

A. A. Vazina, *Liquid crystals and biological mobility*. A muscle is a highly efficient mechanical-chemical machine; contraction is realized by the relative slipping of microfibrils of the muscle fiber; the molecular mechanism of contraction is unknown.

Structurally, a muscle can be viewed as a lyotropic liquid crystal (LC).¹ The hexagonal lattice of the muscle is formed by two types of protein strands: thick strands, consisting of the protein myosin, and thin strands, consisting of actin. The lattice of thick strands overlaps only partially with the lattice of thin strands. In the rest state, there is no contract interaction between the strands: the distance between the thick strands is about 400 Å; the system is stabilized by long-range forces. The actin and myosin strands differ by their periods and symmetry. The heads of myosin molecules, exhibiting ATPase activity, are distributed on the surface of a thick strand in the form of protuberances and

bridges are situated in pairs with an interval of 143 Å; each pair is rotated relative to its neighbors by 120°, so that the strands have a screw symmetry axis 3, and a period of 429 Å. The thin strand is a double helix consisting of actin globules with a noninteger axis 13/6 and a period of 365 Å. The thin strand has a polar structure: it does not have a second-order axis perpendicular to the axis of the strand. The helical structure of the thin strand is modulated by the structure with a different period of 385 Å, which corresponds to the distribution of important regular proteins (tropomyosin and troponin), i.e., the thin strand is an incommensurate one-dimensional crystal. With the limited length of the fibrils (1–2 μm), it represents an aperiodic structure.

Aperiodic polar fibrils, forming LC, form long polar channels, along which there are no equivalent symmetry points. Liquid crystals are prone to polymorphic transitions.² The unique strictly periodic distribution of charges

and active groups on the fibrils forms within a channel a definite force field. Thus the channels in the LC must be viewed as biologically active space, defining the direction and determining the spatial-temporal parameters of the processes occurring in the cell.

An x-ray diffraction pattern of a muscle in the meridional direction consists of two systems of layered lines, formed by the helices of the myosin and actin strands. In the equatorial direction, the diffraction pattern is due to the hexagonal lattice of the thick and thin strands. The diffraction pattern of the muscle changes sharply in the state of rigor mortis, when ATP is absent in the muscle: the intensities of the equatorial reflections are redistributed, the intensity of the reflection from the 10 planes, where only thick strands occur, decreases, while the intensity of the reflection from 11 planes, where both thick and thin strands are situated, increases; the heads move away from the thick strand toward the trunk of the thin strand. The lines form the layers of myosin strands disappear and the actin layer lines are amplified: the heads leave the register of the helix of the thick strand and become incorporated into the structure of the thin strand. It is known that actin and myosin are capable of forming a stable complex, but in the presence of ATP, the complex dissociates. The formation of actomyosin accelerates the stage at which the products of hydrolysis of ATP are released from myosin. The x-ray diffraction picture of the steadily contracting muscle (tetanic contraction) is also characterized by some redistribution of the equatorial reflections and extinction of the myosin layer reflections. This was interpreted (in analogy to the x-ray diffraction pattern of the rigor-mortis state) as an asynchronous emergence of bridges from the register of the thick strand, their approach to the thin strand, and attachment to it, although in this case, an intensification of actin layer reflection was not observed.³

The x-ray experiments formed a serious foundation for the bridge hypothesis of slipping, according to which force is developed due to the periodic attachment of myosin bridges to specific centers of the actin strand. Changing their inclination, the bridges drag the thin strand relative to the thick strand. In this model, the functionally significant structural unit is considered to be a singled out pair of strands, i.e., in principle, two strands and a single bridge are sufficient to develop motion. All theoretical models of slipping are one-dimensional and it is assumed that forces perpendicular to the axes of the fibers are either small or compensated, i.e., the specific properties of a liquid-crystalline ensemble are deemphasized in the models.

