EFFICIENCY OF LIGHT DIFFRACTION BY CROSS-STRIATED MUSCLE FIBERS UNDER STRETCH AND DURING ISOMETRIC CONTRACTION

REINHARDT RÜDEL AND FRANZ ZITE-FERENCZY, *Physiologisches Institut der Technischen Universität München, 8000 München 40, Federal Republic of Germany*

ABSTRACT When light is diffracted by a single frog muscle fiber the intensities I_k of the different orders k (k = 1,2,3) strongly depend on the angle between the axis of the incident beam and the fiber axis. Maximum intensity is not obtained with perpendicular incidence ($\omega = 0°$) but at angles that can be calculated for each order number and sarcomere length using Bragg's formula. In analogy to techniques developed for x-ray structure analysis of mosaic crystals we have rotated the fiber around an axis perpendicular to the fiber axis and to the incident beam axis within an angular range $\Delta\omega = \pm 35°$ and recorded the light intensities I_k. Diffraction efficiencies defined as $E_k = \int I_k d\omega$ were studied as a function of sarcomere length and during isometric contraction. The sarcomere length dependences of the efficiencies E_k of the first three orders show characteristic trends. E_1 increases with fiber stretch, E_2 has a minimum at a sarcomere length near 2.8 μm, and E_3 has a maximum near 2.5 μm. These trends as well as the observed efficiency ratios are in fairly good agreement with predictions by the intensity formula developed for x-ray structure analysis. During isometric contraction, the diffraction efficiencies of the fiber decrease, with the decreases becoming greater the higher the order number. These decreases might be caused by a longitudinal displacement of myofibrils of up to 0.4 μm. The efficiency of light diffraction strongly depends on the tonicity of the bathing fluid. Hypertonic (3/2 × normal) solution reduces E_1 to less than half, hypotonic (2/3 × normal) solution increases E_1 to almost twice the value obtained in normal Ringer's solution.

INTRODUCTION

Two aspects of the light diffraction by striated muscle have been the subject of study by many authors: first, the dependence of the intensity I_k of various orders (k = 1,2,3) of the diffracted beams on the variable sarcomere length of resting muscle, and second, the variation of I_k during isometric contractions. Agreement seems to have been accomplished only with the latter problem (see Table IV of Baskin et al., 1979); the intensity decreases during isometric contraction. However, we still feel that "there is no satisfactory explanation of the intensity effects now at hand," as Kawai and Kuntz put it in 1973. As regards the dependence of I_k of a resting muscle on sarcomere length, the results of different groups have been rather divergent and only recently attempts have been made to fit curves calculated from diffraction models to the experimental data (Fujime, 1975; Fujime and Yoshino, 1978; Baskin et al., 1979). If such

---

Dr. Rüdel's present address is Department Physiologie, Universität Ulm, Postfach 4066, 7900 Ulm, Federal Republic of Germany.

a model, containing physical details of the muscle fiber, like filament lengths, protein densities, etc., can fit the data, one may hope to infer, from intensity measurements, structural information which would otherwise be difficult to obtain. Although we do not claim to have reached this goal, we believe that our observation (Rüdel and Zite-Ferenczy, 1979*a*,*b*) that volume effects play a role in light diffraction by muscle fibers, similar as in thick holographic phase gratings (Burckhardt, 1966), justifies another experimental and theoretical approach toward solving this problem.

METHODS

In contrast to all previous experimenters we have varied the direction of the incident beam with respect to the fiber axis. Fig. 1 schematically illustrates the experimental arrangement. A single fiber dissected from a semitendinosus or tibialis anterior muscle of the frog *Rana esculenta* was suspended in a rotatable semi-cylindrical chamber between two stainless steel hooks. The hooks were situated on a chamber diameter and could be shifted in the direction of the fiber axis to obtain variable sarcomere lengths between 2.0 and 3.6 μm. By shifting both hooks together, a clean fiber segment could be brought into the center of the chamber. The bottom of the chamber was made from glass so that the beam of a 5-mW HeNe laser (model 144, Spectra-Physics Inc., Laser Products Div., Mountain View, Calif., λ = 633 nm, unpolarized) could be directed into the center of the chamber. In contrast to earlier experiments, in the present study, the laser beam was not deflected by mirrors. In most experiments the beam was not narrowed by telemetric optics, its diameter was 1 mm.

