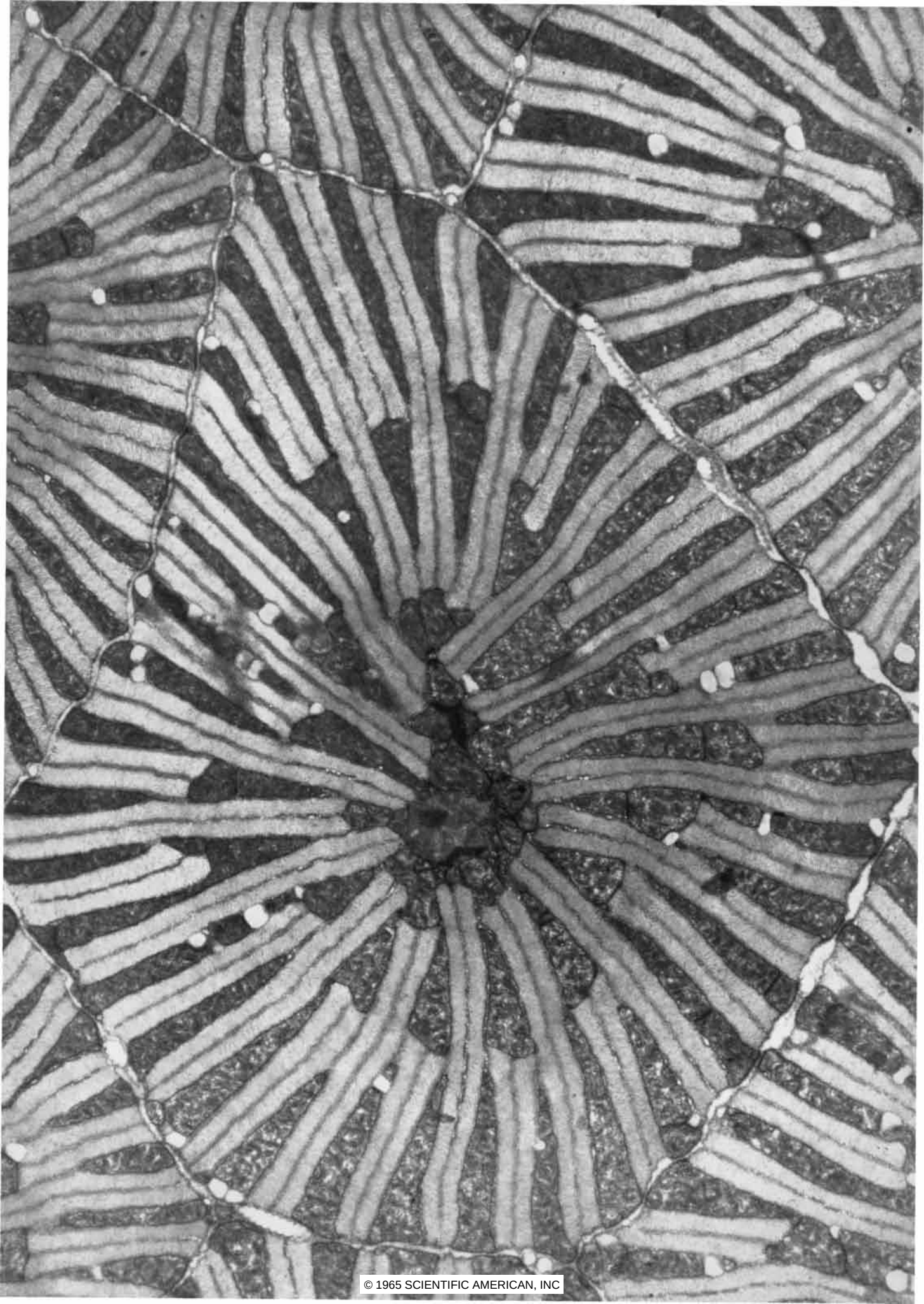

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The Flight Muscles of Insects

The wings of some insects beat hundreds of times per second. The two kinds of muscle that power insect flight give clues to the operation of muscle throughout the animal kingdom

by David S. Smith

The voluntary muscles of almost all animals have an important feature in common: a single nerve impulse gives rise to a single response from a muscle. A significant exception is apparent in the flight of certain insects: their wings can beat many times faster than the most rapid rate at which a muscle responding to a series of nerve impulses can alternately contract and relax. Weight for weight the flight muscle of such insects generates more energy than any other tissue in the animal kingdom, and numerous investigators have attempted to find out how it does so. Before I relate some recent developments in the field the reader may find it helpful to have a few pertinent facts about the evolution of insects and about the study of muscle in general.

Some 350 million years ago—during the Devonian period or perhaps the early Carboniferous—the distant ancestors of today's insects made their first evolutionary experiments with flight. So far the fossil record has not revealed what type of insects these were nor what they looked like, but most students of the matter agree that the first advance was probably the appearance in some insects of stationary horizontal fins that enabled them to glide through the air. These gliding insects were superseded by the true winged insects, whose fins were larger and could be moved up and down around the point at which they joined the body.

Insects of course have an external skeleton, and they move by means of muscles that act on jointed parts of this more or less rigid shell. As insects evolved movable wings they also had to develop muscles to power them; it is believed that at first certain muscles of the legs and body wall were called into service. Insects, however, are highly diversified, and the various orders of flying insects exhibit many different mechanisms of flight. Everyone is familiar with the differences represented by the dancing flight of a butterfly, the hovering flight of a dragonfly and the remarkably maneuverable flight of the housefly and the honeybee.

It is insects of the last kind—the housefly and the honeybee—that are among those whose wings beat at a high rate. This can readily be perceived, but it was not until 1949 that the flight muscle of such insects was recognized as being physiologically unique. In that year J. W. S. Pringle, who was then at the University of Cambridge, was studying the main flight muscles of the blowfly. He observed that nerve impulses arrived in the muscles at a rate that was similar to the rate of nerve impulses arriving in other muscles, but that this rate was much slower than the rate at which the insect's wings beat. Earlier workers had found that cutting off portions of flies' wings had the effect of speeding up the beat; Pringle suggested that the rate of beat was determined not by the nerve impulses but by the load—in terms of wing area—imposed on a natural rhythm that was produced within the flight muscles themselves.

Later studies by Pringle, by Edward G. Boettiger of the University of Connecticut and by Kenneth D. Roeder of Tufts University showed that flight muscles of this kind are found in insects of only four of the 30 or so recognized insect orders: the beetles (Coleoptera); the wasps and bees (Hymenoptera); the flies, mosquitoes and similar forms (Diptera), and certain true bugs (Hemiptera), including the aphids. Because such muscle contracts and relaxes at a much higher rate than the nerve signals it receives it is called asynchronous muscle; the flight muscle of other insects contracts and relaxes in exact response to nerve signals (as do the skeletal muscles of vertebrates) and is therefore called synchronous.

