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STRUCTURAL DIFFERENCES OF FAST AND SLOW EXTRAFUSAL MUSCLE FIBRES AND THEIR NERVE ENDINGS IN CHICKENS

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Kuffler & Vaughan Williams (1953*a*, *b*) have shown that in the frog 'slow' extrafusal muscle fibres occur, which undergo a sustained contracture when the nerve to them is stimulated, rather than a contraction or twitch. It has been shown in the frog that the 'slow' or tonic muscle fibres are of the Felderstruktur type and a single muscle fibre has several '*en grappe*' type nerve endings (diffuse, multiterminal, distributed or 'over-all' innervation), while twitch or 'fast' (phasic) muscle fibres are of the Fibrillenstruktur type and each, in general, has a single '*en plaque*' or end-plate type nerve ending (discrete or focal innervation) (Krüger, 1949; Günther, 1949; Gray, 1957, 1958; Hess, 1960).

Krüger (1950) and Krüger & Günther (1958) have shown in a variety of species of bird that Felderstruktur fibres and '*en grappe*' endings are found in the anterior latissimus dorsi (exclusively) and the medial part of the gastrocnemius (primarily), while Fibrillenstruktur muscle fibres and '*en plaque*' terminations are found in the posterior latissimus dorsi (exclusively), the lateral part of the gastrocnemius (predominantly) and exclusively in the pectoralis major, extensor metacarpi radialis and the flexor metacarpi ulnaris. Ginsborg (1960), by intracellular recording from single muscle fibres in the chicken, found both 'slow' and 'fast' fibres in the biventer cervicis, only 'slow' fibres in the anterior part of the latissimus dorsi, only 'fast' fibres in the posterior part of the latissimus dorsi and the extensor carpi radialis profundus, and some 'slow' fibres in the semispinalis cervicis. In addition, he has deduced from his physiological experiments that multiple or diffuse endings, about 340 μ from each other, occur on the 'slow' muscle fibres.

It is attempted in the present investigation to study further the structure of the muscle fibres in chickens to see if morphological differences do indeed occur and, if so, to define these differences further. Also, it is attempted, by the use of the cholinesterase technique, to see the nerve endings on these muscle fibres, to describe their structure and any differences which might occur in different muscles, and to give direct morphological evidence for the occurrence of diffuse multiterminal endings.

METHODS

Adult chickens, chickens of 2–3 months, and chickens varying in age from newly-hatched to about 1 week in age, were used. The muscles used were the biventer cervicis and both parts, anterior and posterior, of the latissimus dorsi. For study of the structure of the muscle fibres, the muscles or pieces of muscle were fixed in Dalton's or Susa's fluid for 1 hr in an extended state, dehydrated, and embedded in methacrylate. Thin sections were cut for viewing the muscle fibres in the electron microscope, thicker sections were used for the phase-contrast microscope.

For the cholinesterase technique, the muscles were fixed in 10 % glyoxal in tap water treated with calcium carbonate, teased, and stained by a modified Koelle technique, as described previously (Hess, 1960). The teased preparations were incubated in acetyl or butyryl thiocholine iodide with or without previous treatment with di*iso*propylfluorophosphate (DFP). The teased preparations were mounted in glycerine.

RESULTS

The structure of the muscle fibres

In the frog the 'slow' extrafusal muscle fibres were seen to differ structurally from twitch fibres in the distribution of fibrils and a granular sarcoplasm, in the appearance of the Z-disk, and in the presence of lipid droplets (Hess, 1960). The 'fast' Fibrillenstruktur muscle fibre had lipid droplets, discrete fibrils each surrounded by sarcoplasmic granules, and presented a Z-disk running straight across the fibril. The 'slow' Felderstruktur muscle fibre had no lipid droplets. Its fibrils were more haphazard in arrangement and not always surrounded by sarcoplasm, but adjacent fibrils appeared rather to touch or join each other at some places along their length. In addition, the Felderstruktur fibres always had a Z-disk running a zig-zag course across the width of the fibril. In transverse sections of these kinds of muscle fibres viewed in the phase-contrast microscope, the Fibrillenstruktur fibre had a punctate appearance with each discrete fibril visible, while the fibrils of the Felderstruktur fibre appeared more haphazard, irregular and larger, as if several fibrils had joined together.

In the chicken from hatching to about 7 days of age it is difficult to see any obvious differences in transverse sections of the muscle fibres in the phase-contrast microscope because of the small size of the fibres. The differences exist, but are not as obvious as they are in the muscles of adult chickens. Similarly, in transverse sections of muscle fibres viewed in the electron microscope, the differences in the distribution of the fibrils in different muscles of the young chicken are present but not obvious. The contracture which the fibres of the anterior latissimus dorsi undergo during fixation makes it difficult to obtain an exact transverse section. However, in longitudinal sections of muscle fibres from newly-hatched chickens to those of 7 days of age the differences in the muscle fibres are striking (Pl. 2*A*, *B*). The muscle fibres from the posterior part of the latissimus dorsi have lipid droplets, the individual fibrils are discrete and surrounded by a few sarcoplasmic granules, and the Z-disk is always seen running straight across the fibril (Pl. 2*A*). The muscle fibres of the anterior latissimus dorsi are quite different. Here no lipid droplets are present, the fibrils do not appear as individuals and are not surrounded by sarcoplasm but appear to join their neighbours at several places along their length, and the Z-disk takes a zig-zag course across the width of the fibril (Pl. 2*B*). In the biventer cervicis both kinds of muscle fibre can be found.