For a given fiber length the diffracted beams left the chamber at a constant angle irrespective of rotation angle ω of the chamber because the surface of the bathing fluid (dotted in Fig. 1) always kept the same level. A photodiode (PIN 25, United Detector Technology Inc., Santa Monica, Calif.) could be set 60 mm above the center of the experimental chamber on a semicircular rail. The sensitive area of the diode was 25 mm in diameter, but it was masked by tape so that its width along the meridian was reduced to 2–5 mm, depending on the layer line width. The solid angle subtended by the diode was always enough to detect at least 80% of the light intensities contained in a layer line. Thus, the light

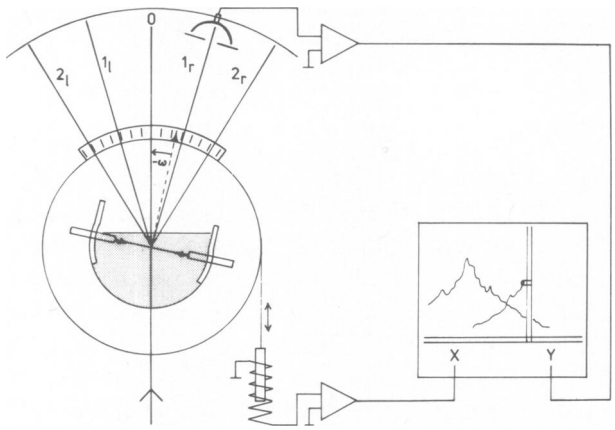

FIGURE 1 Schematic drawing of the experimental arrangement. Lateral view of the rotatable chamber filled with bathing fluid (dotted). The incident laser beam enters through a glass window in the bottom and illuminates the fiber in the center of the chamber. The rotation angle ω is converted into a voltage wired to the *X*-input of an *XY*-plotter. The light intensity of a diffracted beam (here first order to the right) is recorded by a photodiode which is connected to the *Y*-input.

intensity of a particular diffracted beam was monitored while the chamber was rotated by an electric motor by $\omega = \pm 35°$ at a constant speed of 2°/s. The amount of the angle was converted by an inductive position transducer (SS 107, G. L. Collins Corp., Long Beach, Calif.) into a voltage which was used for the horizontal deflection of an *XY*-plotter. Accuracy of angle measurement was <0.5°. The output of the photodiode was amplified and wired to the vertical input of the *XY*-plotter. The intensity of scattered light turned out to be rather independent of ω. Therefore, after each ω-scan the background light intensity was determined at both sides of the layer line and the arithmetic means was subtracted from the plot to define the zero intensity line. Examples of the resulting ω-scans are given in Fig. 2.

For the recording of the fast intensity changes during isometric contractions, the output of the photodiode was wired to a chart writer (Fig. 4 A). The whole experimental run was recorded simultaneously on a storage oscilloscope operated in the *XY*-mode and photographed with a Polaroid camera (Polaroid Corp., Cambridge, Mass.) (Figs. 4 B and 5). Integrated light intensities over all angles ω were obtained by means of a signal averager (NIC 535, Nicolet Instrument Corp., Madison, Wisc.) which was synchronized with the chamber rotor.

Stimulation of the fiber could be accomplished through a pair of platinum plate electrodes extending on each chamber wall over the whole fiber length. Stimulus amplitude was 1.2 × threshold, duration 1 ms, tetanic stimulation was at 50 Hz for 300 ms every 2 min.

Solutions

The bathing fluid contained (mmol/liter): NaCl, 115; KCl, 2.5; Na_2HPO_4, 2.15; NaH_2PO_4, 0.85; $CaCl_2$, 1.8; the pH was 7.2. Hypertonic solution (3/2 × normal) was produced by addition of 37.5 g/liter sucrose, hypotonic solution (2/3 and 1/2 × normal) was produced by dilution with water. The bath was at room temperature (≃20°C).

