From: Anatomical Institute, (Head: Professor Jan Jansen M. D.)
University of Oslo, Norway.

THE LOCATION OF MOTOR END PLATES AND THE DISTRIBUTION AND HISTOLOGICAL STRUCTURE OF MUSCLE SPINDLES IN JAW MUSCLES OF THE RAT

by

KJELL KARLSEN

INTRODUCTION

In recent years an increasing interest has been taken in problems concerned with the innervation of striated muscle, and much work has already been done on the subject, both morphological and physiological.

This paper deals with the location of motor end plates and the distribution and histological structure of muscle spindles in the jaw muscles of rat. Only sparse information is found in the literature concerning the innervation of jaw muscles, and no systematic studies of this problem appear to have been made. Based on examination of different striated muscles from still-born infants *Christensen* (1959) concludes that the end plates of skeletal muscles are found in the middle region of the muscle where they occupy a plane equidistant from the ends of the muscle fibres. *Coërs* (1959) states that with few exceptions this is the case for mammalian muscles in general.

The presence of muscle spindles in striated muscle was first observed by *Kölliker* (1882). In 1894 *Sherrington* presented a very detailed description of spindles from different mammalian muscles. Since that time these structures have been studied by a variety of authors. Recently *Boyd* (1962 a, b), *Eldred et al.* (1962), *Barker* (1962) and *Cooper & Daniel* (1963) have given detailed information concerning the occurrence, distribution and structure of the spindles in various muscles. *Freimann* (1954) investigated the number and location of muscle spindles in human jaw muscles.

MATERIAL AND METHODS

Eight white adult, normal rats were used. The masseter (superficial and profound*), the temporal and the internal and external pterygoid muscles were examined. Miller's, van Gieson's and Bodian's staining methods were used. The animals were anesthetized with nembutal, and the specimens stained according to van Gieson's and Bodian's methods were perfused intravitally with 10 % formalin. Care was taken to obtain a total preparation of the jaw muscles. After routine treatment the muscles were embedded in paraffin and cut in 10 μ transverse or longitudinal sections.

From specimens treated according to Miller's method for examination of motor end plates, very narrow, longitudinal strips of the muscles were removed. Only those reaching from origin to insertion were examined. The specimens treated with van Gieson's and Bodian's stains were used for spindle studies.

OBSERVATIONS

Motor end plates

Microdissection reveals that the muscle fibres run continuously from origin to insertion in all the muscles examined, regardless of their shape. The muscles receive their nerve supply from the trigeminal nerve, the bundles of which in a relatively restricted area penetrate the muscles on their medial aspects. After having passed into the muscle mass the greater nerve trunks divide into smaller bundles, and at the same time ramification of the nerve fibre axons occurs. Thus the perimysium and endomysium of the muscles are penetrated by a great number of gradually dividing nerve bundles. These are of different size.

*) These parts are also referred to as the lateral and medial portions of the muscle.

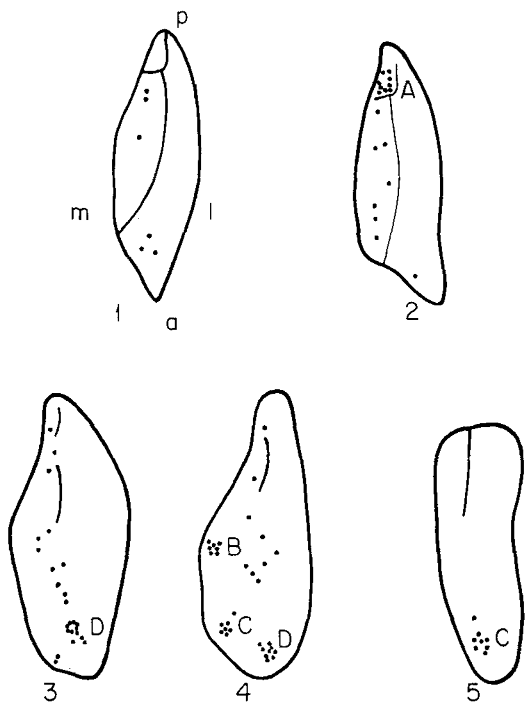

Fig. 1. Drawings of transverse sections of musculus masseter at different levels from origin (1) to insertion (5). Each dot indicates a spindle. Black lines indicate connective tissue septa. Only a few spindles are found in the lateral portion. Distances between drawings are equal (2.5 mm). a anterior, p posterior, m medial, l lateral. Spindle aggregations at A—D.

