translational motion perpendicular to the rod axis contributes predominantly to the depolarized spectra, while fluctuations of the polarized component arise also from lengthwise motion of the molecules. A more detailed interpretation of the CONTIN results is complicated by the polydispersity of the actin filaments, because the time scales for the translational motion of short filaments will probably overlap with the reorientational mode of longer molecules.

Measurements on Different Average Filament Lengths. Next, we studied F-actin of increasing average filament length. Again, we measured both polarized and depolarized DLS spectra. We chose a low scattering angle, $\theta = 20°$, which allowed us to use a lower actin concentration and still get depolarized correlation functions with $\sim 10^6$ counts in the baseline. The experimental results together with theoretical calculations for $51.5 \leq \langle X \rangle \leq 1648$ are presented in Figure 3. Comparison with theoretical predictions is limited, because, as mentioned before, there is no theory available to compute the depolarized dynamic structure factor of semiflexible rods. To circumvent this deficiency, we used the theory of Maeda for rigid rods, but included the effect of flexibility on the diffusion coefficients in our theoretical calculations. We assumed that, at least for the shorter filaments, the contribution of internal modes to the correlation function was negligible.

To estimate the validity of our approach, we tried to understand in more detail the individual contributions of the different relaxation modes to the polarized dynamic structure factor. For that purpose, we separated the contribution of internal modes from changes in the diffusion coefficients due to the flexibility of the molecules to the polarized dynamic structure factor in the following way. First, we did the model calculations for rigid rods, using the transport coefficients of semiflexible molecules, and second, we computed the VV spectra as usually using the theory for semiflexible macromolecules with $\gamma^{-1} = 15$ μm. Figure 4 shows that for an average degree of polymerization $\langle X \rangle = 100$ the theories for rigid and semiflexible rods with a Kuhn length of 15 μm provide almost identical correlation functions. For longer filaments, $\langle X \rangle = 200$, the effect of flexibility lead to a significantly faster decay profile for semiflexible molecules. But Figure 4 also indicates that most of the difference can be accounted for by using the expression for the diffusion coefficients of flexible molecules in the rigid-rod calculations. Going to even higher actin/gelsolin ratios, $\langle X \rangle = 500$, the interal modes give a significant contribution to the polarized component of scattered light.

In general, our calculations have shown that for low scattering vector and $\gamma \langle L \rangle < 0.04$ the contribution of internal modes to the polarized dynamic structure factor is probably negligible. The question remains, whether these estimates are relevant for the corresponding depolarized DLS spectra. Therefore, it is desirable to have a theory that explicitly considers flexibility in the expression for the depolarized dynamic structure factor of rodlike macromolecules. Aragon[14] has given expressions for the forward depolarized dynamic structure factor of a wormlike chain polymer in dilute solution. His theory, which neglects hydrodynamic interactions, predicts only a small contribution of bending motions to the depolarized dynamic structure factor in the rigid rod-limit. This provides support to our simple approximation for short filaments as discussed above.

As expected from our previous measurements[2] and shown in Figure 3, we observed a good agreement of the experimental polarized correlation functions for filaments of $\langle X \rangle \leq 350$ ($f_X = 1.17$) with theoretical predictions for semiflexible rods. In the same way, the depolarized spectra were well recovered by our simulated correlation functions using the rigid rod approach, but including the diffusion coefficients for semiflexible molecules in the model calculations. Thus, we can conclude that for such stiff molecules the internal bending modes do not contribute significantly to the depolarized dynamic structure factor. For $\langle X \rangle = 350$ the experimental VH correlation function reveals a slight deviation for longer decay times. This might be an artifact, using the multi-τ option of the correlator, or it might indicate that, in the depolarized component of scattered light, the dilute–semidilute transition becomes evident at lower concentration than observed in the polarized spectra. With $[A_F] = 6.5$ μM and $\langle X \rangle = 350$ the value of $c\langle L \rangle^3$ is calculated to 10, certainly in the dilute solution regime considering the polarized DLS spectra. Contribution from internal bending modes however would result in a faster initial decay of the depolarized correlation function.

For the longest average length ($\langle X \rangle = 1648$) we observed strong deviations between measured and calculated spectra for both the polarized and depolarized data, respectively. With $c\langle L \rangle^3 = 140$ we are far in the semidilute regime. In the polarized spectra a slow relaxation mode leads to a long tail in the correlation function. This has been observed in a more detailed study on the concentration effect on the dynamics of F-actin and was also reported for other polymers. On the other hand, the experimental depolarized correlation function revealed a significantly faster decay than the simulated spectra. A possible explanation is that for filaments this long the influence of internal bending motions, definitely of importance but

