appears that lymphocytes possess a specific mechanism that is based on some kind of interaction with mesothelial cells and results in the formation of basal lamina-bound passageways of the exact size of the traversing cells. Conceivably, this mode of cooperation with mesothelial or endothelial cells also enables lymphocytes to cross tissue barriers in vivo. Further studies with the yolk sac model may contribute to a better understanding of the dynamic interaction of migrating cells and the extracellular matrix.

1 M.-F. Maignan, Biol. cell., in press.
2 G. Haemmerli and H. Felix, Leukemia Res. *1*, 79 (1977).
3 G. Haemmerli, H. Felix and P. Sträuli, Virchows Arch. B, Cell Path. *20*, 143 (1976).
4 H. Felix, G. Haemmerli and P. Sträuli, in: Dynamic Morphology of Leukemia Cells, p. 8. Springer-Verlag, Berlin/Heidelberg/New York (1978).
5 G. Haemmerli and P. Sträuli, Virchows Arch. B, Cell Path. *29*, 167 (1978).
6 S. Wood, Jr, Arch. Path. *66*, 550 (1958).
7 F.S. Steven and S. Itzhaki, Biochim. biophys. Acta *496*, 241 (1977).
8 M.K. Dabbous, A.N. Roberts and B. Brinkley, Cancer Res. *37*, 3537 (1977).
9 C. Biswas, W.P. Moran, K.J. Bloch and J. Gross, Biochem. biophys. Res. Commun. *80*, 33 (1978).

Sarcomere shortening and tension development during 'isometric' tetanus of muscle[1]

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Summary. Laser diffraction and tension measurements from frog muscle during isometric tetanus reveal that the sarcomeres contract more rapidly than tension develops.

During muscle activation sarcomeres contract in response to the cycles of attachment, force-generation and detachment of crossbridges unless the muscle is kept strictly isometric[2]; this is only possible by the use of a servo-system such as the spot-follower[3]. In a nominally isometric experiment the sarcomeres may contract by as much as 5%, depending upon the compliance of the end-tissues and the mountings, until the tetanic level of tension is established. We have used an optical technique to measure the changes in sarcomere length of a frog sartorius muscle throughout the development of tetanus and also in the subsequent relaxation. By taking measurements at successive points along its length we obtained an average sarcomere contraction for the whole muscle and compared this with the corresponding development of tension.

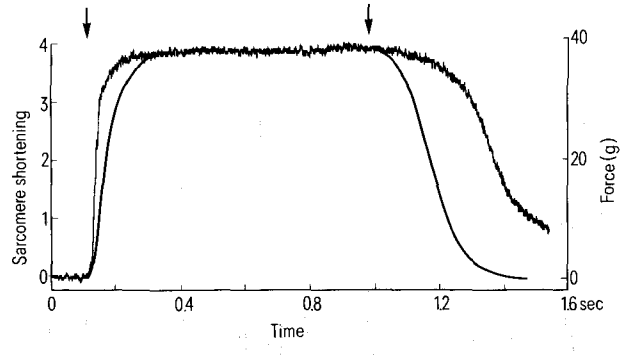
Methods. The essentials of the experimental system have been outlined elsewhere[4,5]. An He-Ne laser is directed normally on a muscle specimen and the angular spacing of the first-order beams is sampled at 420 µsec intervals by chopping them with a rotating slotted disk. The sarcomere length at any instant is calculated from a knowledge of the system geometry and the time interval between the outputs of 2 photodiodes on which the 2 diffracted beams fall. Systematic noise is removed using a Hewlett Packard 2100S computer which also provides digital data every 420 µsec. Successive experiments were carried out, traversing the muscle length in 1 mm steps (approximately the diameter of the laser beam) in order to obtain sarcomere length records from all regions of the specimen. Each region provided a digital data file that was used to produce a summed and averaged data file equal to the total length change of all sarcomeres in the muscle occurring in response to the applied supramaximal stimulus. Tension was recorded using a Harvard 363 transducer.

Results. The summed and averaged response of sarcomeres from the full length of a frog sartorius is shown in the figure together with the tension record. The stimulus pulses commenced 100 msec after the computer began collecting diffraction data for noise reduction purposes. On the plateau of the sarcomere length record no sarcomere oscillation can be seen within a resolution of 2 nm, i.e. if periodic oscillations were present, their amplitude was less than 0.1%.

The figure also shows that the sarcomere length change procedes more rapidly than the development of tension. For instance the half-maximum of contraction is reached approximately 16 msec ($\Delta t_{1/2}$) before the half-maximum of tension. There is an even greater difference between the time-course of force and contraction following the cessation of stimulation. The sarcomeres expand much more slowly than the rapid fall in tension, reaching their half-maximum value some 200 msec after the tension. The sarcomere length in this 24 mm long muscle was 2.2 µm at rest, whilst the tension in full tetanus was 0.36 N. The temperature was controlled at 5 ± 0.25 °C.

Discussion. The variations in slope of the sarcomere shortening curve in the figure show that the sarcomeres start to contract at about the same time as tension starts to develop. By about 20 msec after the initial stimulus they reach their maximum rate of contraction ($250 \pm 50\%$ sec^{-1}) which remains constant for approximately a further 20 msec. This rate is substantially the same as V_{max}, the maximum velocity that can be generated when a frog muscle at this temperature contracts against zero load[5].