When the innervation zone is reached, the terminal bundles usually contain less than 30 and often less than 10 fibres (Fig. 4). Ultimately, these fibres separate and as sole axons cross a few muscle fibres before terminating. The course of these terminal axons is mostly straight. Having reached the muscle fibre, the terminal arborization of the motor axon and the subneural apparatus of the muscle fibre contribute to the end plate (Fig. 5). As a rule, each muscle fibre is provided with one end plate only. In a very few cases, however, two plates seem to lie on the same muscle fibre, but so close to each other that they are both situated within the limits of the general innervation zone. In cases of double end plates it is difficult to ascertain whether their nerve supply is due to a terminal branching of an axon or not.

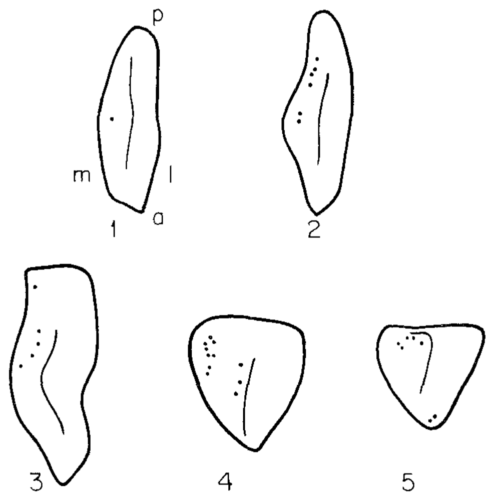

Fig. 2. Drawings of transverse sections of musculus temporalis at different levels from origin (1) to insertion (5). Each dot indicates a spindle. Black lines indicate connective tissue septa. No spindles found in the lateral portion. Distances between drawings are equal (1.6 mm). a anterior, p posterior, m medial, l lateral.

In the Miller stained sections the end plates appear as circular or oval dots with relatively indistinctly marked limits. The end plates stain dark red and display a somewhat meshy appearance. Furthermore, as Figure 5 reveals, the end plate in its whole ex-

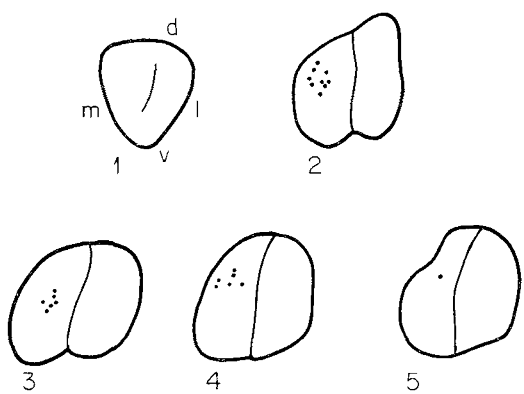

Fig. 3. Drawings of transverse sections of musculus pterygoideus internus at different levels from origin (1) to insertion (5). Each dot indicates a spindle. Black lines indicate connective tissue septa. Distances between drawings are equal (1 mm). d dorsal, v ventral, m medial, l lateral.

Fig. 4. Innervation zone of temporal muscle. Terminal nerve bundles and motor end plates. Miller method. × 620.

tent is filled by lots of small roundish or thread-like formations, irregularly distributed and very darkly stained. Among these the final branches of the motor axon can be seen in some of the end plates. The innervation band is in all muscles situated equidis-

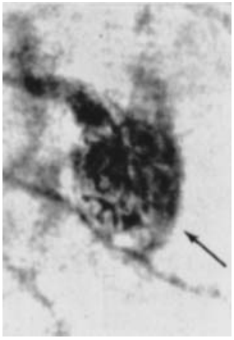

Fig. 5. Extrafusal end plate of the internal pterygoid muscle. Details in the structure of the end plate are seen. Miller method. × 900.

tantly from both ends of the muscle, almost perpendicular to the fibre direction. In none of the muscles does any sign of double innervation zone exist.

Muscle spindles

Masseter muscle

The masseter of the rat consists as in other mammals of a superficial and a profound portion. The former is the most voluminous. The fibres of the two parts have a slightly different course. This accounts for a somewhat different fibre appearance in the sections. Despite this, the two parts of the muscle were included in the same block and examined together, since a separation might have caused damage to muscle spindles along the midline region. In the masseter altogether 130 spindles are found.*) The region of origin and insertion of the muscle are devoid of spindles. In the whole lateral portion of the muscle only 6 spindles are observed, most of them close to the midline. The distribution of the spindles in the transverse direction is highly uneven, while the distribution in the longitudinal direction is even and continuous. A conspicuous concentration of spindles in the transverse plane is found in four places (Fig. 1 A, B, C, D). At some distance from the origin of the muscle 10 spindles are concentrated in a restricted posterior area (Fig. 1 A). Likewise, in the middle region of the muscle and towards the insertion 3 heaps of spindles are situated (Fig. 1 B, C, D) each heap consisting of 6—12 spindles. Accordingly, also great areas of the medial portion of the masseter are without spindles.