RESULTS

Relative Intensity in Different Orders of Light Diffraction of a Resting Fiber at Fixed Length

Fig. 2 shows six ω-scans carried out for I_1, I_2, and I_3 to the left and right sides, respectively, using the same illuminated fiber field. Each light intensity distribution spans a range of ~50° with a half width of ~15° and a peak which is situated at the angle expected by the Bragg condition:

$$2d \sin \theta_k = k\lambda/n_F \; (k = 1,2,3), \tag{1}$$

where d, distance between lattice planes ≃ sarcomere length; θ_k, glancing angle between incident beam of light and lattice planes to give diffraction of the kth order; λ, wavelength of light; $n_F = 1.377$, mean refractive index of the fiber.

For the sarcomere length $L_s = 2.6$ μm used in this experiment, $\theta_1 = \pm 5.1°$, $\theta_2 = \pm 10.2°$, $\theta_3 = \pm 15.4°$. Intensity distributions of the same order to the left and right have similar shape and display corresponding local maxima and minima. The fact that they are almost identical but separated by $2\theta_k$ along the ω-axis can be interpreted as Bragg reflexion from the same sets of planes once to the left and once to the right (Rüdel and Zite-Ferenczy, 1979*a*).

Fig. 2 makes obvious why all previous measurements with normal light incidence ($\omega = 0°$) gave spurious results. The ratios $I_1{:}I_2{:}I_3$ at $\omega = 0°$ are 1:0.09:0.05, and at the peaks they are 1:0.17:0.39. We consider comparison of peak intensities more sensible than of intensities at a fixed angle of beam incidence because only in the former case diffraction by the same partial volume is compared, viz., by myofibrillar clusters whose lattice planes have no inclination

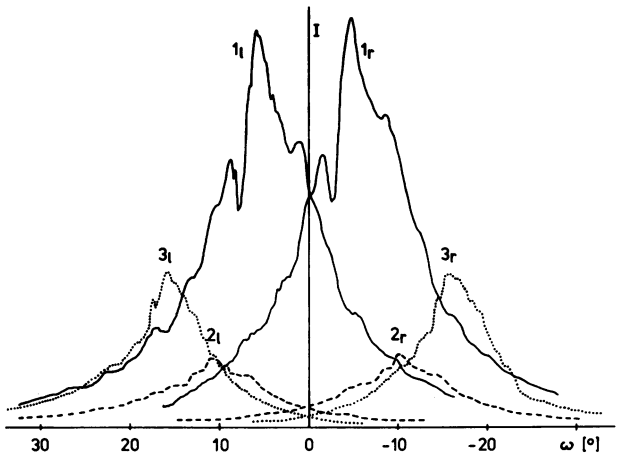

FIGURE 2 Dependence of the intensity of the first three orders to the left *(l)* and right *(r)* of diffracted beams on the rotation angle ω ($\omega = 0^0$ corresponds to normal light incidence). Same arbitrary linear scale for all six intensity distributions. Anterior tibial fiber, sarcomere length $L_s = 2.6$ μm.

against the fiber axis. To obtain the most relevant measure of diffraction intensity and in analogy to methods applied in x-ray diffraction studies on polycrystalline material we propose to integrate I_k over the whole relevant angular range $\Delta\omega$. Since for each ω the photodiode integrates over most of the length l of the layer line we can define an efficiency E_k by

$$E_k = \int\int I_k \, dl d\omega. \tag{2}$$

The ratios $E_1{:}E_2{:}E_3 = 1{:}0.18{:}0.30$ in the example of Fig. 2 are similar to the ratios of the peak intensities.

The result illustrated in Fig. 2 is qualitatively representative for all fibers that we have investigated. However, in many fibers there was a preponderance of inclination to either side, i.e., all intensity distributions were found to be shifted to positive or negative angles with respect to $\omega = 0°$ along the ω-axis.

Efficiency of Light Diffraction as a Function of Sarcomere Length

Recording of absolute efficiencies at varied sarcomere length turns out to be rather difficult. One has to make sure that, after each fiber stretch, the same segment is illuminated again; changes in fiber cross-section have to be taken into account; sometimes irreversible changes occur during stretch. We therefore mainly studied the efficiency ratios E_2/E_1 and E_3/E_1 which are much more accurate with respect to changes of the illuminated fiber field or of the fiber cross-section. The result of six experimental series with different fibers is illustrated in the lower two diagrams of Fig. 3. Special care was taken to determine the sarcomere lengths $L_s = 2.84 \pm 0.07$ μm, at which E_2/E_1 was minimal, and $L_s = 2.55 \pm 0.09$ μm, at which E_3/E_1 was maximal (means ± SD of seven measurements).