Chickens 2–3 months after hatching also present these obvious differences in structure (Pl. 2*C*, *D*). However, no lipid droplets were encountered in the anterior or posterior latissimus dorsi of chickens of this age.

Adult chickens also present this picture (Pl. 3). Here the muscle fibres are large and the muscle fibrils can be seen quite clearly. In Susa-fixed material cut in transverse section and viewed in the phase-contrast microscope, the differences in the arrangement of fibrils in the muscle fibres can be seen (Pl. 1). The muscle fibres of the posterior latissimus dorsi have a punctate appearance (Pl. 1*A*), while the fibrils of those of the anterior latissimus dorsi are larger and more irregular and haphazard in appearance (Pl. 1*B*). The adult chicken differs from the younger chickens examined in the occurrence of lipid droplets; both kinds of muscle fibre can have lipid droplets. As in younger chickens, the biventer cervicis has both kinds of muscle fibre (Pl. 3*A*, *B*).

Thus, the posterior latissimus dorsi consists *almost* entirely (see below, p. 224) of 'fast' Fibrillenstruktur muscle fibres, while the anterior latissimus dorsi is composed entirely of 'slow' Felderstruktur muscle fibres. The biventer cervicis has both kinds of muscle fibre; although counts were not made, the general impression is that one kind of muscle fibre is about as numerous as the other in the latter muscle. The presence of lipid droplets is apparently not a significant difference between 'fast' and 'slow' muscle fibres in chickens.

The nerve endings of the muscle fibres

The morphology of the endings. Staining of cholinesterase reveals the motor endings. The posterior latissimus dorsi of the newly-hatched to 7-day-old chicken has endings that are variable in shape (Pl. 4*D*). They can appear as a dark line or blob of material on the muscle fibre. Frequently the endings appear annular and form hollow circles. The endings can also be seen to be surrounded in many instances by a darker staining border of cholinesterase, which is apparently the sub-neural apparatus.

The anterior latissimus dorsi of the newly-hatched to 7-day-old chicken has endings that vary very much in shape (Pl. 4*C*). The endings appear as a line or sometimes two or just a few streaks of cholinesterase-stained material. Circular endings, as seen in the posterior portion of the muscle, have not been found in the anterior part of the latissimus dorsi. A darker-stained border, probably equivalent to a sub-neural apparatus, can also be seen on some endings, although not as frequently or as clearly as in the nerve endings in the posterior latissimus dorsi.

The adult chicken reveals a rather drastic transformation in the shape of its nerve endings, compared to the newly-hatched chicken. The end-plates of the posterior latissimus dorsi (Pl. 4*E*, *H*, *I*, *J*) sometimes appear as relatively long finger-like extensions of cholinesterase-stained material. In other instances a series of intensely stained droplets comprises the ending. The endings of the anterior latissimus dorsi (Pl. 4*G*) are typically '*en grappe*' in structure. They appear as clusters or groups of droplets of cholinesterase-stained material and are very variable in shape. The biventer cervicis has many muscle fibres with end-plates and many other fibres have '*en grappe*' endings (Pl. 4*A*, *B*, *F*). The posterior latissimus dorsi also has a few muscle fibres with '*en grappe*' endings (Pl. 4*K*). The end-plates of the posterior latissimus dorsi are easily differentiated from the '*en grappe*' endings of the anterior latissimus dorsi after cholinesterase staining. The end-plates are stained more intensely, occupy a greater extent of the muscle fibre, and as will be seen below, occur singly on a muscle fibre, whereas the '*en-grappe*' endings are stained relatively lightly, consist of only a few droplets or a small cluster, and several endings always occur on a single muscle fibre.

All chickens of all ages have both true and pseudo-cholinesterase in their motor nerve endings, whichever the kind of ending. Incubation in acetyl thiocholine iodide after treatment with DFP reveals all nerve endings stained somewhat less intensely than without DFP treatment. Incubation in butyryl thiocholine iodide also reveals all nerve endings, although all the endings, especially the '*en grappe*' type, are stained much more lightly. Incubation in butyryl thiocholine iodide after DFP treatment inhibits the staining of all nerve endings.

The distribution of the endings. End-plates and '*en grappe*' terminations were never found on the same muscle fibre.