Temporal muscle

The temporal muscle is also divided in a medial and a lateral part by a strong connective tissue septum which extends through the entire muscle. The two portions are of approximately the same size. The lateral part contains no spindles. Both the origin and insertion areas of the medial portion are devoid of spindles, the number of which gradually increases towards the middle region where spindles occur most abundantly. Altogether 46 spindles are observed in the temporal muscle. Also in this muscle single spindles occur, but conspicuous concentrations, espe-

*) In this and the following muscles this number is based on countings in one total muscle where every section of the entire series was examined. In addition, representative parts of identical muscles on the other side, and in various animals, were examined for comparison.

cially in the medial posterior region contain about half the total number of spindles (Fig. 2).

Internal pterygoid muscle

The internal pterygoid muscle too is in its entire length separated into a medial and a lateral portion, both of approximately the same volume. Immediately after origin one spindle occurs in the core of the medial portion. In the following sections the number of spindles gradually increases, and they disappear at a distance about two thirds from the origin of the muscle. This means that the distal third of the medial portion of the muscle is completely devoid of spindles, and so is the entire lateral portion. Altogether, only 16 spindles are found. Within the medial portion they are distributed in a transversely strongly restricted area (Fig. 3). About one third of the spindles occur singly; the rest forms heaps of 2 to 4 spindles, extending through a great part of the muscle.

External pterygoid muscle

In this muscle no signs of spindles were observed, neither in the end regions nor in the belly.

General features of the spindles

The masseter, temporal and internal pterygoid muscles have many features in common concerning their spindles. When the same muscles of both sides of the same animal are compared, the distribution patterns of the spindles of the two sides are in broad features the same, even if they are not identical. This is also the case from one animal to the other. In other words, the number of spindles varies slightly from side to side, and from animal to animal.

Each spindle is enclosed in a capsule of connective tissue, which also contains blood vessels and nerves. The capsule tapers gradually towards both ends or poles. At its midpoint, the equatorial region, the capsule displays for a short distance a slight swelling, indicating the lymph space. Here there is a gap between the capsule and the intrafusal fibres. Beyond this region they lie close together.

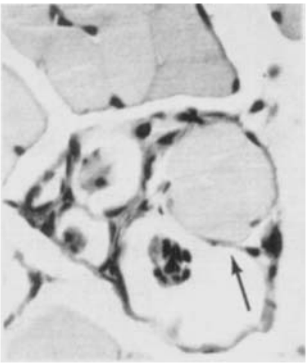

Fig. 6.

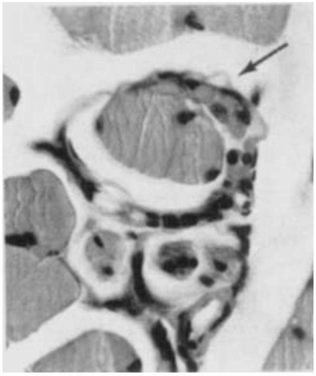

Fig. 7.

Fig. 6. Extrafusal fibre bundle (arrow) enclosed in the spindle capsule at the equatorial level. Masseter, van Gieson stain. × 620.

Fig. 7. The same extrafusal fibre bundle as shown in Fig. 6 joining the intrafusal fibres in the polar region (arrow). Masseter, van Gieson stain. × 620.

The length of the single capsule in the examined muscles varies from 0.7 to 1.5 mm when no correction is made for histological shrinkage and a slightly oblique fibre direction in parts

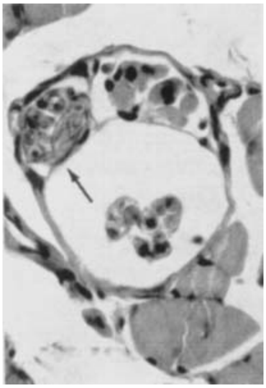

Fig. 8. Two spindles sharing a common capsule which at this level is penetrated by a nerve (arrow). Temporal muscle, van Gieson stain. × 620.

of the muscles. The longer spindles are mostly situated in the middle region, the shorter towards the ends of the muscles, but exceptions occur.

