Reports

Mechanism of Supercontraction in a Striated Muscle Fiber

Abstract. *Cross-striated muscle fibers may contract reversibly to less than 30 percent of their rest length and it is not easy to reconcile this fact with the sliding filament model of muscular contraction. The mechanism of supercontraction has been studied in fibrils obtained from the giant muscle fibers of the barnacle* Balanus nubilus. *They were examined by phase-contrast light microscopy and electron microscopy. Contraction beyond the 50-percent stage was found to be achieved largely by the passage of thick filaments through the Z-disks, which are perforated. The overlap of thick filaments from adjacent sarcomeres causes the appearance of the contraction bands about the Z-disks. Subsequent contraction is associated with a folding and loose coiling, but not a shortening, of the thick filaments.*

Cross-striated muscle fibers show a wide range in their capacity to shorten. Ordinary vertebrate skeletal fibers, representing the mean position, can shorten reversibly by about 40 percent of the *in situ* rest length. At one extreme of the scale of shortening ability are insect flight muscles, which may be able to shorten by no more than 8 percent (*1*). At the other extreme are striated muscles from several different invertebrate phyla which can shorten to as little as 10 percent of rest length (*2*).

The slight degree of shortening found in insect flight muscle is considered to be due to the high A-band/sarcomere length ratio (that is, short I-band length). However, the converse situation, low A-band/sarcomere ratio, cannot explain the extremes of contraction observed. The difficulty arises acutely as a result of the currently accepted model of muscular contraction, which is the sliding filament hypothesis of Huxley and Hanson (*3*) and Huxley and Niedergerke (*4*). On this model, two sets of relatively rigid, interdigitating filaments slide past each other during contraction. Thin filaments are attached to the Z-bands and end in an H-zone at the center of the sarcomere. Thick filaments occupy the A-band. Overlap of thin and thick filaments is regarded as essential for contraction to occur. Even if the overlap is minimal and the I-band length maximal, less than 50-percent shortening is the most that can occur before the thick filaments crash into the Z-bands and the thin ones meet each other.

It is generally considered that at this stage in contraction the thick filaments crumple and the thin ones either crumple or overlap. New bands, termed contraction bands, appear at the Z-lines and in the center of the H-zone (M-lines) as a result of contraction. Such changes can explain a small additional degree of contraction, but they do not help us to explain the enormous extent of contraction found in some muscle.

Recently, giant striated muscle fibers of the barnacle *Balanus nubilus* were found to be capable of great degrees of contraction (*5*). These fibers are beautifully striated, and they have normal relative lengths of A- and I-bands. Hence it was of interest to examine them by light and electron microscopy in the relaxed and contracted states.

Single fibrils were obtained by standard procedures, after mincing whole fibers from glycerinated depressor scutorum muscles and observed by phase-contrast microscopy. By examining fibrils from muscles in different stages of contraction, and by inducing them to contract with adenosine triphosphate, the various stages of contraction could be outlined. These are quite standard, and similar to those observed in other fibrils. The I-bands decrease in length while the A-bands remain at constant length.

With further contraction the I-bands are obliterated and the Z-bands then appear to broaden. At the same time, the A-band lightens. The sarcomere has meanwhile shortened by about 70 percent and increases in diameter to just less than double the original diameter. The band which appears around the Z-band is the contraction band (*C*). A very significant feature of the fibril contracted down to this stage is that the distance between the proximal edge of a contraction band of one sarcomere, and the distal edge of the contraction band of the next sarcomere (*X* in Fig. 1) measured after passing across the nearest Z-band, and the next one in line, is of constant length. Furthermore, this length is equal to the length of the A-band.

The simplest interpretation of this finding is that the A-band is composed of filaments which pass through the Z-disk and do not change in length during this degree of shortening. In Fig. 1 are shown photomicrographs of a relaxed fibril (*A*) and one contracted down to about 30 percent of rest length (*B*). Below each picture is given an interpretation of the contraction. In order that these events may occur, the Z-disks must be perforated or reticular. They appear solid in the light microscope, but the spaces are probably beyond the limit of resolution and in any case may open up only during the stretching which must occur after contraction and consequent thickening of the fiber. Lightening of the A-band can be explained simply on the basis of a reduced optical density consequent upon thickening of the fiber.

The possibility of perforation of the Z-disks and the hypothesis of penetra-

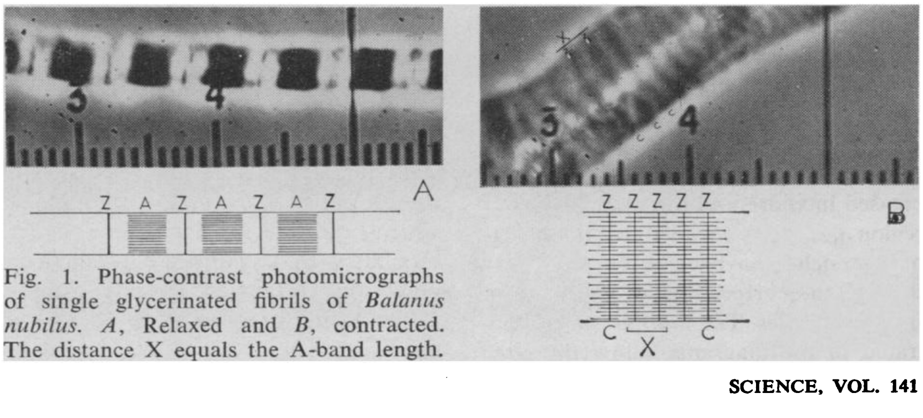

Fig. 1. Phase-contrast photomicrographs of single glycerinated fibrils of *Balanus nubilus*. *A*, Relaxed and *B*, contracted. The distance X equals the A-band length.