In the newly-hatched to 7-day-old chicken individual muscle fibres are difficult to tease, and are about 10 μ in thickness. However, when individual fibres are teased, it is possible to see a difference in the distribution of the endings between the muscle fibres of the anterior and posterior parts of the latissimus dorsi. The posterior latissimus dorsi, as far as can be determined, has one ending per muscle fibre, while the anterior latissimus dorsi has several endings per muscle fibre, distributed rather evenly along the muscle fibre at distances of about 250–350 μ (Pl. 4*C*). It is difficult to tease the small muscle fibres of the newly-hatched chicken for any great length and thus difficult to ascertain if only one ending occurs per muscle fibre in the posterior latissimus dorsi.

In the adult chicken the teasing of the muscle fibres becomes relatively easy, and the fibres are about 60 μ in diameter. Fibres of 1 cm or more in length were teased from the posterior latissimus dorsi and on none of these fibres on which an end-plate occurred was there more than one nerve ending. The few fibres from the posterior latissimus dorsi with '*en grappe*' endings always had several endings along their length (Pl. 4*K*). The endings of adjacent muscle fibres occur at about the same level.

It is relatively more difficult to tease the fibres of the anterior latissimus dorsi, even in the adult, probably because of the 'slow' characteristics of these fibres and their tendency to undergo a contracture. Fibres were teased for distances of about 8 mm. All fibres revealed several '*en grappe*' endings along their length, separated by distances of about 1000 μ from each other. The endings are separated from each other by rather regular distances. The endings of adjacent fibres also occur nearly at the same level on the muscle fibre.

The fibres of the biventer cervicis present an advantage for preparing teased preparations in that the 'slow' fibres, mixed in with twitch fibres, are rather easier to tease. Muscle fibres with '*en grappe*' endings were teased for distances of 1 cm or more. As an example, one fibre about 12 mm in length had 11 '*en grappe*' endings at distances of 1200 μ, 900 μ, 800 μ, 1000 μ, 1000μ, 900μ, 1200 μ, 1700 μ, 1000 μ and 1100 μ from each other, which indicates the rather regular disposition of '*en grappe*' endings along the 'slow' muscle fibres of the chicken (Pl. 4*A*, *B*).

DISCUSSION

Extrafusal muscle fibres are of two kinds and their similarities and differences may be generally summarized as follows: (*a*) 'slow' muscle fibres which undergo contracture and do not give rise to a propagated potential when repetitively stimulated are of Felderstruktur type and are innervated by small motor nerve fibres which form multiple '*en grappe*' endings on each muscle fibre; (*b*) 'fast' muscle fibres which undergo a twitch and have a propagated potential with every stimulus are of Fibrillenstruktur type and are innervated by large motor nerve fibres which form usually one '*en plaque*' ending on each muscle fibre. End-plates and '*en grappe*' endings never occur on the same muscle fibre. This will be referred to as the general scheme of muscle fibre innervation in the ensuing discussion.

Fish muscle fibres deviate from this scheme. 'Fast' muscle fibres of the fish have 'over-all' innervation (Barets, 1955; Barets & Le Touzé, 1956; Takeuchi, 1959) or nerve endings at each end of the muscle fibre ('myoseptal' endings) (Barets, 1952; Barets, Fessard & Le Touzé, 1956). Nevertheless, these fibres are called 'fast' because they have 'aborted' action potentials which, although not identical to the twitch fibres of the frog, resemble the propagation of 'fast' frog fibres more closely than the 'slow' fibres of the frog (Barets & Le Touzé, 1956; Barets *et al.* 1956; Takeuchi, 1959). The 'slow' fibres of the fish conform more closely to the scheme, undergo contracture and have multiple endings (Barets, 1952; Barets & Le Touzé, 1956; Takeuchi, 1959). The 'slow' muscle fibres of the fish are innervated by small nerve fibres, the 'fast' fish muscles by large fibres (Barets, 1952, 1955). Fish muscle fibres differ in their internal structure. However, muscle fibres with the same internal structures can be found in both 'slow' and 'fast' muscles. It is rather in the distribution of muscle fibres of different internal structure in 'fast' and 'slow' muscles by which the morphological contrasts between these kinds of muscle can be seen (Barets, 1952).

Amphibian muscle fibres conform to the scheme, as has already been mentioned in the introduction. However, there are amphibian muscle fibres which have myoseptal endings (Mackay, Muir & Peters, 1960; Lewis & Hughes, 1960) and which presumably would also have membrane characteristics different from typical 'fast' or 'slow' fibres. Their internal structure is as yet unknown.