To get absolute efficiency values we recorded the sarcomere length dependence of E_1/E_0 in a selected semitendinosus fiber that was of large diameter (150 μm at $L_s = 2.2$ μm), fairly round and clean. The diameter of the incident beam was reduced to 100 μm using telemetric optics (Zite-Ferenczy and Rüdel, 1978) to have all the light pass the fiber. The result of this

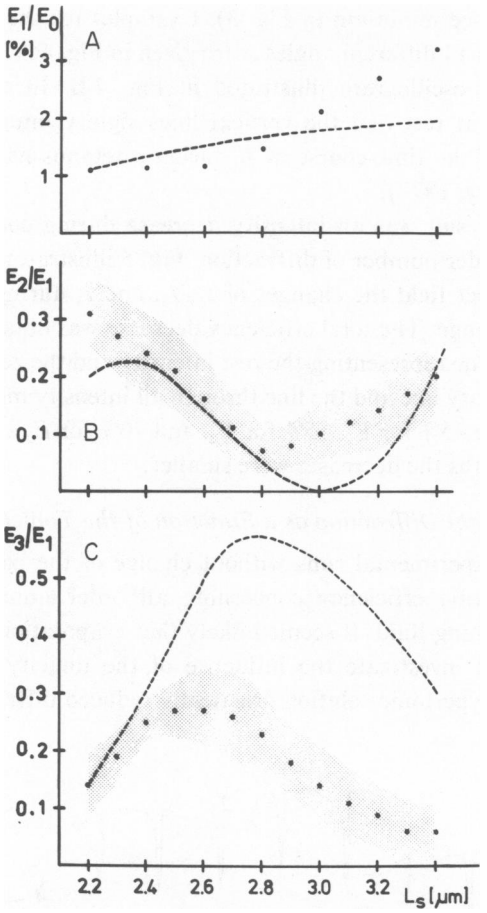

FIGURE 3 Dependence of efficiency ratios on sarcomere length L_s. (A) E_1/E_0, the intensity of one first order beam integrated over the whole angular range ω, normalized to the incident beam intensity. Experimental values from a semitendinosus fiber, having a diameter of 150 μm at L_s = 2.2 μm. Incident beam diameter reduced to 100 μm. (B, C) E_2/E_1 and E_3/E_1, respectively. Means and standard deviations (dotted) of the results from six different fibers. Dashed lines calculated values, using Eq. 3 of text, normalized to the experimental value of E_1/E_0 at L_s = 2.2 μm.

experiment is illustrated on top of Fig. 3. E_1 remains constant with fiber stretch from L_s = 2.2 to 2.6 μm and then increases up to threefold at L_s = 3.4 μm.

Efficiency of Light Diffraction during Isometric Contraction

An ω-scan lasted ~25 s. To avoid exhaustion of the fiber by tetanic stimulation for such a long time we performed the ω-scans with the resting fiber in steps of ~2°, stimulating twitches or brief tetani of 300-ms duration at each step.

The intensity changes usually showed three phases: a quick initial phase, a slower phase during contraction, and a relaxation phase. The changes did not always go in the same direction. The greatest variability in the intensity changes was observed when the intensity at rest was already small, i.e. when ω was very much different from the Bragg angle calculated for lattice planes normal to the fiber axis, and especially for I_2 and sarcomere lengths around

2.8 μm at all angles ω (see minimum in Fig. 3). Examples for the time-course of I_1 during twitches (L_s = 2.6 μm) at 14 different angles ω are given in Fig. 4 A. The angles ω can be read from the accompanying oscillogram illustrated in Fig. 4 B. In this plot the curved line represents the intensity at rest and the vertical lines signify intensity changes during the twitches. An example of the time-course of I_1 during a tetanus has already been published (Rüdel and Zite-Ferenczy, 1977).

The most consistent result was an intensity decrease during contraction, which was the greater the higher the order number of diffraction. Fig. 5 illustrates an experiment where for the same illuminated fiber field the changes of I_1, I_2, and I_3 during twitches were recorded over each respective ω-range. The total efficiency decrease was obtained by subtracting from the area defined by the line representing the rest intensity and the zero intensity line, the area defined by the rest intensity line and the line through all intensity minima. The resulting total efficiency decreases were 45% for E_1, 55% for E_2, and 70% for E_3 at L_s = 2.6 μm. At shorter or longer sarcomere lengths the decreases were smaller.

