words such as desertification, desertization and aridization.

Irrigated lands in arid to semi-arid climates which have increased water tables and/or direct salt input from the irrigation water eventually support lowered crop production. Even some originally forested lands in southern Australia develop such problems when the high transpiration draw-downs affected by the forest are eliminated after tree removal. The only plants that can grow on some of the most heavily salinized former farm- or forestlands are shrubs normally found in desert regions. The soil moisture is excessive, but the soils are physiologically dry to non-desert species. The term xerification would more usefully describe these processes than the narrow word salinization.

Clearly it will be difficult to distinguish natural xerification from that induced by man. But palaeoecological evidence shows that deserts are relatively young ecosystems on all continents, and thus have arisen naturally. Therefore it is important to elucidate natural, as well as man-made, mechanisms. □

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Muscle contraction

Crossbridges, force and motion

from Richard T. Tregear

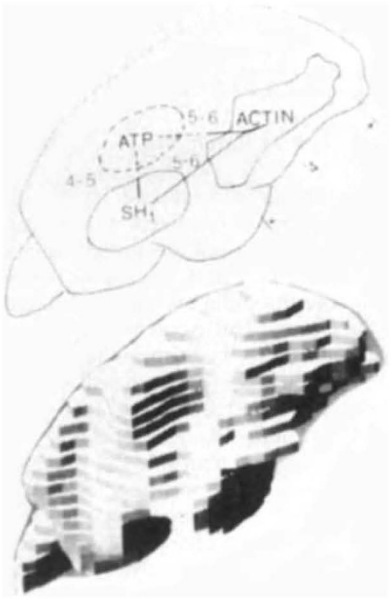
THE basic question that concerns those interested in crossbridges is 'what makes muscle pull?'. Many different answers have been suggested over the years. Some simple and elegant experiments described at a recent workshop* exclude several of them. Other experiments place constraints on the part of the myosin head (or crossbridge) responsible for the generation of force consequent on ATP hydrolysis. The picture which emerges is of a crossbridge (which projects from the thick filament of muscle fibres) that can easily attach and detach from actin (in the thin filament) in the first part of the enzymatic cycle and then 'harden' its attachment and produce force in the later part of the cycle. The contractile process occurs in the middle of the myosin head, does not need the other head of the myosin molecule, much of the tail region of the molecule or even, perhaps, the light chains of the head itself. The process probably involves only a small change in the shape of the head, is reversible and can sometimes couple to a huge interfilament movement. Altogether this picture is not very like the usual undergraduate idea of crossbridge rotation and force production.

The evidence for these statements comes from a wide variety of approaches. The idea of the rapidly attaching weak-binding crossbridge comes from enzymatic studies (E. Eisenberg, NIH), and fits both with the way in which measurements of crossbridge attachment by X-ray diffraction (H. Huxley, Cambridge; K. Wakabayashi, Osaka) and mechanical stiffness (R. Simmons, London) are seen to rise before tension during activation and with the large number of disorganized myosin heads still seen by electron proton resonance (EPR) when a muscle is contracting strongly (D. Thomas, Minneapolis). On the other hand, the strong-binding, tension-generating state may be best seen by electron microscopy of muscle in rigor (M. Reedy, Duke); at any rate, no regular crossbridge angle other than that of rigor (thought to represent the maximal force-producing state) has been detected by EPR or polarized fluorescence in actively contracting muscle.

The resolution of immuno-electron microscopy is now good enough to divide the myosin head into a regulatory neck and an operative body, and within that body to locate the three regions most likely to transfer energy across it: the nucleotide- and actin-binding regions and the interlinking part close to the active thiol residue (T. Wakabayashi, Tokyo; see figure). Furthermore, both the sequence near the thiol and the purine-binding sequence have turned out to be highly conserved, being invariant from slime mould to rabbit, as if they perform an essential function (J. Spudich, Stanford).

Optical microscopy has now improved to such an extent that one can see the motion of unrestrained actin filaments over myosin, or of particles coated with myosin over actin (Spudich; T. Yanagida, Osaka). Such motion occurs even when the myosin is single-headed or its tail is greatly reduced in length. These experiments appear to eliminate contractile mechanisms dependent on either head–head interaction[1] or a change in tail structure[2].

Chemists have managed to attach a photolysable group to ATP (caged ATP) that can be diffused into muscle before lysis releases the ATP itself[3]. The resultant synchronized events indicate that phosphate release and tension generation occur together and that both processes are reversible (Y. Goldman, Philadelphia). It follows that tension can be regenerated without coupled ATP hydrolysis, which was not envisaged in earlier ideas of the crossbridge cycle[4].



Location of the ATP-binding and reactive thiol (SH_1) sites on the surface of the myosin head (top), determined from avidin binding and three-dimensional reconstruction of the actin-myosin head complex (bottom). ATP binds to the back of the head. Units, nm. (Courtesy of M. Tokunaga, A. Tomioka, C. Toyoshima, K. Sutoh, K. Yamamoto & T. Wakabayashi, unpublished observations.)

An ingenious argument was presented from a couple of conceptually simple experiments. If actin is proteolytically cut loose in a myofibril or if myosin heads are floated into a brush of actin filaments, they remain still until ATP is added and then they move, quite rapidly. Yanagida measured the speed of motion and the rate of ATP hyrolysis and deduced that each crossbridge stroke using ATP moves the myosin molecule by at least 60 nm, which is too far for the crossbridge to stretch[5,6]. Is there something wrong with Yanagida's logic, or with the crossbridge theory itself? □

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* Workshop on the interaction between actin and myosin in skeletal muscle held at Alpbach, Austria, 17-22 March 1986. Supported by the European Molecular Biology Organization and the Muscular Dystrophy Association of America.