Chicken muscle fibres, as shown in the present study, conform very well to the scheme. The size of the nerve fibres innervating the 'fast' or 'slow' chicken muscle fibres has not yet been determined. Although preliminary studies of the nerve to the anterior latissimus dorsi indicate that there are many small myelinated fibres, a more crucial study of deafferented nerves is necessary before making any further statement on the size of motor nerve fibres innervating the 'slow' extrafusal fibres of chickens. This problem is further complicated by the occurrence of spindles and intrafusal fibres in the anterior latissimus dorsi of the chicken which have been seen to have multiple endings (Hess, unpublished observations) and which would presumably be innervated by the same size nerve fibres as those innervating the 'slow' extrafusal fibres. In addition, Ginsborg (1959) and Ginsborg & Mackay (1960) have reported that 'diffusely innervated (chicken) fibres are capable of responding to adequate stimulation with propagated action potentials'. Amphibian 'slow' fibres apparently do not react in this way. This difference might be accounted for by the distribution of the multiple nerve endings, which are scattered and irregular and can be very close together in the frog (endings were seen with only 60 or 120 μ between them (Hess, 1960)), while in chickens of the age used by Ginsborg, the '*en grappe*' endings appear to be rather evenly distributed along the length of the muscle fibres (about 250–350 μ between endings), are perhaps less concentrated than those of the frog, and occur at about the same level on adjacent muscle fibres.

More work must be done before it can be determined if mammalian extrafusal muscle fibres fit into this scheme. The occurrence of muscle fibres of Felderstruktur or Fibrillenstruktur types in mammals has not yet been confirmed, although the discoverer of such muscle fibres in frogs and birds believes that they occur (Krüger & Günther, 1955). The situation is especially difficult since '*en grappe*' endings are said not to occur on the extrafusal muscle fibres of mammals (except in eye muscles, see Tiegs, 1953) and 'slow' extrafusal muscle fibres are not found physiologically in mammals (Kuffler *et al.* 1953*b*), although Krüger (1960) believes that they do occur and that the same correlations can be made in mammals as in frogs and birds. In addition, the small motor nerve fibres in mammals are said to go to intrafusal muscle fibres only (Kuffler & Hunt, 1952).

Intrafusal muscle fibres have also been investigated with this scheme in mind. Frog intrafusal fibres receive large or small motor fibres (Katz, 1949) and can have '*en grappe*' multiple terminations or end-plate type endings (Gray, 1957). The membrane characteristics of the frog intrafusal fibre, even those with multiple nerve terminations, resemble twitch fibres more closely than 'slow' fibres (Koketsu & Nishi, 1957*a*). The differences between 'slow' extrafusal fibres and intrafusal fibres might be accounted for by the multiple terminations on intrafusal fibres being less concentrated than on 'slow' fibres (Koketsu & Nishi, 1957*b*). Similarly, in mammals, intrafusal fibres with multiple motor terminations react physiologically with propagated potentials like 'fast' muscle fibres (Eyzaguirre, 1960). Intrafusal mammalian fibres receive large or small motor fibres and have end-plate endings or multiple endings (Boyd & Davey, 1959; Diete-Spiff & Pascoe, 1959; Hess, 1961). However, the multiple motor endings are restricted to the juxta-equatorial region of the intrafusal fibre adjacent to the equatorial region where the sensory innervation occurs (Hess, 1961). This restriction of multiple motor nerve terminations to a limited region of the muscle fibre might account for the physiological similarities of the intrafusal muscle fibre and a 'fast' muscle fibre. Krüger (1960) and Barker & Gidumal (1960) have found differences in the myofibrillar arrangement in mammalian intrafusal muscle fibres. The correlation between kind of muscle fibre and kind of nerve ending remains to be worked out.

The source or origin of the multiple terminations remains to be determined in many of the above cases. I have concerned myself here only with the occurrence of multiple motor endings. These endings could come from the branches of a single axon in a peripheral nerve and hence from a single cell in the spinal cord or the branches of axons of several nerve cells could end on a single muscle fibre (polyneuronal innervation). In some cases, a single axon has been seen to pass along a muscle fibre and make endings. In other instances, polyneuronal innervation has been proven. I have not dealt directly with this problem in this investigation.

The multiply innervated muscle fibre seems to make its appearance first in the phylogenetic series of animals. Invertebrate muscles are innervated in this manner (see Hoyle, 1957). The similarities of invertebrate muscles and those of fish, where even the 'fast' muscle fibres are multiply innervated, are striking. The presence of 'slow' multiply innervated fibres in frogs and chickens and the multiply innervated intrafusal fibres of frogs, chickens and mammals indicates that these multiply innervated fibres, 'slow' or 'fast' or classified in between these two extremes, are present throughout all animal groups. Just as 'the chief and most characteristic functions of nervous and other excitable tissues are performed by means of graded responses' and the 'all-or-none response is a special case of the general property of excitability' (Bishop, 1956), so it may be that the 'slow' multiply innervated muscle fibre appears first phylogenetically, undergoes modification in the distribution of its nerve endings and its ability to propagate an impulse and can be either 'fast' or 'slow' or in between, and is still present, highly modified, as the intrafusal muscle fibre in the highest animals.