Efficiency of Light Diffraction as a Function of the Tonicity of the Bathing Fluid

During longer lasting experimental runs without change of the bathing fluid we noticed a decrease of the diffraction efficiency concerning all order numbers. The decrease was reversible with fresh bathing fluid. It seemed likely that evaporation of the bathing fluid was involved. This led us to investigate the influence of the tonicity of the bathing fluid on diffraction efficiency. Hypertonic solution drastically reduced diffraction efficiency, a result

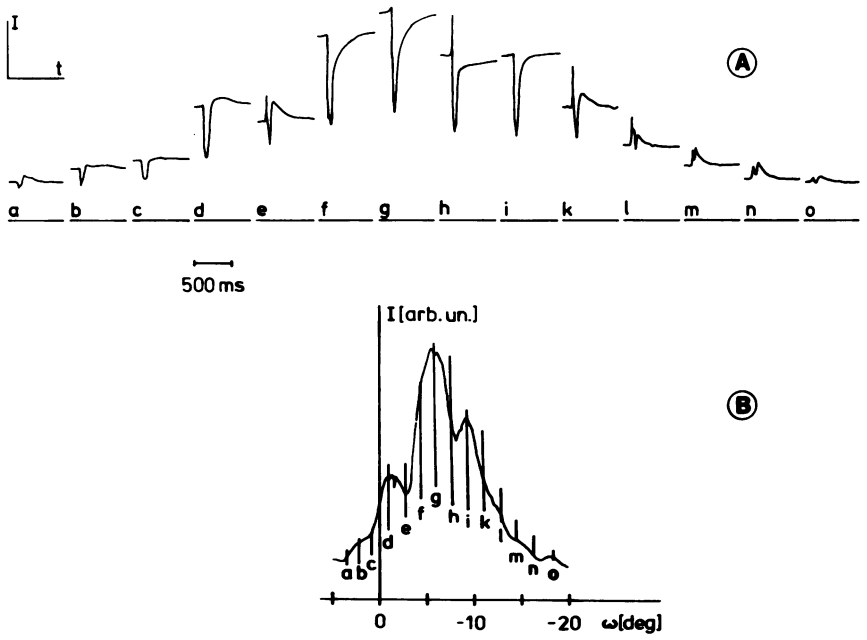

FIGURE 4 (A) Time-course of I_1 during isometric twitches of a tibialis anterior fiber (L_s = 2.6 μm) at various rotation angles ω. Same linear intensity scale for all records. (B) simultaneously recorded ω-scan. The same intensity variations during contraction are represented as vertical lines superimposed on the resting intensity distribution.

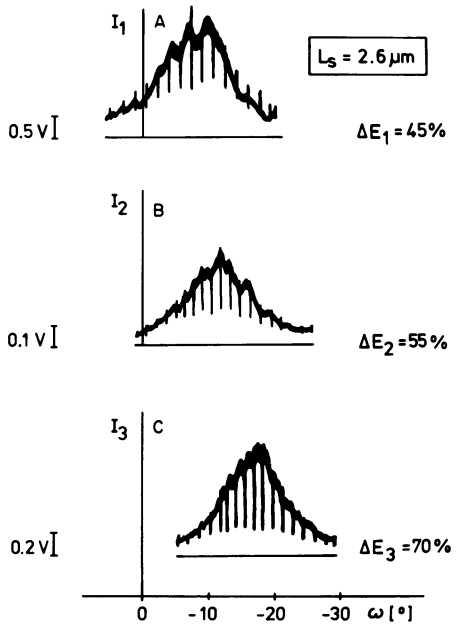

FIGURE 5 The intensity variations of I_1 (A), I_2 (B), and I_3 (C) during isometric twitches (L_s = 2.6 µm) at various rotation angles ω. Note changes in intensity calibration. For details see text.

already reported by Blinks (1965*a*,*b*). Hypotonic solution increased diffraction efficiency. At L_s = 2.6 µm the following results were obtained from six fibers (E_1 in normal solution taken as 100%). At ½ × normal tonicity, E_1 was 44 ± 14%, at ⅔ × normal tonicity, E_1 was 182 ± 33%. At the even higher dilution of the bathing fluid of ½ × normal tonicity, the value of E_1 was less increased to 162 ± 39% (mean values ± SD). Efficiencies of higher orders E_2 and E_3 showed similar trends.

