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Liquid-Crystalline Aspects of Muscle Fibers

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Abstract—The physical-chemical factors which affect the filament separation in striated muscle are reviewed. It is suggested that muscle fibers are a " liquid-crystalline " superphase, and that the physical nature of this phase is of importance in the contractile mechanism.

Recent X-ray studies of muscle fibers have been reviewed by Hanson.[1] That review supplemented Huxley's comprehensive review[2] of many well-documented studies of striated muscle structure. Our purpose here is to discuss certain aspects of the striated muscle fiber which seem likely to be of importance in the physical-chemical understanding of the contractile process, but which have not, perhaps, received the attention they merit.

The inter-filament distance in glycerinated striated muscle (rabbit psoas) is a function of (i) sarcomere length, (ii) *p*H of the inter-filament medium, (iii) ionic strength of the medium, (iv) valency of the positive ions in the medium.[3,4,5] The variation can be large; for example the myosin-myosin center-to-center distance in " rest length " glycerinated rabbit psoas increases from 450 Å to 540 Å when the ionic strength decreases from 0.1 to zero. Nevertheless the order in the lattice is maintained.

The general form of the *p*H and ionic-strength behavior in glycerinated muscle is similar to that observed by Bernal and Fankuchen[6] for equilibrium gels of tobacco mosaic virus. Apart

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from (iv) all these effects have also been demonstrated in living resting muscle (toad and frog sartorius).[4,5,7,8] In contracting muscle, as in resting muscle, it is known that the inter-filament separation varies over a considerable range as a function of sarcomere length.[9,10]

We have suggested[11,4] that in striated muscle (both living muscle, at rest and during contraction, and glycerinated muscle) the inter-filament separation is controlled by the balance of van-der-Waals attraction, electrical double-layer repulsion and hydration. On this basis the observed effects can be understood at least qualitatively. Verwey and Overbeek[12] made detailed calculations of van-der-Waals and double-layer energies, using planar and spherical geometry. Calculations have now been made for systems of parallel cylinders,[13] making assumptions reasonable for the muscle system. The indications are that a stable balance can be obtained at the observed inter-filament separations. The van-der-Waals and electrostatic energies are considerable, and it is possible that contraction might involve perturbation of these energies.

The striated muscle fiber, which changes length by a sliding filament mechanism,[14,15] can therefore be considered as two interleaving 'smectic' superphases (using superphase in the sense defined by Zocher and Török).[16] These superphases are certainly " liquid crystalline ", though whether they come within the definition of a liquid crystal depends on the usage of the term. The " liquid-crystalline " nature of the two interleaving superphases (one of the protein actin and one of the protein myosin) is clearly of importance in the contractile mechanism. The water layers probably act as a lubricant, the high dielectric constant of water may make possible high surface charges and thick double-layers.[16] The particular role of water is not understood in detail. Derjaguin[17] has focussed attention on the ability of glass and quartz surfaces to change the physical properties of many polar liquids to a great depth; it is possible that the surfaces of protein molecules act similarly. Bernal[18] has discussed the special nature of water and the gradation of water structure round a protein

from an ice-like structure at close range (~ 10 Å) to the free water structure at long-range (~ 4000 Å). The distances of interest in muscles, actin surface to myosin surface, are about 200 Å, in the intermediate range.

The potential gradients in the double-layers can be large, of the order of 10^5 volt cm^{-1} according to the model calculations.[13] This must give rise to separate regions and pathways for mobile positive and negative ions. In addition, any event which alters the surface charge on one of the filaments will also, because of the operation of Gauss' Theorem of electrostatics, change the potential gradients throughout the inter-filament region. Thus the arrival of a Ca^{++} ion on the surface of the actin filament could "switch on" the ATP-splitting enzyme, which is known to project from the myosin filament (see the review articles,[1,2]) if the enzyme is sensitive to potential gradient, as seems plausible.

From the point of view of the production of the contractile force the important interaction may be a local one between the head of the myosin molecule and the actin monomer. A dipole-dipole interaction seems possible, for example see reference 19. However the longer-range interactions which we have discussed here can hardly be disregarded in any complete description of the contractile process, and they are probably vital to that process.

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