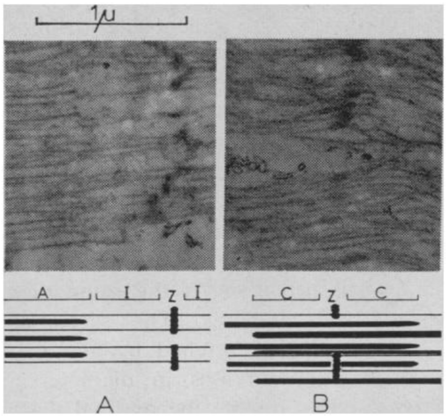

Fig. 2. Electronmicrographs of longitudinal ultrathin sections of *B. nubilus* muscle. (*A*) Partially contracted; the A-band is approaching the Z-band. (*B*) Contracted to the stage at which contraction bands (*C*) appear. The I-bands have disappeared and thick filaments have passed through spaces in the Z-disk into the next sarcomere. The region of overlap of thick filaments forms the contraction bands.

tion of the disk by the A-band filaments, can be tested by electron microscopy. Relaxed and contracted fibers were prepared for electron microscopic examination by osmium fixation and staining, followed by epon embedding and diamond-knife ultrathin sectioning. They were examined in a Siemens Elmiskop I.

In electronmicrographs the Z-bands are seen to be composed of a number of irregular bars about 0.5 μ long and 300 Å thick separated, even in weakly contracted sarcomeres, by spaces. When cut in certain places, the bars are simply transected and appear as large, round particles. Thin filaments are attached to the bars, and pass into the A-bands which are composed of 120-Å thick filaments (Fig. 2*A*). Although there is interdigitation of filaments, the array is not very regular, as it is in rabbit psoas and insect flight muscle. However, a clear zone of thin filaments, corresponding to the I-band region, is seen on either side of the Z-band in the extended and weakly contracted muscle. There are some unfilled spaces in this zone, and these probably correspond to regions opposite the spaces between Z-band bars.

The situation in the contracted fibril is strikingly different (Fig. 2*B*). The spaces between Z-band bars have increased in width and the original I-band region has been invaded by thick filaments. These have come to pass right through the perforations in the Z-bands, from both sides. The mechanism is illustrated in the diagrams below the electron micrographs in Fig. 2. It is evident that the contraction bands are formed by the overlapping of thick filaments passing across the Z-bands from adjacent sarcomeres. Probably not all the thick filaments succeed in finding spaces to go through. These become bent back in their own sarcomere.

In fibers contracted down to below 30 percent, the length referred to above is reduced. Thus there is no further overlap once the thick filaments approach those from the next-but-one sarcomere. They do not themselves shorten, but at this stage the filaments start to bend or to form a loose spiral. The filaments which have gone through the Z-disks are not well-oriented and may take up bizarre positions, becoming bent and pressed back against the Z-band.

These observations provide an explanation for the classically described changes (*6*) which occur in the banding of arthropod muscle during contraction and supercontraction. They also provide a striking confirmation of the sliding filament model of muscular contraction.

They do, however, raise a number of problems regarding the nature of excitation-contraction coupling, and the details of the interaction between filaments (*7*).

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References and Notes

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Indium Telluride Metal

Abstract. *Metallic indium telluride, InTe(II), is metastable up to 125°C at one atmosphere pressure. It has a cubic crystal structure and has a light blue color.*

The indium-tellurium temperature-pressure phase diagram (*1*) which shows a metallic phase above 32,000 bars has led us to attempt to isolate the metallic phase in a metastable state under ordinary laboratory conditions just as we isolated indium antimonide (*2*). This attempt has proven successful. The new metal is metastable to about 125°C, and has properties of considerable general interest. Its x-ray diagram shows it to be a simple cubic structure as reported earlier (*1*). Our parameters are given in Table 1. The lattice spacing is 3.07 Å corresponding to a theoretical density of 6.69 g/cm^3. Our density, directly measured, is slightly lower presumably because of imperfections in the crystalline compact arising from the high pressure preparation.

Indium telluride (I) was prepared by heating In and Te, each 99.999 percent pure, in an atom ratio of 1.000 to 1.000 ± 0.001, in an evacuated quartz tube, while being thoroughly mixed at approximately 100°C above the melting point of the compound (*3*).

Debye-Scherer x-ray diffraction patterns, Fig. 1, of the InTe(I) showed no lines attributable to In or Te above the background, thus indicating that the reaction was at least 98-percent complete.

Our technique for the preparation of metallic indium telluride, InTe(II), was similar to that used for the preparation of the indium antimony metal (*2*)—heating at high pressure to remove nucleation centers, followed by chilling with liquid nitrogen while under pressure, and subsequent pressure release and removal from the pressure apparatus. This metal is more easily isolated than indium antimonide. The latter requires temperatures below −63°C while the indium telluride is metastable at temperatures below about 125°C. X-ray diffraction of metallic indium telluride

Table 1. Lattice spacings of metallic indium telluride, InTe(II). The lattice spacing is 3.07 Å, theoretical density 6.69 g/cm^3, CuKα radiation.

h k l	*d* (Å)
100	3.056
110	2.174
111	1.773
200	1.536
210	1.374
211	1.255