DISCUSSION

Sarcomere Length Dependence of Diffraction Efficiency

The dependence of diffraction efficiencies on sarcomere length illustrated in Fig. 3 is completely different from that of diffraction intensities reported earlier, e.g., by Baskin et al. (1979). The increase of intensity with sarcomere length found by these authors is explained by the fact that with fiber stretch the intensity distributions (Fig. 2) move together according to the Bragg condition (1) so that the $\omega = 0°$ line intersects them more closely at the peak.

Our sarcomere length dependence of diffraction efficiencies is similar to the one calculated by Baskin et al. (1979) in their Fig. 5 using the simple grating equation. These authors, however, do not accept this as a model and we agree that the plane-grating concept is not very adequate because it does not imply volume effects. The problem of the intensity of light diffracted by gratings with a thickness much greater than the wavelength of incident light has been mathematically treated by several authors (Burckhardt, 1966, 1967; Kogelnik, 1967; Kaspar, 1973; Su and Gaylord, 1975; Magnuson and Gaylord, 1977). The dependence of the relative intensity of diffracted light on the angle of beam incidence calculated by Burckhardt

(1967) for a grating of 100 μm thickness and a refractive index variation of $\Delta n = 0.01$ (in frog muscle fiber $\Delta n = 0.015$, Huxley and Niedergerke, 1958) with sinusoidal index variation, is similar to the one shown in our Fig. 2, in particular maximum intensity is obtained at the Bragg angle.

However, the formulas used by Burckhardt and others are highly idealized because they assume a homogenous index modulation along the grating thickness. This would apply to a muscle fiber only if the A–I-band pattern of all myofibrils were exactly in register or at least systematically displaced. Inspection of a muscle fiber with interference contrast (Huxley, 1974) shows that even the latter idealization is not verified. The myofibrils seem to be organized in clusters of 10–15 μm in diameter with different inclination of striation so that for each cluster "reflexion planes" and therefore Bragg angles are differently defined. To scan all clusters it thus seems necessary to vary the angle of light incidence. A further complication is given by the observation that even within such a cluster the orientation of the striation may vary within tenths of a millimeter along their length. We suggest that this is reflected in the large width of our intensity distributions obtained with an incident beam of 1 mm diameter. With 0.1-mm beam width several sharp lines can be resolved (Rüdel and Zite-Ferenczy, 1979*a*).

Considering diffraction intensities we therefore assume that for a given angle of light incidence not the whole illuminated fiber cross-section is able to contribute but only those clusters whose orientation fulfills the Bragg condition. The grating thickness would therefore be 10–15 μm instead of ~100 μm. Intensity-angle of incidence relationships calculated by Burckhardt (1966) for this grating thickness resemble those of Bragg reflexion in crystals. For this reason we have adopted the view of the muscle fiber as a mosaic crystal and applied the formalism of x-ray crystallography to our problem.

For the integrated intensities of x-ray diffraction in crystals the following formula has been developed (e.g. Bragg, 1949, chapter IX and Appendix V)

$$E_k/E_0 = C \cdot N^2 \cdot L_k \cdot P_k \cdot |F_k|^2 \cdot \Delta V, \quad k = 1,2,3 \tag{3}$$

with E_0, incident radiation intensity; C, constant containing natural constants and wavelength of radiation used; N, number of pattern units (unit cells, i.e., one sarcomere of one myofibril) per unit volume; $L_k = 1/(\sin 2\theta_k)$, Lorentz factor; $P_k = (1 + \cos^2 2\theta_k)/2$, polarization factor; F_k, structure factor representing the diffraction by a unit cell; and ΔV, illuminated volume.

The volume of a muscle fiber remains constant when the fiber is being stretched (Blinks, 1965*a*). Therefore, N, the number of unit cells per unit volume, remains constant with fiber stretch. The illuminated fiber volume ΔV decreases with stretch because the fiber diameter decreases. We have accounted for this by multiplying ΔV with a factor which is 1 at $L_s = 2.2$ μm and gradually decreases to 0.75 at $L_s = 3.4$ μm. Lorentz and polarization factors can easily be calculated. The structure factor F_k of a unit cell and its dependence on sarcomere length is the most uncertain factor in Eq. 3.