A few examples will make clear just how extraordinary the performance of asynchronous muscle is. O. Sotavalta of the University of Helsinki has measured the wingbeats of many insects; the wings of the swallowtail butterfly, for instance, oscillate through five cycles per second and those of the dragonfly through 35 cycles per second. Both insects have synchronous flight muscles; indeed, these frequencies are within the range of performance of vertebrate skeletal muscles. Among the insects with asynchronous flight muscles, beetles beat their wings at frequencies between 55 and 175 cycles per second, the honeybee at frequencies between 208 and 247 cycles and the mosquito at frequencies as high as 587 cycles. One midge (*Forcipomyia*) attains the almost incredible rate of 1,046 cycles per second. The special tissue that powers this sort of performance has been of great importance in the evolution of body shape and wing size in the insects that possess it; synchronous muscle can drive the large, lightly loaded wings of the butterfly but would be quite unable to lift the relatively bulky, small-winged body of a fly or bee.

Toward the end of the 19th century,

FLIGHT MUSCLE of a damselfly is shown enlarged 9,000 diameters in the electron micrograph on the opposite page. The cells are seen end on; the individual fibrils in which contraction takes place form a radial array (*light areas*). Between them are mitochondria (*dark areas*) that furnish the required power. Oblong fibrils are typical of primitive synchronous muscle, the less energetic of the two kinds of flight muscle.

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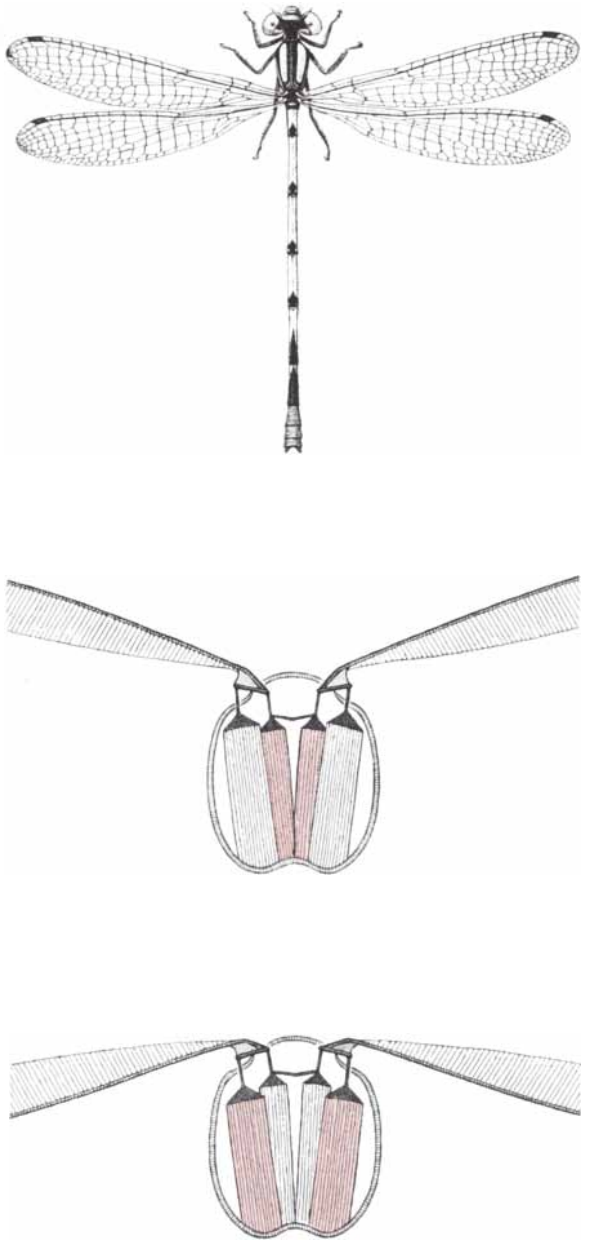
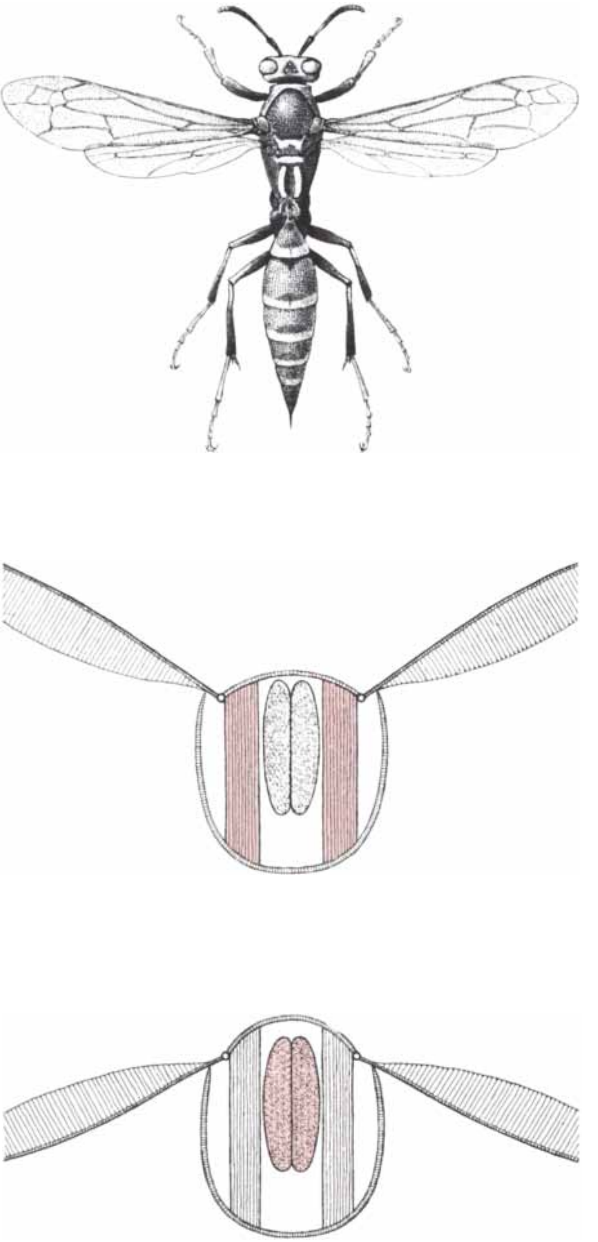


SYNCHRONOUS FLIGHT MUSCLE distinguishes all but four orders of insects; illustrated is a damselfly of the genus *Enallagma*. As the first thorax section shows (*middle*), contraction of an inner pair of muscles, applying force to a lever-like portion of the wing base, raises the wings. Then a more robust outer pair of muscles contracts to provide the downward power stroke (*bottom*). The muscles are called synchronous because each contraction is in response to a separate stimulus from the central nervous system.



ASYNCHRONOUS FLIGHT MUSCLE has evolved among bees and wasps, flies and mosquitoes, beetles and some bugs; shown here is a wasp of the genus *Polistes*. The muscle arrangement is antagonistic: the outer bundles contract vertically and the inner ones horizontally. Both do so alternately and in an oscillatory fashion. The contractions deform the wasp's thorax so that the wings are driven up (*middle*) and then down (*bottom*). This cycle is much faster than the nerve-signal rate, hence the muscle is called asynchronous.

when ideas about the structure of muscle almost equaled the number of investigators interested in the matter, it was realized that vertebrate skeletal muscle, in contrast to "smooth" muscle such as that of the vertebrate intestine, is "striated." This is to say that each of the many fibers, or cylindrical cells, comprising such muscle appears regularly striped or banded when it is viewed in the light microscope. These striations are present whether the fiber is living or has been fixed and sectioned; moreover, their pattern changes during the cycle of contraction and relaxation. There were various interpretations of what the striations meant. Some investigators thought they were part of a contractile network embedded in a gelatinous ground substance; others held that the ground substance alone was able to contract.