SUMMARY

1. The extrafusal muscle fibres of chickens were studied in the electron and phase-contrast microscopes. Their nerve endings were examined in teased preparations after staining with the cholinesterase technique.
2. Fibrillenstruktur muscle fibres have regular fibrils, each surrounded by sarcoplasm and granules. The Z-disk runs straight across the width of the fibril. These are the twitch or 'fast' fibres.
3. Felderstruktur muscle fibres have irregular fibrils apparently joining with each other at certain points along the length of the fibrils, the fibrils are not regularly surrounded by sarcoplasm and granules, and the Z-disk appears zig-zag across the width of the fibril.
4. The presence of lipid droplets is apparently not a significant difference between 'fast' and 'slow' muscle fibres in chickens.
5. End-plate endings are the ordinary kind of ending and occur one per muscle fibre on Fibrillenstruktur muscle fibres only.
6. Several '*en grappe*' terminations occur on each muscle fibre and only on fibres of Felderstruktur.

7. The posterior latissimus dorsi of the chicken from hatching to 1 week of age, from 2 to 3 months of age, and adult, consists almost entirely of muscle fibres of Fibrillenstruktur which have one ordinary end-plate on each fibre. There are, however, a few fibres which receive several '*en grappe*' terminations in the posterior latissimus dorsi and are probably of Felderstruktur type.

8. The anterior latissimus dorsi of such chickens consists entirely of muscle fibres of Felderstruktur. Several '*en grappe*' terminations are found on each of these muscle fibres, occurring regularly along the length of the muscle fibre and separated by distances of about 250–350 μ in 1- to 7-day-old chickens, and by about 1000 μ in adults.

9. The biventer cervicis consists of mixed Fibrillenstruktur and Felderstruktur muscle fibres, the former with one end-plate type ending per muscle fibre and the latter with several '*en grappe*' terminations on each muscle fibre.

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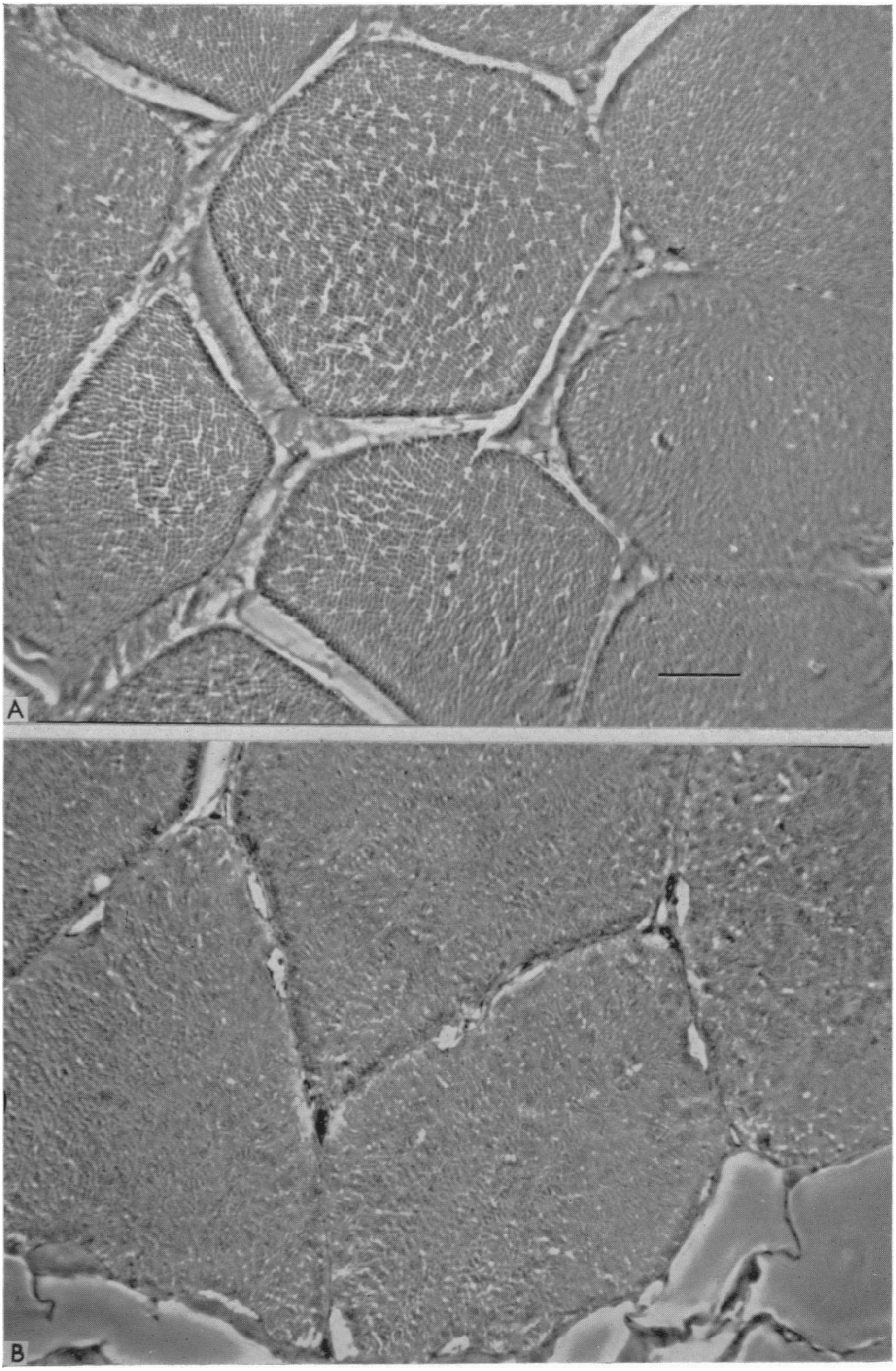
EXPLANATION OF PLATES