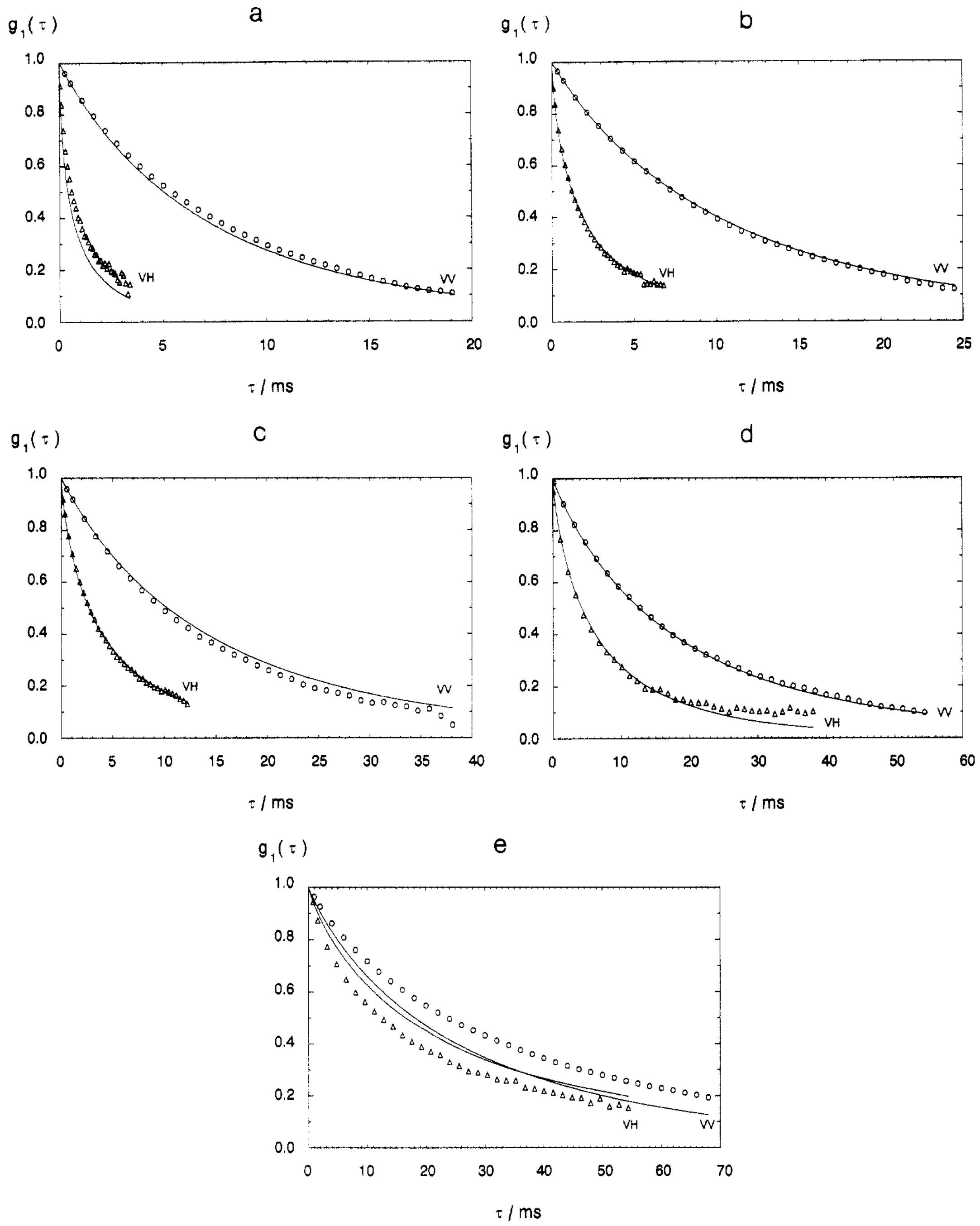

Figure 3. Comparison of polarized and depolarized first-order correlation function from F-actin with different average filament lengths at θ = 20°: [A]:[G] = (a) 50, (b) 100, (c) 200, (d) 300, (e) 1600. The solid lines represent model calculations for semiflexible rods. For computing the depolarized dynamic structure factor only the flexibility effect on the transport coefficients has been included. The contribution from internal motions was not considered. Details on the model calculations are given in the text.

not considered in our calculations, is not compensated by the decrease of the diffusion coefficients due to hydrodynamic interactions and topologic constraints.

Semidilute Solution Regime. To study the concentration effect on the depolarized dynamic structure factor, we prepared samples with an average degree of polymerization $\langle X \rangle = 350$ and varied the actin concentration in the range 6.5 μM $\leq$ [A_F] $\leq$ 105 μM. For the reason of clarity, we have shown in Figure 5 only exemplary depolarized correlation functions, measured at θ = 20°. The corresponding polarized spectra have been discussed in the preceding paper.[2] (See Figure 7 of ref 2 for comparison.)