At that time insect muscles were widely examined in the microscope as a convenient tissue for the study of muscle. The German anatomist Anton Kölliker showed in 1888 that the individual cells of some insect flight muscles could be teased apart into tiny fibrils, or cylindrical subunits, each with a diameter of about two microns (.002 millimeter). The fibrils too were banded; when they were lined up side by side, they pre-

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sented the characteristic striped appearance of the whole fiber. Kölliker also observed small spherical objects in the sarcoplasm: the fluid-filled space between the individual fibrils of the muscle cell. These spherical bodies, named sarcosomes, took up stains and dyes in the same way another cellular subunit did; this was the rodlike mitochondrion, which microscopists were then discovering in many types of cells. The two later proved to be identical.

These early observations with light microscopes go a fair way toward providing a basic model of striated muscle. Whether the muscle is vertebrate or invertebrate, each cell is a cylinder containing contractile fibrils in a sarcoplasmic matrix. In recent years, however—particularly during the past decade—biologists have been able to refine the model by using the electron microscope, which of course provides far higher magnification and resolution than the light microscope. Electron microscopy has made it possible to describe the structures within the muscle cell in considerable detail and has contributed much to modern theories of muscle contraction and relaxation and of the processes by which energy is supplied to the contractile mechanism.

On the basis of electron-micrograph studies H. E. Huxley of the University of Cambridge and Jean Hanson of King's College have developed the now generally accepted model of vertebrate muscle-fibril structure and function [see "The Contraction of Muscle," by H. E. Huxley; SCIENTIFIC AMERICAN, November, 1958]. They found that the fibril subunit was itself composed of subunits; cross-sectional micrographs looking, as it were, at the fibrils from the side reveal that each fibril is made up of two overlapping sets of filaments. The filaments of one set are thick and those of the other are thin; cross-sectional micrographs looking at the filaments from the end show that they lie together in a hexagonal array [*see illustration on this page*]. The thick filaments are made up of the protein myosin; the thin ones, of the protein actin. Huxley and Hanson propose that a muscle fibril contracts and relaxes not by any change in the length of its constituent filaments but by the fact that two sets of filaments slide past each other. The energy required for the sliding process is provided by adenosine triphosphate (ATP), and the utilization of this molecule within the fibrils during contraction requires the presence of calcium ions.

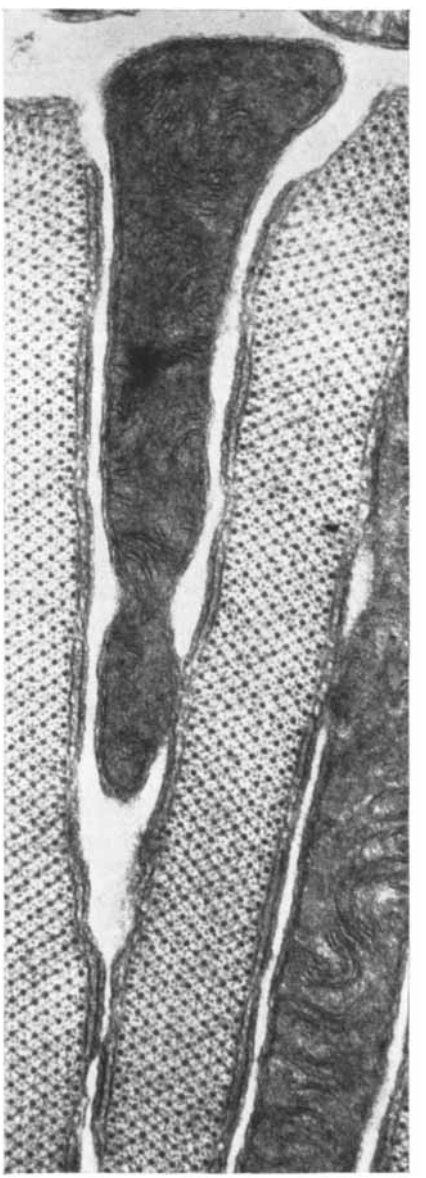
The contraction of a muscle cell is preceded by a chain of events, the first of which is the arrival of a nerve impulse at one or more localized regions where the endings of motor nerves are quite close to the muscle cell's thin surface membrane. A transmitter substance is released from the nerve ending into the narrow gap between the membranes of nerve and muscle; it initiates a wave of electrical activity—a loss of electrical polarity by the muscle membrane—that spreads over the whole fiber. A few milliseconds after the nerve impulse has arrived at the surface of the muscle cell the cell starts to contract.

This is only part of the story, and yet even this part presents an acute problem. Some 15 years ago A. V. Hill of the University of Cambridge pointed out a paradox: the response to electrical depolarization is so swift that even the fibrils farthest from the surface of the muscle cell begin to contract before it seems possible for any substance to have diffused inward from the depolarized surface membrane. The solution to this paradox was to remain unknown for more than a decade.

As I have indicated, in vertebrate muscle each nerve impulse gives rise to a single contractile event. In "fast" muscles (muscles that are able to contract and relax quickly) the event is a discrete twitch; in "slow" muscles successive impulses advance the contraction in a stepwise manner. A fast-muscle cell has only one junction with a nerve fiber; a slow-muscle cell has several junctions.

With these facts as background, the similarities and differences between vertebrate and insect muscle can now be examined. All insect muscle fibers resemble the "slow" fibers of vertebrates in having several nerve-muscle junctions rather than one. Electron micrographs of insect muscle show that the structure of these synapses between nerve and muscle is similar to that in vertebrates: the end of the axon—the elongated portion of the nerve cell—is in close contact with the membrane of the muscle cell and contains concentrations of vesicles, or minute sacs. Bernhard Katz of University College London and his co-workers have advanced the hypothesis that these synaptic vesicles hold "packets" of a transmitter substance that in the case of vertebrate synapses has been identified as acetylcholine. Although it is not definitely known what the insect transmitter substance is, it seems safe to infer that insect and vertebrate nerve endings have a common mechanism of transmitter-substance release.

The damselfly *Enallagma*—a familiar fluttering insect of streams and lakesides—provides an example of synchronous insect flight muscle in action. The insect's thorax, or mid-body, is divided into three segments; its flight apparatus consists of two pairs of wings, one pair mounted on the middle thoracic segment and the other on the rear segment. The segments are almost completely filled with the muscles that beat the wings [*see illustration at left on opposite page*]. Each muscle is made up of many separate fibers packed tightly together; each fiber is between 20 and 30 microns in diameter, a size common in vertebrate muscle. A low-power electron



FIBRIL SUBUNITS lie in a geometric array; the large dots are filaments of the protein myosin, the small are actin. These fibrils, seen end on and enlarged 50,000 diameters, are from dragonfly flight muscle.