All photo-micrographs are from chicken muscles. The scale marks on the electron photomicrographs represent 1 μ; those on the light and phase-contrast photomicrographs represent 10 μ.

Pl. 1. Susa-fixed, embedded in methacrylate, transverse sections, phase-contrast micrograph. *A*. The posterior latissimus dorsi, Fibrillenstruktur. *B*. The anterior latissimus dorsi, Felderstruktur.

Pl. 2. *A*, *B*. Chickens from hatching to 7 days, longitudinal section, electron micrograph. *A*. The posterior latissimus dorsi, Fibrillenstruktur. *B*. The anterior latissimus dorsi, Felderstruktur. C, D. Chickens of 2–3 months, longitudinal section, electron micrograph. *C*. The posterior latissimus dorsi, Fibrillenstruktur. *D*. The anterior latissimus dorsi, Felderstruktur.

Pl. 3. *A*, *B*. Adult chickens biventer cervicis, longitudinal section, electron micrographs. A Fibrillenstruktur muscle fibre is on the top of each photograph; a Felderstruktur muscle fibre is on the bottom of each photograph.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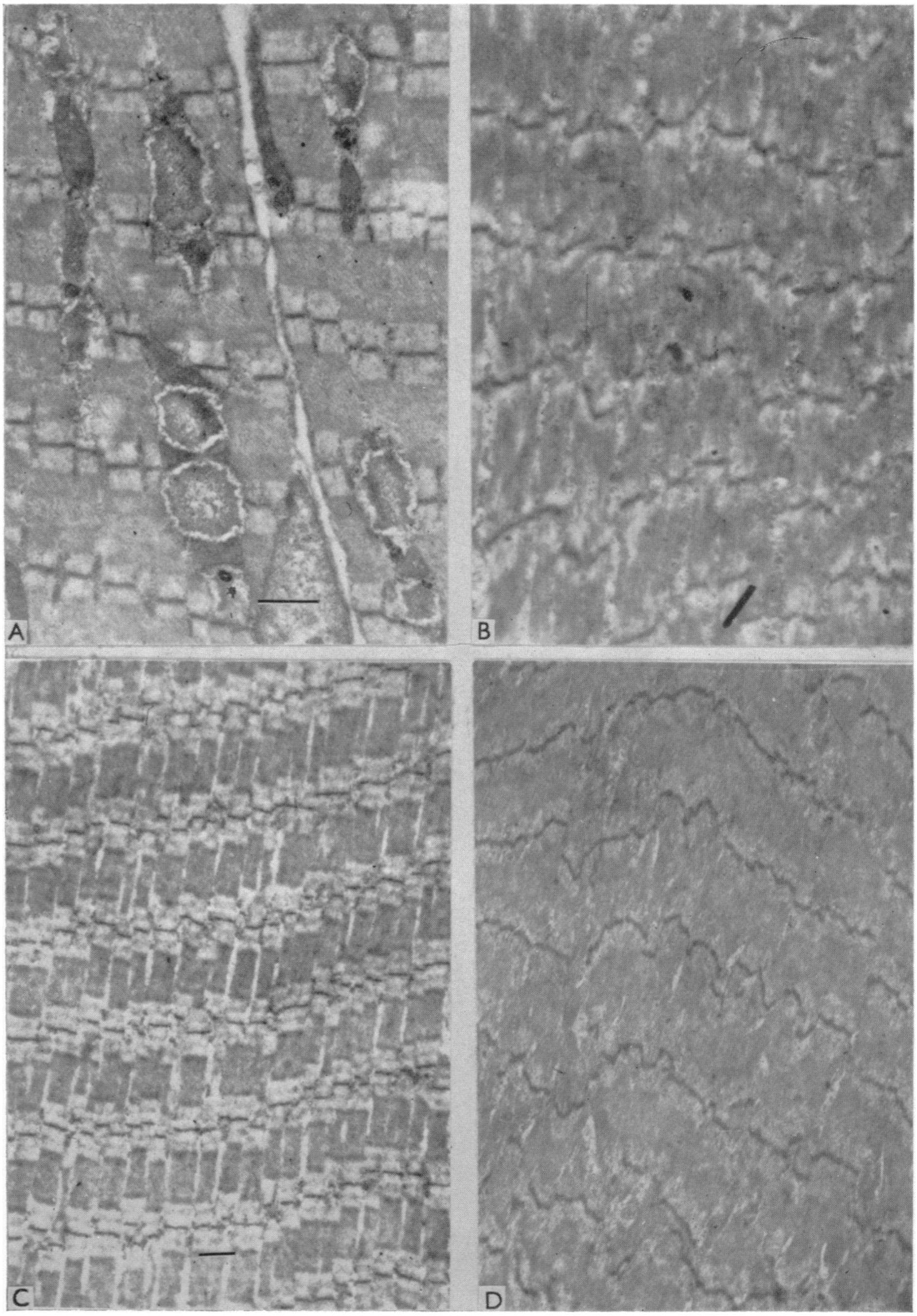