With increasing concentration a slow relaxation mode appeared in the depolarized spectra, just as observed for the corresponding polarized correlation functions. Though, there are some differences to consider: In the polarized spectra the amplitude of the slow mode seemed to reach a constant level for $c\langle L \rangle^3 > 60$ μM. In contrast, Figure 3 indicates that the long tail behavior in the depolarized becomes more distinct with increasing concentration. We will suggest a qualitative explanation for this observation. Electric birefringence measurements on fd virus in aqueous solution[15] revealed that the rotational motion of the rodlike particle is severely hindered in the semidilute regime. For the polarized spectra, we have discussed[2] that the decrease of the rotational diffusion coefficient with concentration gives rise to a decrease in the initial decay rate at θ = 90°. We suggested that the slow mode in the correlation function results from a decrease in the diffusion coefficient, $D_\perp$, for sidewise translational motion due to topological constraints, probably combined with a collective diffusional mode of temporarily formed clusters. The decrease of $D_\perp$ with concentration has been observed in a Brownian dynamics simulation of rodlike molecules in semidilute and concentrated solution.[16] With increasing concentra-

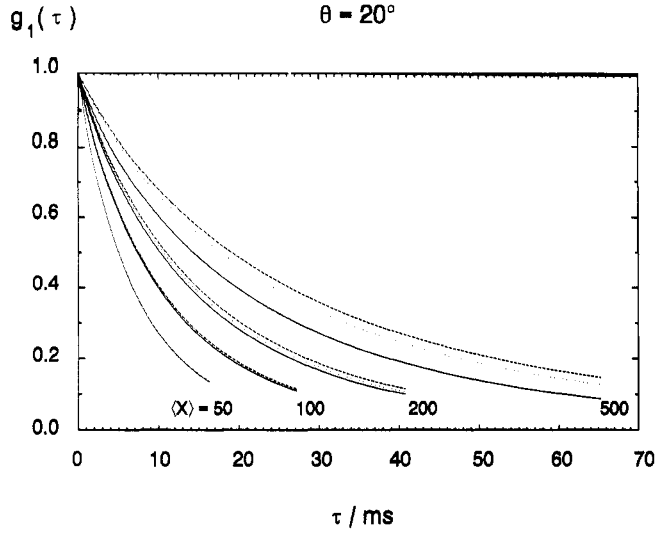

Figure 4. Calculated polarized correlation functions for actin filaments with different degrees of polymerization to estimate the contribution of internal bending motions: (- - -) rigid rod model; (···) rigid-rod model, but considering the transport coefficients for wormlike chains[9,10] in the calculations; (—) semiflexible rods with γ^{-1} = 15 μm.

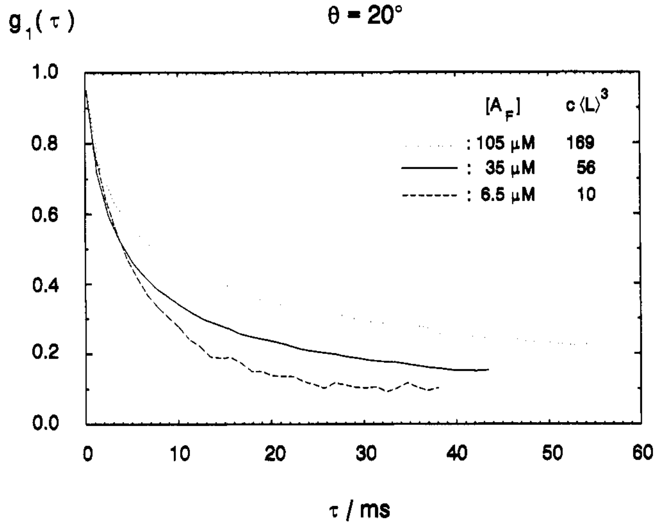

Figure 5. Depolarized first-order correlation function profiles for different concentrations in semidilute solution for ⟨X⟩ = 350. θ = 20°.

tion, the decrease of $D_\perp$ might be compensated by an increase of $D_\parallel$ that results from repulsive rod–rod interactions. As a consequence, the slow relaxation mode reaches a constant amplitude. (See Figure 7 of ref 2.) Similar observations have been made for DNA in solution.[17] According to eq 3, only $D_\perp$ contributes to the depolarized component of scattered light at low scattering angle, if we neglect the coupling term. This could explain why the amplitude of the slow mode in the depolarized correlation function still increases at the higher concentrations where the decay profile of the polarized spectra did not change significantly. In addition, the restricted rotation of longer filament could have a stronger influence on the VH than on the VV spectra.

Furthermore as discussed above, the depolarized spectra seemed to be more sensitive to concentration effects in the transition range from dilute to semidilute solution. Again, this effect is probably based on the dominant contribution of reorientational motion to the depolarized intensity at low scattering vector.

Conclusions

To our knowledge, this work presents the first detailed comparison of angular dependent polarized and depolarized dynamic light scattering measurements on rodlike macromolecules in solution. For short actin filaments with ⟨L⟩ = 390 nm (⟨X⟩ = 141), the experimental data are in quantitative agreement with theoretical calculations for rigid rodlike molecules. Considering the transport coefficients for semiflexible macromolecules in the rigid rod model is sufficient to describe the decay profile of the experimental depolarized correlation functions for F-actin with ⟨X⟩ ≤ 350. Contributions from internal bending motions are necessary to characterize the dynamics of the longer filaments studied.

There is more experimental data and theoretical work necessary to clarify the dynamics of rigid and semiflexible rodlike macromolecules in semidilute solution. More elaborate comparisons of polarized and depolarized dynamic light scattering experiments are certainly one possibility to achieve this objective. The actin filaments offer the opportunity to perform such investigations over a broad range of filament lengths from basically rigid to semiflexible molecules, the only drawback being the polydispersity of the system.

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