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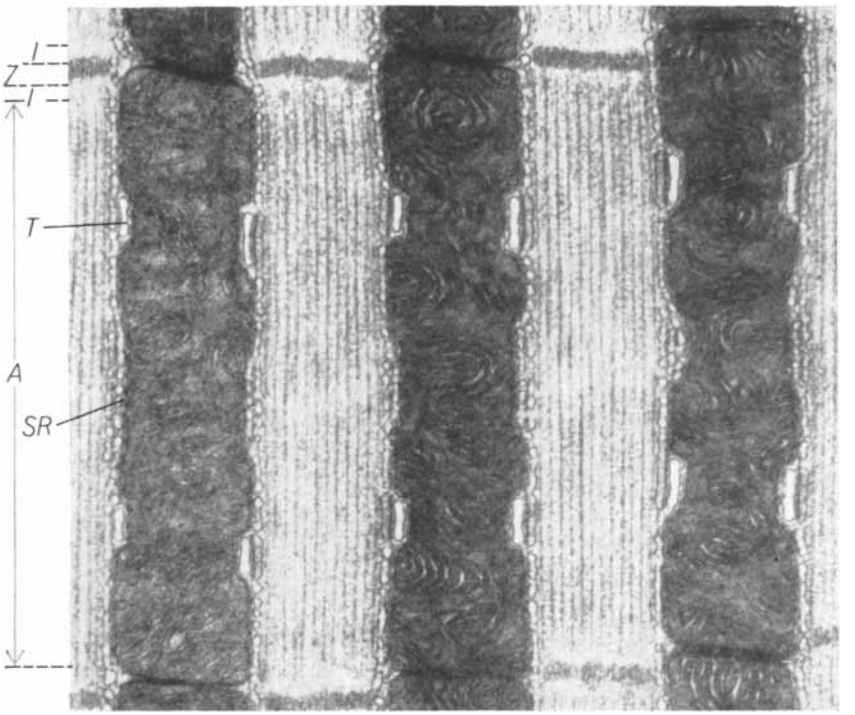
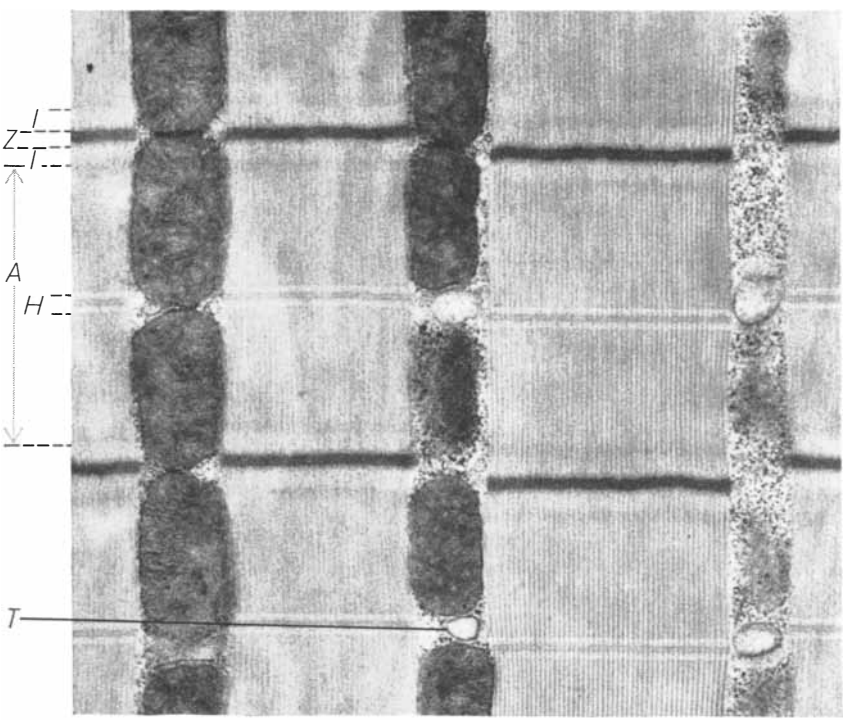


SYNCHRONOUS MUSCLE, seen in longitudinal section enlarged 40,000 diameters, shows the subunits of muscle cells along their long axes, bounded at each end by dark transverse "*Z* lines." These lines are flanked on both sides by narrow, light "*I* zones," whereas the bulk of each subunit is composed of a wide, medium-density "*A* band." One of the tubules comprising the "transverse" system of ducts is labeled *T*; *SR* identifies the chains of vesicles making up the sarcoplasmic reticulum that separates fibril from adjacent mitochondrion.



ASYNCHRONOUS MUSCLE, also in longitudinal section but enlarged only 16,000 diameters, contains subunits similarly bounded by dark *Z* lines flanked by narrow *I* zones. Each broad *A* band, however, is bisected by an "*H* zone" that is precisely aligned with the tubules of the transverse duct system (*most clearly visible among the mitochondria at center and right*). One major difference between this and synchronous flight muscle is the virtual absence of sarcoplasmic reticulum vesicles (*see illustration on opposite page*).

micrograph of these fibers in transverse section shows the striking arrangement of their contents: the sheetlike contractile fibrils form a radial array and alternate with dense mitochondria [*see illustration on page 76*]. At higher magnification the fibril structure is further resolved into its thick and thin filaments of myosin and actin, arranged in a hexagonal lattice. The radial arrangement of the sheetlike fibrils in damselfly flight muscle is typical of the leg and body muscles of insects in general, which are also synchronous.

There is a correlation between the metabolic activity of a muscle fiber and the number of mitochondria within it; these bodies house the enzymes that manufacture the ATP molecules necessary for muscular contraction [see "The Mitochondrion," by David E. Green; SCIENTIFIC AMERICAN, January, 1964]. One of the characteristic features of insect flight muscle, which is metabolically the most active insect tissue, is that it contains large numbers of mitochondria. As an example, although the damselfly has preserved in its flight muscle the primitive radial pattern of fibrils evolved in leg and body muscle, there is a great difference between the two kinds of tissue: to cope with higher metabolic demand the flight muscles have been much more abundantly endowed with mitochondria. Whether synchronous or asynchronous, however, most insect flight muscle has departed from the radial pattern of fibril organization; instead the contractile part of the fiber is divided into fibrils that are circular when seen in transverse section. Butterfly flight muscle, for example, contains cylindrical fibrils about which large mitochondria are wrapped [*see bottom illustration on page 82*].

One of the contrasts between insect and vertebrate muscle involves their provision for the supply of oxygen (and the removal of carbon dioxide). In vertebrates oxygen reaches all the organs in chemical combination with hemoglobin, the respiratory pigment of the red blood cells; in vertebrate muscles blood capillaries are located between the fibers. In insects the situation is different: the fluid hemolymph in the insect's body cavity contains no respiratory pigment. Instead atmospheric oxygen diffuses to the cells throughout the insect's body by way of a branching system of tubes—the tracheae—that are open to the exterior. The finest branches of this ramifying system are called tracheoles; they are present most abun-