On the basis of the distribution of structural proteins within a sarcomere, Fujime and Yoshino (1978) have calculated the scattering form factors F_I and F_A for the I and A bands as a function of sarcomere length (see their Figs. 2 and 3). From these a structure factor $F_k = F_{I,k} + (-1)^k F_{A,k}$ can be calculated which we have used to compute theoretical sarcomere length dependences of E_1/E_0, E_2/E_1, and E_3/E_1 (Fig. 3). The absolute value of the calculated E_1/E_0

at $L_s = 2.2$ μm was normalized to the measured value of E_1/E_0, all other values are then determined by Eq. 3. The calculations fit the measured sarcomere length dependence of diffraction efficiencies (Fig. 3) in a qualitatively satisfying manner. This indicates that Eq. 3 together with Fujime and Yoshino's structure factor is an adequate approximation for describing the diffraction process. Quantitative comparison of the two sets of curves shows that the calculated minima and maxima fall outside the standard deviations of our experimental results. Moreover, the absolute value of the calculated third order is too high.

These discrepancies could be the result of insufficient experimental techniques which limit the gathering of all the light along a layer line, in particular of the more widely spread third order. As mentioned before, the structure factor entering Eq. 3 is another point of uncertainty. This is indicated by our results with varied tonicity.

Effects of Varied Tonicity

In hypertonic solution the fiber shrinks and therefore ΔV decreases. In contrast, N increases by the same factor because N is proportional to the reciprocal of the fiber volume. Because the efficiency is proportional to $N^2 \cdot \Delta V$ an efficiency increase should result, but the opposite effect was recorded. Obviously the water loss alters the protein concentrations within the fiber and thus changes the structure factor. An even dehydration of the A and I bands should increase the difference in protein concentrations which should result in increased diffraction efficiency. Thus, our opposite results suggest that dehydration effects A and I band in uneven manner. Perhaps, diminution of diffraction efficiency could be used to determine the degree of hydration of one or the other set of myofilaments.

Intensity Changes during Isometric Contraction

The fast phase of intensity changes observed during isometric contraction might be related to the activation process. More experiments will be needed to clear up this point. As a possible explanation for the intensity decrease during contraction, we propose a modification of Fujime's (1975) suggestion of myofilament displacement. If the myofibrils within a cluster develop slightly different forces, perhaps owing to different activation, the reflecting planes which are reasonably well defined at rest would become distorted. This would resemble a "static" thermic distortion of the reflecting Bragg planes which can be described by the Debye-Waller formalism (e.g., Bragg, 1949, chapter IX). If we assume that while at rest the diffracting units within a cluster possess a certain mean square displacement $\overline{u^2_{\text{rest}}}$ from their ideal lattice position, the real intensity at rest E_{rest} is only a fraction of the ideal intensity E_{ideal}

$$E_{k,\text{rest}} = E_{k,\text{ideal}} \cdot \exp(-16 \cdot \pi^2 \overline{u^2_{\text{rest}}} \cdot \sin^2\theta_k/\lambda^2). \tag{4}$$

During contraction the mean square displacement will increase to $\overline{u^2_{\text{con}}}$ and $E_{k,\text{con}}$ can be described by a similar expression. Dividing the intensity at rest into the intensity during contraction yields the mean increase in displacement $(\overline{u^2_{\text{con}}} - \overline{u^2_{\text{rest}}})$ from

$$\frac{E_{k,\text{con}}}{E_{k,\text{rest}}} = \exp[-16 \cdot \pi^2 \cdot \sin^2\theta_k/\lambda^2 \cdot (\overline{u^2_{\text{con}}} - \overline{u^2_{\text{rest}}})]. \tag{5}$$

From the decrease of E_1 during contraction in the experiment of Fig. 5 a mean displacement of $\simeq 0.45$ μm can be calculated. It seems more plausible that relative displace-

ments of this order of magnitude occur between adjacent myofibrils rather than myofilaments (Fujime, 1975), although fluctuations on the filament level have also been reported (Bonner and Carlson, 1975; Carlson, 1975).