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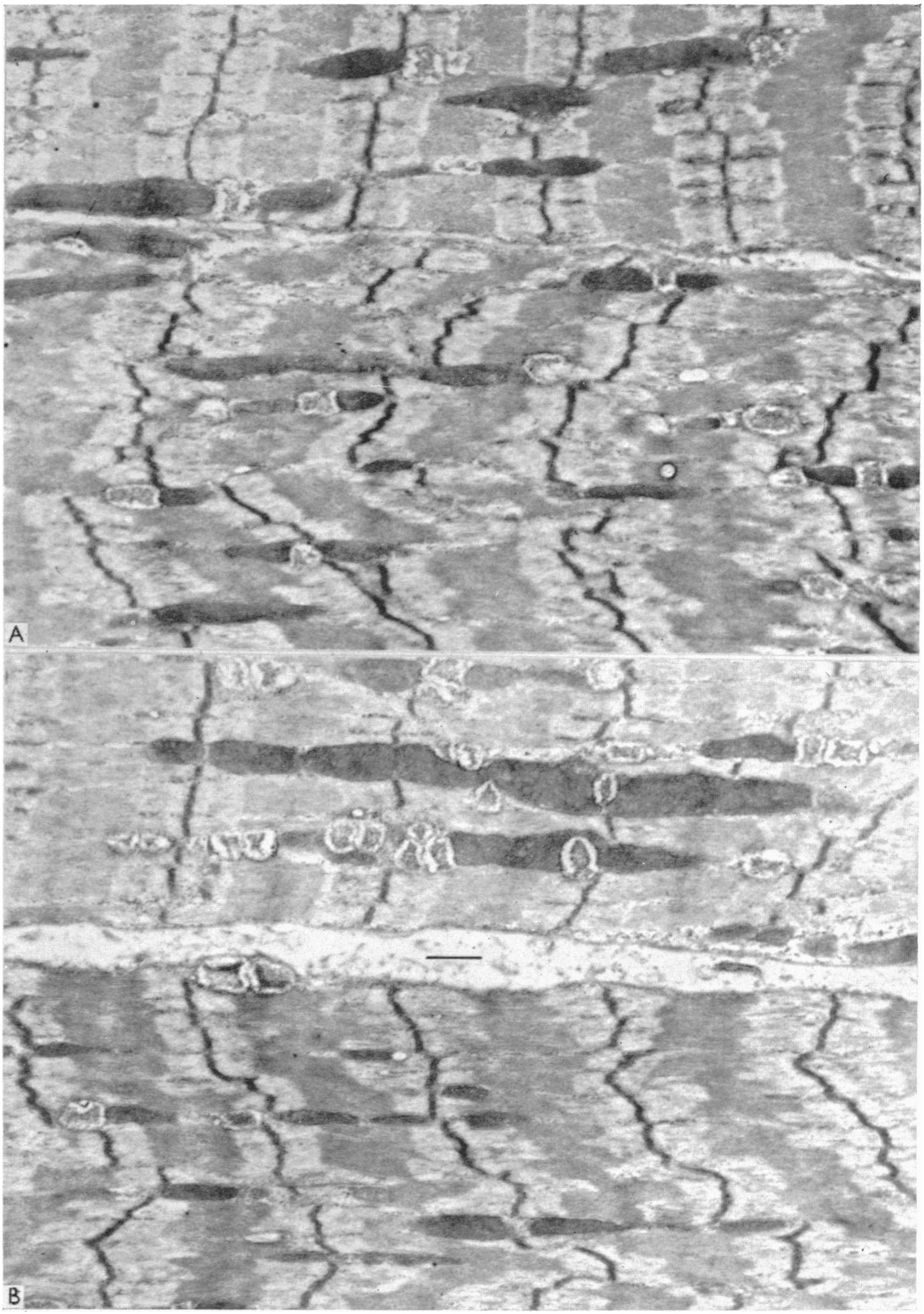