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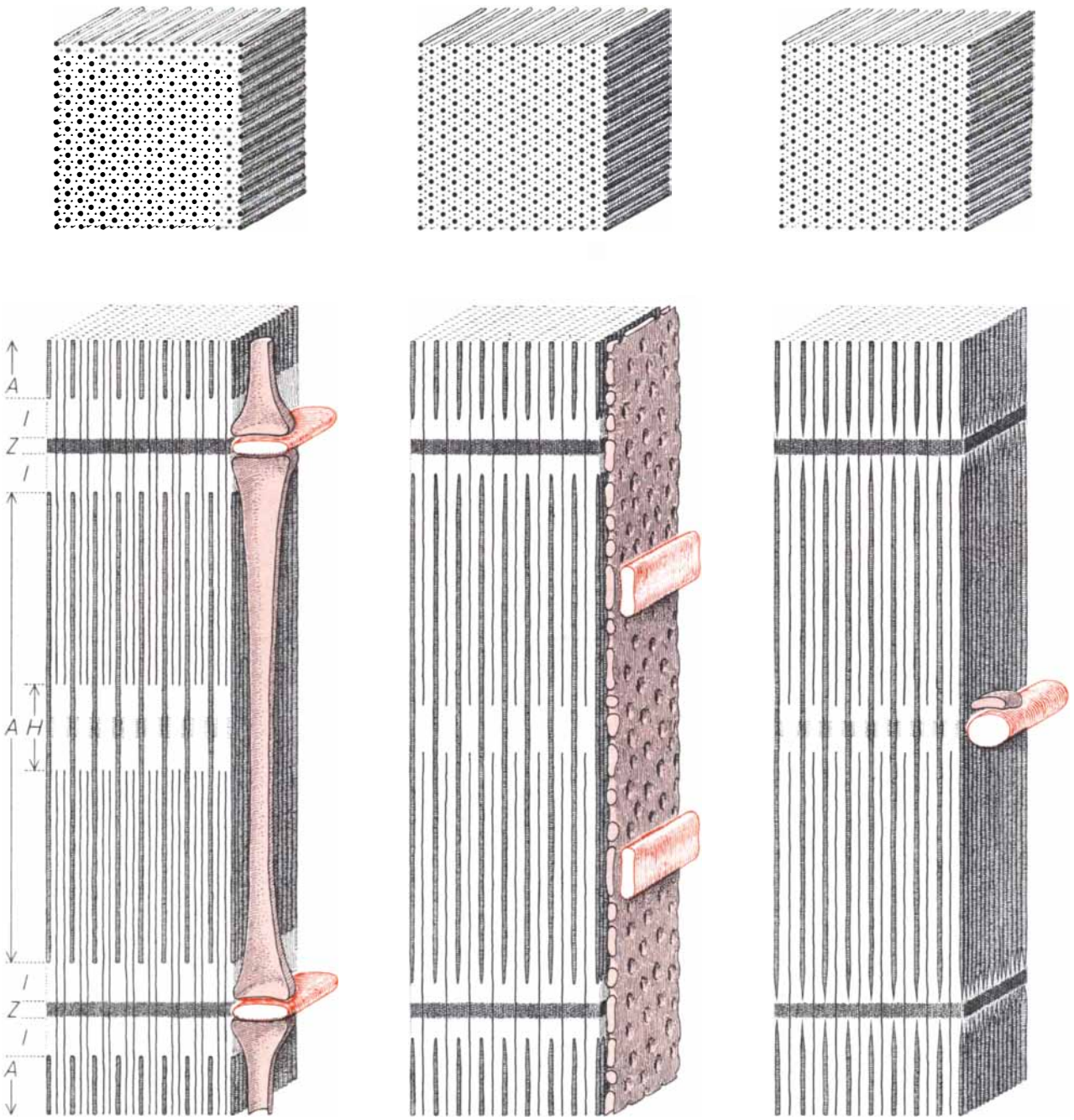
dantly in the organs that have the highest oxygen requirement—notably the flight muscles. Insect leg muscles (and flight muscles such as those of the damselfly, in which the diameter of the muscle fiber is rather small) are equipped with tracheoles that pass between the fibers as the capillaries in vertebrate muscle do; the oxygen simply diffuses inward from the surface of the fiber. In most insect flight muscles, however, the tracheolar system brings the oxygen much closer to the mitochondria by passing deep into the fibers, rather like fingers pushed into a toy balloon. (The tracheoles do not actually penetrate the muscle fiber; they are sheathed in the muscle cell's thin external membrane.) The result of this arrangement is that oxygen does not have to diffuse across the entire radius of the flight muscle



THREE KINDS OF MUSCLE are compared schematically at the level of fibril structure. At left is a vertebrate fibril; in center, an insect synchronous fibril; at right, an insect asynchronous fibril. The forward face of the cube above each of the longitudinal sections shows the hexagonal pattern formed by the filaments of myosin and actin when viewed in transverse section. The zones and lines that give muscle fiber its characteristic striated appearance are labeled at left. Asynchronous muscle is structurally different from the other kinds in two major respects. The tapering ends of its myosin filaments appear to reach almost to the *Z* line; actin filaments alone occupy the *I* zones bordering the *Z* line in other relaxed muscles. Although asynchronous muscle contains *T*-system tubules (*color*) as do other muscles, the membrane linked to fibril relaxation, the sarcoplasmic reticulum (*tint*), is greatly reduced.

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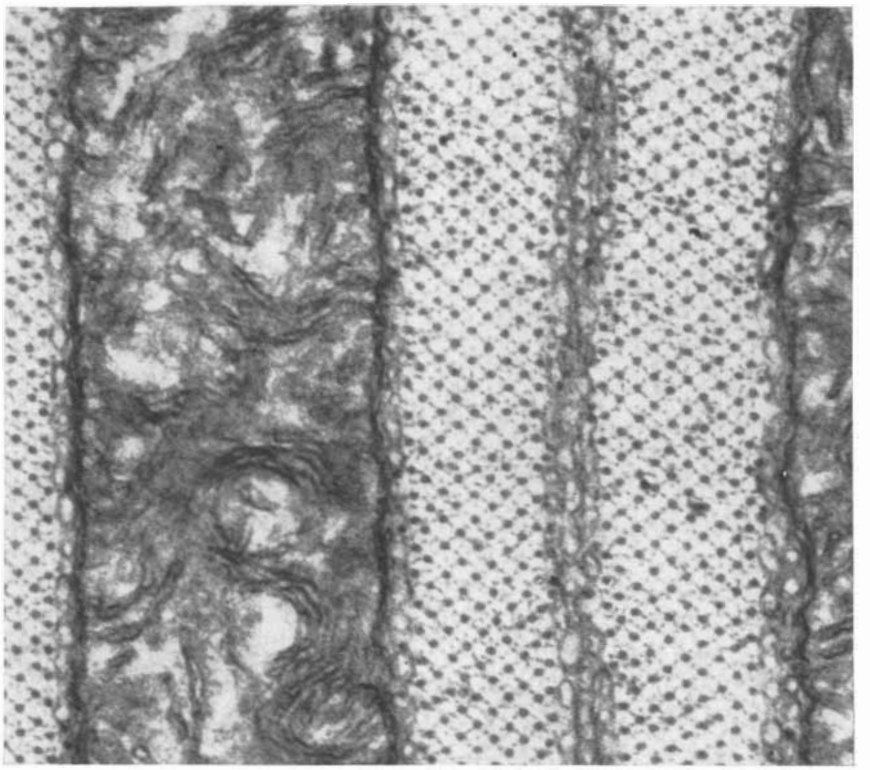
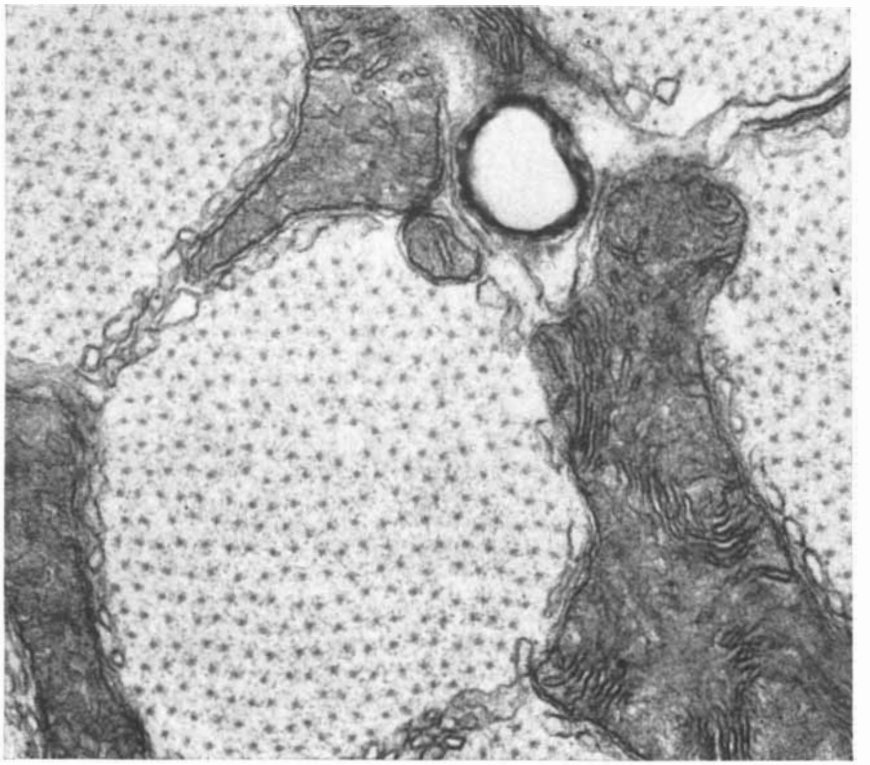