Results obtained in recent years by us and abroad in x-ray diffraction experiments with high temporal resolution up to 1 ms (diffraction motion picture), revealed and paradoxical nature of the changes of the intensity during the contraction process.^{1,4-6} (The diffraction motion picture technique was developed based on the use of SI and sensitive detectors.⁴) The temporal behavior of the intensity of the reflection at 429 Å follows the stress curve, while the change in the intensity of reflection at 143 Å (third-order reflection), reveals an anomaly: the curve is a biphasic curve, there is a distinct increase in the reflection intensity at 143 Å at maximum stress. A considerable reversible change in the intensi-

ty of the reflection at 143 Å compared to the stability of the reflection at 429 Å is observed in experiments with fast mechanical actions on the contracting muscle. The temporal behavior of the intensity of the 11 equatorial reflection leads the 10 curve in phase. It should be emphasized that no intensification of the actin layer strands was recorded in these experiments.

The results presented above cannot be explained within the framework of the bridge contact model. To interpret them, it is necessary to have some notion of the dynamic structure,¹ which is formed in the interior of the LC; this lattice is not a morphologically independent structure, it is formed by bridges of three different strands at the time of contraction; its lifetime is a hundredth of a second.

Thus a trigonal channel of the liquid-crystalline ensemble, which is formed by fibrils with different periods and symmetries and not a pair of isolated strands must be viewed as the functionally significant element. When the interaction between the thick and thin strands is switched on, the system goes over into a nonequilibrium state and uncompensated longitudinal forces appear. In the presence of a degree of freedom and in view of the polarity of the structure, any vector of forces leads to a unidirectional motion of the thin strand along the axis of the myosin channel and when set in motion, the system becomes an equilibrium system. The principle of dynamic coupling of symmetries can determine the mechanism of biological mobility in its various manifestations.⁸

The elementary acts of motion will be manifested in the form of vibrations and quivering of the strands. Indeed, with a given strand length (1 μm) and with a given ratio of periods of the helices of the thick and thin strands, there cannot be two identical distances r_{AM} between the interacting centers of the actin and myosin strands and, therefore, the elementary interaction forces f_{AM} , which are a function of r_{AM} , will also have different magnitudes; the width of the dispersion of r_{AM} and f_{AM} will be determined by the ratio of the periods of the helices of the thick and thin strands. We do not make any assumptions concerning the nature of the forces. It is important that these are long-range forces. In view of the different symmetry of the strands in the trigonal channel, forces will be applied to the thin strand from the side of the thick strands at nonequivalently symmetrical points. This will lead to the appearance of a moment of forces and to rotation around an axis by some angle. In this system, with complete determinateness of the structure, the interactions will be realized as quasistochastic interactions. Vibration leads to stability of the system, and the force of dry friction is converted into friction of a liquid. The statistical nature of the vibrations around the axis guarantees the possibility of a complementary interaction of specific centers of myosin and actin in the isometric contraction regime, which is necessary in order to complete the act of fermentation hydrolysis of ATP (release of products of hydrolysis from myosin) and which makes it possible for the cycle to be repeated.

The mechanism of mobility cannot be represented in terms of models with physicists are familiar. The contraction systems are apparently reminiscent of systems with mixing and it is possible that such ideas will be fruitful here.

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³H. E. Huxley and W. Brown, J. Mol. Biol. **30**, 383 (1967).

⁴A. A. Vazina, Vestn. Akad. Nauk SSSR, No. 8, 14 (1978).

⁵A. A. Vazina *et al.*, in: Otchet o rabote po ispol'zovaniyu sinkhrontron-nogo izlucheniya v IYaF SO AN SSSR (Report on the Use of Synchrotron Radiation at the Institute of Nuclear Physics, Siberian Branch of

the USSR Academy of Sciences), SO AN SSSR, Novosibirsk (1981), p. 20.

⁶H. Huxley *et al.*, Proc. Nat. Acad. of Sci. USA **78**, 2297 (1981).

⁷H. Huxley *et al.*, Nature **284**, 140 (1980).

⁸A. A. Vazina in: Proceedings of the IVth International Conference on Liquid Crystals, Tbilisi (1981), p. 142.

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