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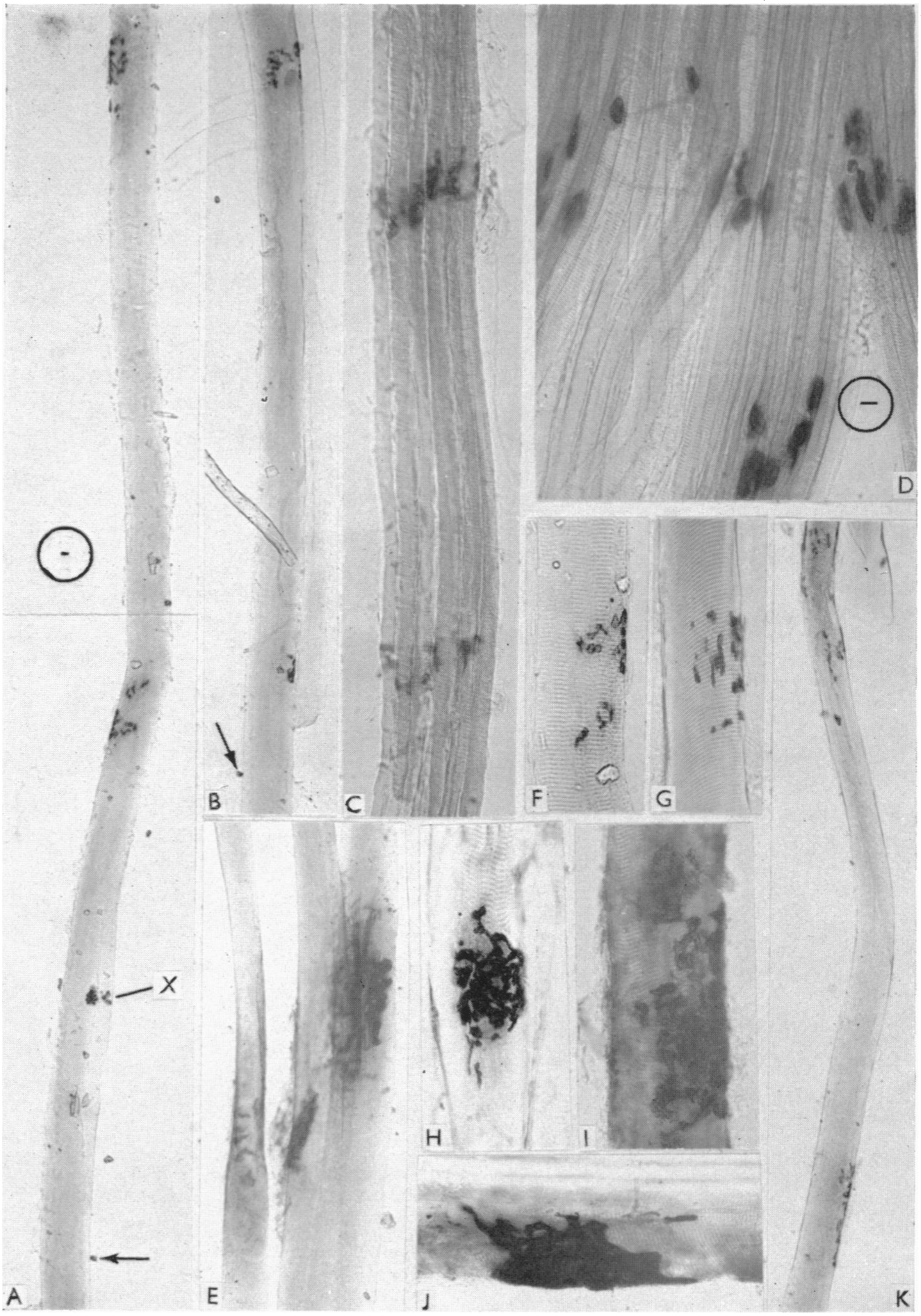

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Pl. 4. Teased muscle fibres, cholinesterase stain. *A*, *B*, *E*, *K* are the same magnification; *C*, *D*, *F*–*J* are the same magnification. *A*, *B*. '*En grappe*' endings from the biventer cervicis of adult chicken. Montage; the fibre in *A* and *B* is continuous at the arrow. Four out of 11 '*en grappe*' endings on this fibre are seen. *X* is a piece of dirt, not an ending. *C*. '*En grappe*' endings from anterior latissimus dorsi of 3-day-old chicken. *D*. '*En plaque*' endings from posterior latissimus dorsi of 3-day-old chicken. *E*. '*En plaque*' endings from posterior latissimus dorsi of adult chicken. *F*. '*En grappe*' ending from biventer cervicis of adult chicken. *G*. '*En grappe*' ending from anterior latissimus dorsi of adult chicken. *H*, *I*, *J*. '*En plaque*' endings from posterior latissimus dorsi of adult chicken. *K*. '*En grappe*' endings from posterior latissimus dorsi of adult chicken.