PRIMITIVE SYNCHRONOUS MUSCLE is characteristic of the dragonfly and damselfly; the platelike fibril structure is very much like that of insect leg and body muscle in general but the flight muscles are far more abundantly equipped with energy-supplying mitochondria. This is a transverse section of a damselfly flight muscle, enlarged 70,000 diameters.



ADVANCED SYNCHRONOUS MUSCLE has its fibrils distributed in cylindrical rather than platelike structures; the mitochondria are wrapped around these cylinders. This is butterfly flight muscle in transverse section, enlarged 70,000 diameters. The tube at the top is a tracheole, part of the system that carries oxygen to and carbon dioxide from the tissues.

fiber but only across a much shorter distance—on the average about five microns.

The existence of this network for oxygen supply hints at the solution to Hill's paradox concerning surface excitation and interior response. Could there not be some structure, similar to the structure for oxygen transport, that would channel excitatory signals deep into the muscle cell? If so, the signal would have to travel only a micron or so to influence the innermost fibrils. As has only recently been made clear, such a structure does exist. Called the *T* (for transverse) system, it extends deep into muscle fiber in association with a separate system of ducts and cavities known as the sarcoplasmic reticulum [see "The Sarcoplasmic Reticulum," by Keith R. Porter and Clara Franzini-Armstrong; SCIENTIFIC AMERICAN, March].

Even after electron microscopy had revealed the *T* system of vertebrate muscle in detail, it was uncertain that its component tubules actually communicated with the exterior of the muscle cell. By means of a simple but elegant experiment Huxley has shown that the system is indeed open to the exterior. He soaked fibers of frog muscle in a solution of ferritin, a protein that contains iron particles .011 micron in diameter. These particles are readily recognized in electron micrographs, and in examining thin sections of soaked muscle Huxley found the iron in the tubules of the *T* system. The particles were never found in any of the cavities of the sarcoplasmic reticulum. Clearly the *T* system is an extension of extracellular space throughout the muscle cell. If very large molecules such as ferritin can diffuse freely through this system, it scarcely presents a barrier to the diffusion of ions and of molecules of a transmitter substance. Thus Hill's paradox is solved; a path is open so that excitation both at the surface and in the interior of the muscle fiber can be virtually simultaneous.

In insect muscle—except for asynchronous muscle—the organization of the *T* system is quite as clear-cut as it is in vertebrate muscle. The two systems are not identical, however. The striations of striated muscle consist of a repeating pattern of "*Z* lines" and "*A* bands." The light region between each *Z* line and *A* band is the "*I* zone"; the *A* band is also bisected by an "*H* zone." In vertebrate muscle the *T* system lies at right angles to the long axis of the muscle fiber, either in the plane of the *Z*

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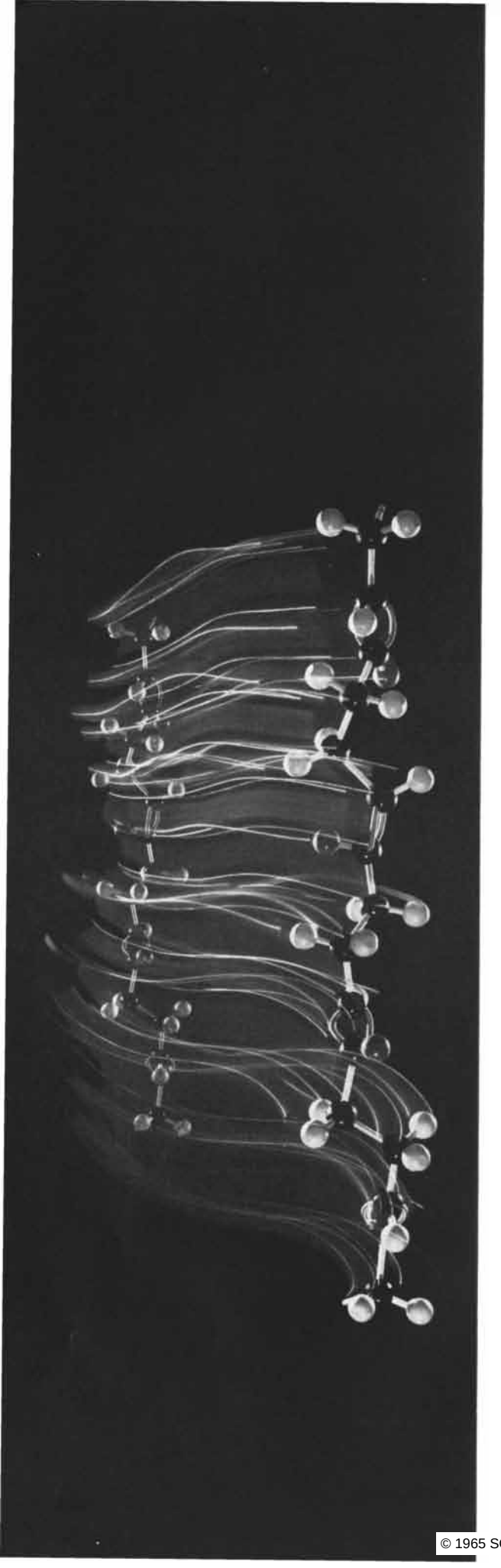

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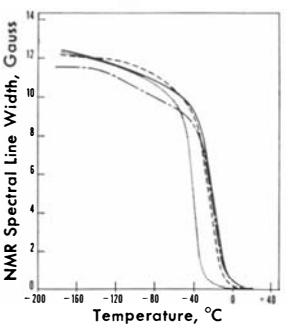

Effects of plasticizers on NMR spectrum of neoprene. The best plasticizer produces spectral line narrowing (due to increased molecular motion) at lowest temperature.
—From a recently published GMR paper.