At the end of this period of maximum contraction velocity the tension has reached only about 20% of its full tetanic



Average sarcomere shortening and tension developed in frog sartorius muscle throughout tetanus at 5 °C. Length and force scales have been chosen to assist in making comparisons. Arrows indicate the beginning and the end of the stimulating train of 40 V 200 µsec pulses.

value (P_o) but it is increasing rapidly. At this stage the increase in stiffness closely follows the increase in tension after correcting for the compliance of the external connective tissue[6]. As tension rises to P_o the sarcomere contraction velocity falls and values derived from the figure show that a conventional (A.V. Hill-type) hyperbolic force-velocity relationship is applicable even in this non-steady state situation of developing tetanus.

Recent high time-resolution X-ray diffraction experiments have shown that the proportion of crossbridges that have moved out to the actin filaments during tetanus[7] and twitch[8] also increases more rapidly than the tension ($\Delta t_{1/2} = 15$ and 30 msec resp. at 0–2 °C). It appears that most of the sarcomere shortening is complete and most of the tetanic crossbridge attachments are made before the tension has reached more than 80% of its final value. The smallness of the further shortening as the remaining tension is built up reflects the high non-linearity of the muscle system – particularly the tendon at either end which stiffens by several orders of magnitude as the full tetanic tension is developed.

That the time course of the 1,1 and 1,0 X-ray diffraction reflections is paralleled by the time course of sarcomere contraction before tension develops may in part be ex plained by the fact that sarcomeres shorten at the expense of elastic elements including tendon. Thus actin and myosin filament overlap increases more rapidly than if the muscle was held rigidly isometric during the development of tension.

The behaviour after stimulus ceases appears paradoxical but is explained by heterogeneity in the muscle. As activity decreases the sarcomeres which weaken first expand abruptly allowing the rest of the muscle to contract further; this has been observed both directly[4,9] and indirectly[10]. The net effect is for the average sarcomere length to decrease only slightly while the tension falls quite steeply, as seen in the figure.

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2 A.F. Huxley, J. Physiol. *243*, 1 (1974).
3 A.M. Gordon, A.F. Huxley and F.J. Julian, J. Physiol. *184*, 143 (1966).
4 J. Borejdo and P. Mason, J. Mechanochem. Cell Motil. *3*, 155 (1976).
5 J.A. Barden and P. Mason, Science *199*, 1212 (1978).
6 P. Mason, Biophys. Struct. Mechanism *4*, 15 (1978).
7 H.E. Huxley, Int. Conf. Fibrous Proteins, Massey University, New Zealand 1979. Academic Press, New York, in press 1979.
8 I. Matsubara and N. Yagi, J. Physiol. *278*, 297 (1978).
9 H. ter Keurs, T. Iwazumi and G.H. Pollack, J. Gen. Physiol. *72*, 565 (1978).
10 A.F. Huxley and R.M. Simmons, J. Physiol. *210*, 32P (1970).

The non-inheritance of the direction of foliar spiral in coconut

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Summary. The leaves on a coconut crown are arranged in 5 spirals, all running clockwise in one palm, and counter-clockwise in another. The 2 types of palms in any plantation are distributed more or less equally. Data on the foliar spirality of the progeny obtained by different kinds of parental matings clearly show that the direction of foliar spiral in the coconut is not genetically determined. Additional data presented on 7860 palms show that the left-spiralled ones are in excess of the right-handeds.

The leaves of the coconut (*Cocos nucifera* L.) are produced one after another (spiral phyllotaxis), the angle of deflection between any 2 consecutive leaves being about 138 degrees[2–9]. By following the production sequence of leaves, one can trace out a single spiral in a crown which is the genetic spiral. In addition to this, there are 5 clearcut spirals running opposite the single genetic spiral. In this communication we always refer to the 5 obviously visible spirals. All the 5 spirals in one crown veer clockwise and in another, counter-clockwise[2,6,7]. There are also other ways of determining the direction of foliar spirals. If in a palm the spadix appears on the right side of its supporting leaf, the foliar spiral is left-handed. In a tree where the bunch appears on the left side of leaf, the palm is right-handed. The figure shows the 2 kinds of palms. On the basis of limited data relating to only 205 progeny of 4 pollen parents and 24 seed parents, Davis[2] reported that the direction of foliar spiral in the coconut is not determined genetically. At the research farms of the Industrial Crops Research Institute, Manado, there are large collections of parent palms and their progeny raised through different kinds of pollination. Some 25 years ago, A.F. Ihne and his colleagues effected controlled cross pollination between 41 selected palms (now about 52 years old) at the Mapanget Farm involving 49 parent-combinations. The foliar spirals of all the parents and the surviving 1023 progeny (now about 22 years old) at the Kima Atas Farm were checked and the data given in table 1.

As seen from the data in the table 1, 53.96% of the total progeny are left-spiralled. When we look for an association

Table 1. *Cocos nucifera:* Foliar spiralities of parents and progeny

Parent-combinations	No. of combinations	Progeny Lefts	Rights	(L+R)	(L−R)
Left ♀ × left ♂	14	156	164	320	−8
Left ♀ × right ♂	13	150	130	280	20
Right ♀ × left ♂	10	131	89	220	42
Right ♀ × right ♂	12	115	88	203	27
Total	49	552	471	1023	81