Application of Eq. 5 to E_2 and E_3 yields smaller displacement values of $\simeq 0.25$ and $\simeq 0.20$ μm, respectively. Obviously, as with the previous example of the structure factor, the Debye-Waller formalism is not sufficient to describe all changes in diffraction properties associated with isometric contraction. Changes in intracellular water distribution or in the chemical valency of proteins may have to be considered. Many more experiments will be needed to clear these questions.

We would like to thank Professors Sir A. F. Huxley, W. Wilke, and Dr. J. Krueger for helpful discussions and for criticizing the manuscript. We are grateful to Ms. E. Köster and to Mr. L. Müller for technical assistance.

Received for publication 31 July 1979 and in revised form 15 January 1980.

REFERENCES

BASKIN, R. J., U. P. ROOS, and Y. YEH. 1979. Light diffraction study of single skeletal muscle fibers. *Biophys. J.* **28**:45.

BLINKS, J. R. 1965*a*. Influence of osmotic strength on cross-section and volume of isolated single muscle fibres. *J. Physiol. (Lond.).* **177**:42.

BLINKS, J. R. 1965*b*. Influence of hypertonic solutions on optical diffraction spectra of living striated muscle fibers. *Proc. Int. Union Physiol. Sci.* **6**:334.

BRAGG, L. 1949. The Crystalline State. A General Survey. Reprint with corrections. *G. Bell & Sons, Ltd., London.*

BONNER, R. F., and F. D. CARLSON. 1975. Structural dynamics of frog muscle during isometric contraction. *J. Gen. Physiol.* **65**:555.

BURCKHARDT, C. B. 1966. Diffraction of a plane wave at a sinusoidally stratified dielectric grating. *J. Opt. Soc. Am.* **56**:1502.

BURCKHARDT, C. B. 1967. Efficiency of a dielectric grating. *J. Opt. Soc. Am.* **57**:601.

CARLSON, F. D. 1975. Structural fluctuations in the steady state of muscular contraction. *Biophys. J.* **15**:633.

FUJIME, S. 1975. Optical diffraction study of muscle fibers. *Biochim. Biophys. Acta.* **37**:227.

FUJIME, S., and S. YOSHINO. 1978. Optical diffraction study of muscle fibers. I. A theoretical basis. *Biophys. Chem.* **8**:305.

HUXLEY, A. F. 1974. Muscular contraction. *J. Physiol. (Lond.).* **243**:1.

HUXLEY, A. F., and R. NIEDERGERKE. 1958. Measurement of the striations of isolated muscle fibers with the interference microscope. *J. Physiol. (Lond.).* **144**:403.

KASPAR, F. G. 1973. Diffraction by thick, periodically stratified gratings with complex dielectric constant. *J. Opt. Soc. Am.* **63**:37.

KAWAI, M., and I. D. KUNTZ. 1973. Optical diffraction studies of muscle fibers. *Biophys. J.* **13**:857.

KOGELNIK, H. 1967. Bragg-diffraction in hologram gratings with internal reflections. *J. Opt. Soc. Am.* **57**:431.

MAGNUSON, R., and T. K. GAYLORD. 1977. Analysis of multiwave diffraction of thick gratings. *J. Opt. Soc. Am.* **67**:1165.

RÜDEL, R., and F. ZITE-FERENCZY. 1977. Intensity behaviour of light diffracted by single frog muscle fibres from narrow laser beams. *J. Physiol. (Lond.).* **272**:31P.

RÜDEL, R., and F. ZITE-FERENCZY. 1979*a*. Interpretation of light diffraction by cross-striated muscle as Bragg-reflexion of light by the lattice of contractile proteins. *J. Physiol. (Lond.).* **290**:317.

RÜDEL, R., and F. ZITE-FERENCZY. 1979*b*. Do laser diffraction studies on striated muscle provide evidence for stepwise sarcomere shortening? *Nature (Lond.).* **278**:273.

SU, S. F., and T. K. GAYLORD. 1975. Calculation of arbitrary-order diffraction efficiencies of thick gratings with arbitrary grating shape. *J. Opt. Soc. Am.* **65**:59.

ZITE-FERENCZY, F., and R. RÜDEL. 1978. A diffractometer using a lateral effect photodiode for the rapid determination of sarcomere length changes in cross-striated muscle. *Pflügers Arch. Eur. J. Physiol.* **374**:97.