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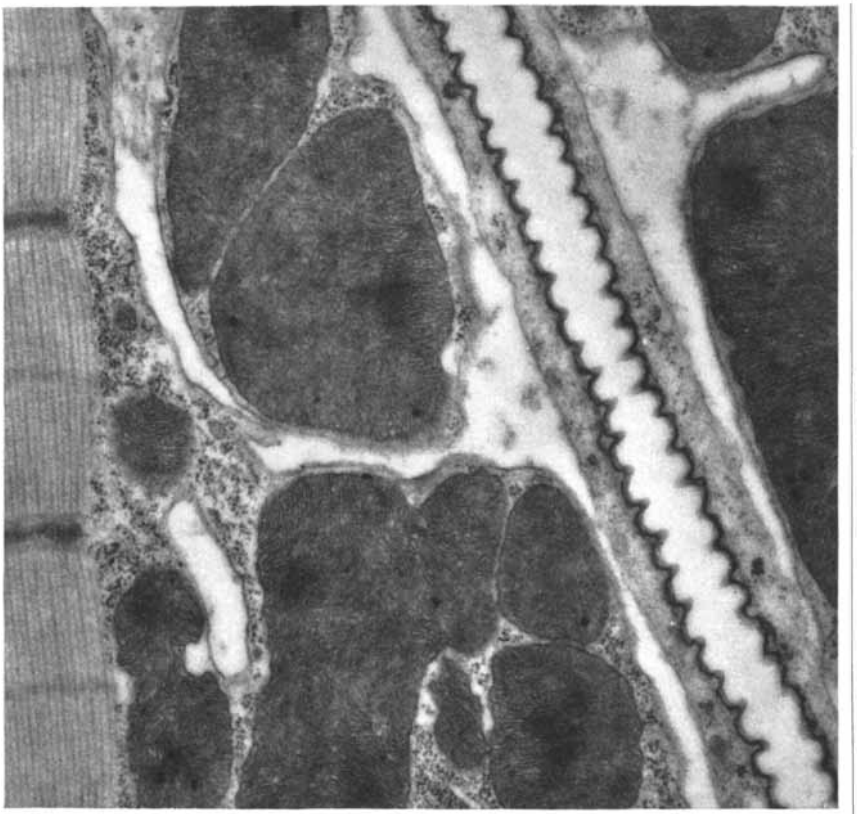

APHID FLIGHT MUSCLE, seen in longitudinal section and enlarged 16,000 diameters, is somewhat less regularly organized than the flight muscle of a wasp, although it is also asynchronous. The fibril (*left*) shows orderly banding, but the tubules of the *T* system (*light areas at top left, center and top right*) are neither uniform in shape nor aligned with the fibril bands. The indented diagonal structure is one of the tubes of the tracheolar system.

line or in the plane at the junction of the *A* band and the *I* zone [*see illustration on page 81*]. In insect muscle the *T* system lies instead in a plane midway between the *Z* line and the *H* zone. This arrangement is shown in longitudinal section in the top illustration on page 80 and in transverse section in the illustration on page 79.

The sarcoplasmic reticulum is at right angles to the *T* system; that is, it is oriented along the long axis of the muscle fiber. Its function is probably to provide regions of concentration for calcium ions in resting muscle fiber; the arrival of an excitation in the tubules of the *T* system evidently triggers the release of these ions from the sarcoplasmic reticulum, thus initiating the breakdown of ATP that powers the contraction of the fibrils. The sarcoplasmic reticulum then recaptures the activating ions, thereby halting the breakdown of ATP within the fibrils and allowing them to relax.

Although this picture of calcium ions being rapidly shuttled into and out of the fibrils has been put together on the strength of experiments with vertebrate muscle, the synchronous flight muscles of insects have an equally well-developed sarcoplasmic reticulum. In damselfly muscle fibers the sarcoplasmic reticulum almost fills the sarcoplasm between the elements of the *T* system; in butterfly muscle the sarcoplasmic reticulum is seen as chains of vesicles around transversely sectioned fibrils. Hence it appears that physiologically similar muscles in organisms as widely separated in the evolutionary scheme of things as insects and mammals are constructed on the same plan. The muscles contain not only the specialized array of protein filaments whose movements enable the muscle to do work but also the intricately related internal membranes that ensure that the muscle fibers give correctly timed responses to the directions issuing from the central nervous system.

In what ways has insect evolution modified normal synchronous striated muscle and enabled it to work in asynchronous fashion? The paper wasp *Polistes* will serve as an example of an insect whose wing mechanism is driven

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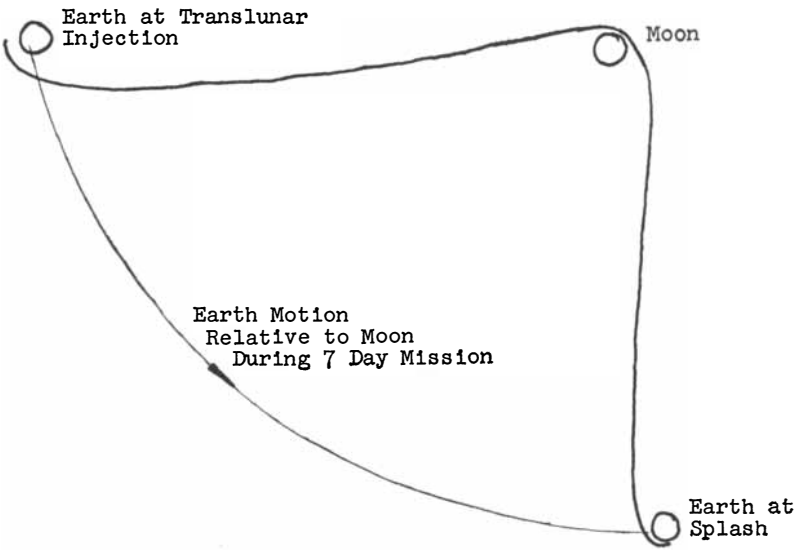

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by these evolutionarily advanced fibers. Its bulky middle thoracic segment is almost filled with horizontal and vertical blocks of flight muscle. They serve to drive both pairs of wings, which are coupled together and work as one. The two sets of muscles, aligned at right angles to each other, contract alternately; each action slightly deforms the shape of the thorax, and this in turn operates a delicate lever mechanism at the base of each wing. Contraction of the horizontal fibers lowers the wings and contraction of the vertical fibers raises them; they click up and down in time with the oscillatory shortening of the two antagonistic sets of muscles.

Electron micrographs immediately reveal one structural difference between asynchronous and synchronous muscle. This is in the way the myosin and actin filaments are fitted together at the ends of each repeating unit of striations. In relaxed synchronous muscle the *I* zones contain only filaments of actin; during contraction the ends of the myosin filaments are thought to slide into this region. In asynchronous muscle, however, the myosin filaments have tapered ends that seem to reach the central Z line. There they meet the actin filaments in a complicated arrangement; this has been shown by the work of J. Auber and R. Couteaux of the University of Paris.

When an asynchronous muscle contracts, it shortens much less than a synchronous one, but this fact has shed no light on how the myosin filaments of asynchronous muscle move in the vicinity of the Z line. Although the sliding of overlapping filaments—along the lines of Huxley and Hanson's proposed model—may well occur here, there are still only a few hints as to how these muscles achieve their characteristic high-frequency oscillation. In any case it is certain that the fibrils of asynchronous muscle are able to utilize ATP. Experiments I have carried out in collaboration with Lois Tice of Columbia University show that a calcium-activated enzyme that splits ATP is present in the *A* bands of blowfly flight muscle and that the sites of this enzymatic activity are at the periphery of the myosin filaments.

The most striking difference of all between synchronous and asynchronous muscle fiber is found in the arrangement of the membranes situated between the fibrils. Electron micrographs make it clear that *T*-system tubules are present throughout asynchronous fiber just as they are in other muscle. In the wasp

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Another RD and E capability report from ALLIS-CHALMERS

First 28-volt fuel-cell system to pass 500-hour test at NASA!

Successful completion of this test demonstrated Allis-Chalmers capability to respond to RD & E challenges. The challenge was to fabricate and assemble two 28-volt, 1.8kw fuel-cell systems — subject one system to a 400-hour verification test and deliver the second system to NASA's Manned Spacecraft Center, Houston, Texas, within TWO AND ONE-HALF MONTHS after contract go-ahead!

The challenge was met on schedule. On arrival at MSC, the second system was successfully run by NASA personnel with assistance from Allis-Chalmers for 200 hours.

Next, NASA personnel took over and ran the system without assistance — through the four-segment load profile as specified — for 300 hours. Test time totaled 500 hours of operation under load, exceeding contract requirements and still operating within an acceptable performance range. Tests are continuing.

The test load profile varied from 480 to 1800 watts, a considerably more severe profile than would be expected during actual missions or qualification demonstrations.

Achieving design performance as predicted represents years of work . . . a result of constantly advancing fuel-cell capability:

- First fuel cells in a land vehicle, 15-kw tractor, applied in 1959.
- First fuel cells to successfully pass zero gravity tests, Wright Patterson AFB, in 1962.
- First fuel cells "qualified for space" with the Air Force, in March, 1964.
- First fuel cells to power an underwater vehicle — Electric Boat Division, General Dynamics Star I submarine, in July, 1964.
- First 28-volt fuel-cell system to pass 500-hour test at NASA.

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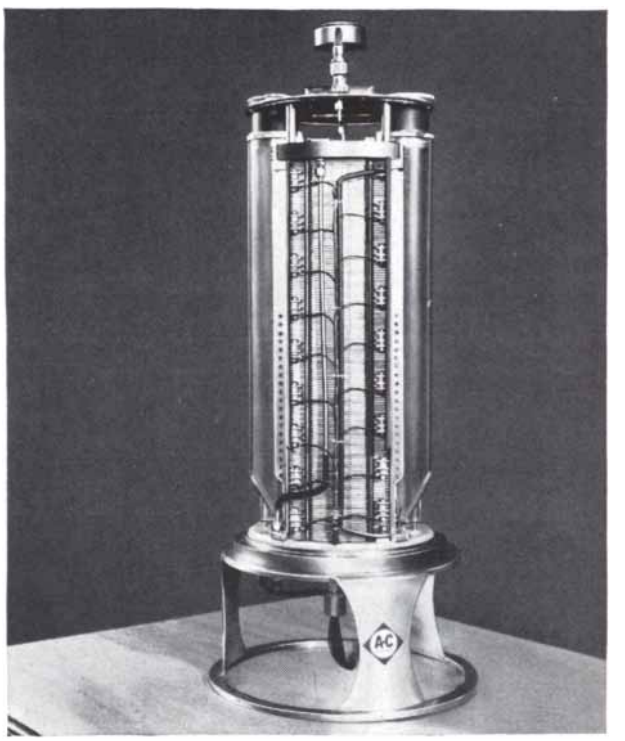
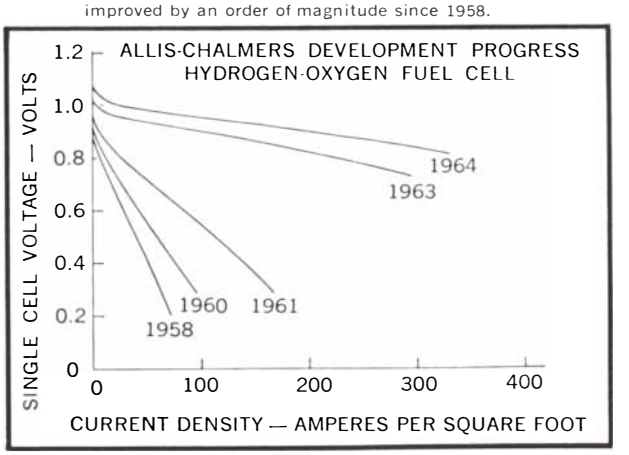


Allis-Chalmers 28-volt, fuel-cell system is the first to successfully pass 500-hour test at NASA.

Chart shows Allis-Chalmers fuel-cell technology has improved by an order of magnitude since 1958.



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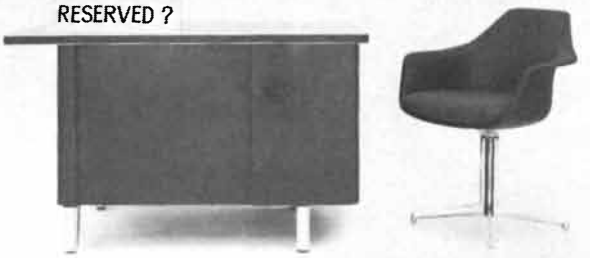

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they are aligned with the *H* zone, in register with the middle of each repeating unit of striation [*see bottom illustration on page 80*]. Presumably the *T* system in asynchronous muscle fulfills the same role of transmitting excitatory signals that it does in other muscles. Although the frequency of oscillation in asynchronous muscle is much higher than the frequency of nerve impulses, a succession of excitations is necessary to maintain activity. In asynchronous muscle, however, there is almost no trace of the other membranous system so evident in synchronous muscle—the sarcoplasmic reticulum.

It is most interesting that the very structure that is believed to control the contraction-relaxation sequence in synchronous insect and vertebrate muscle is virtually absent from asynchronous muscle. Rather than alter our interpretation of the role of the sarcoplasmic reticulum, it is tempting to conclude that the flies, wasps, beetles and bugs have evolved a variety of muscle exceptional enough to prove the rule. Quite recently, however, Pringle and two of his colleagues at the University of Oxford, B. R. Jewell and J. C. Rüegg, have conducted experiments that may help to clarify at least one aspect of the function of asynchronous muscle. They took muscle cells of this type from two species of giant water bug and treated them with glycerine, a process that leaves the filaments of the fibrils intact but removes the sarcoplasm. When the treated muscle cells were placed in a medium containing calcium and ATP, they contracted and relaxed in an oscillatory fashion!

This result makes it clear that the mechanism that enables asynchronous muscle to oscillate resides within the contractile system of protein filaments that compose the fibrils. This being the case, perhaps it is no longer surprising to find that asynchronous muscle is poorly supplied with sarcoplasmic reticulum; the calcium ion give-and-take that operates synchronous muscle may not even occur in these specialized cells. In any case, when the details are fully elucidated of how the filaments in these muscles are organized, how they move with respect to one another and what chemical events are involved in their movement, we shall have not only an overall picture of the function of the most spectacularly active tissue that animals have evolved but also further insight into the mechanism of muscle in general.

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