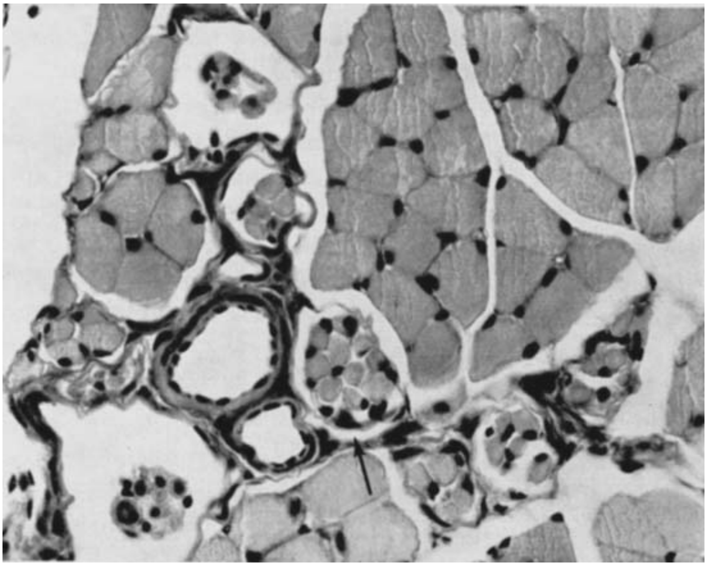

Fig. 9. Great spindle unit from the masseter. At this level 8 individual units are found. Centrally, a giant spindle with 10 fibres (arrow) surrounded by other spindles. van Gieson stain. × 620.

In most spindles some of the intrafusal fibres are seen to extend somewhat beyond the capsule at both poles, terminating on neighbouring structures or extrafusal fibres. The capsule of some spindles also encloses a small bundle of extrafusal muscle fibres from its equatorial (Fig. 6) towards one of its polar regions. In this end of the spindle the intrafusal fibres join the enclosed extrafusal fibres already within the capsule (Fig. 7). At the opposite end, however, the spindle fibres join another extrafusal fibre bundle after having left the capsule. Enclosing of extrafusal muscle fibres in a spindle mainly occurs in connection with a spindle unit, as illustrated in Figures 6 and 9. As far as could be seen, only one of the spindles making up a spindle unit is attached to the enclosed extrafusal fibre.

When enclosing of extrafusal fibres occurs in the middle region of the muscle, it has in a few cases been possible to trace a small nerve bundle to the enclosed area of the extrafusal fibre.

As has been mentioned, the spindles may occur singly or in greater units. With some exceptions spindle units occur most frequently in areas of the muscle with a high total number of spindles. The spindle units are composed of 2 to 12 single spindles. The smallest units are found in the internal pterygoid, then follows the temporal, while the masseter muscle displays the greatest units (Fig. 9). In many of the units one of the spindles contains a much larger number of fibres than the other spindles. Figure 9 from the masseter illustrates such a giant spindle of 10 fibres surrounded by spindles of 5 fibres. In these units the single spindles usually overlap each other to the equatorial region, and the great units may therefore extend through large parts of the muscle. *Sherrington* (1894) termed these structures compound spindles.

Each of the spindles in the unit is surrounded by its own capsule which joins those of the neighbouring spindles (Fig. 9). Thus there is in both planes established a great continuous capsule which permits the individual spindle to join its extrafusal fibres. It has never been seen that the fibres of different spindles in a unit make contact.

In a very few places tandem formations were observed. In these, 2 separate capsules share one or a few continuous intrafusal fibres. The few tandems occur both in spindle units and in simple spindles. More than one tandem structure has not been found in a spindle unit, not even in the greatest. Nor have tandems including more than two capsules been observed.

Spindle structure

All the examined spindles contain intrafusal fibres which differ in certain respects. They differ in diameter, even if this often is little pronounced. Furthermore, they usually differ in length. More characteristic is, however, the difference in number and arrangement of nuclei in their equatorial region. All fibres are multinucleated the nuclei being situated centrally as well as peripherally. In the lymph space region, however, the nuclei of some fibres are packed together, almost superseding the cytoplasm in this area. These fibres, therefore, are named bag fibres. The other category is named chain fibres since their nuclei through the lymph space region are arranged centrally in a con-

Fig. 10. Spindle with only one bag fibre (arrow) but several chain fibres. Masseter, van Gieson stain. × 620.

tinuous row, thus forming a chain-like arrangement (according to the terminology of *Boyd,* 1960). Different staining properties of bag and chain fibres could not be found.

Most of the spindles contain 5 to 7 fibres, of which 1 to 3 usually are of the bag type (Figs. 10 and 11). The bag and chain regions of adjacent fibres within the same spindle are always situated at the same level with minimal differences. The number of intrafusal fibres, however, shows great variations from 2 fibres in a very few spindles to 12 in some of the giant spin-

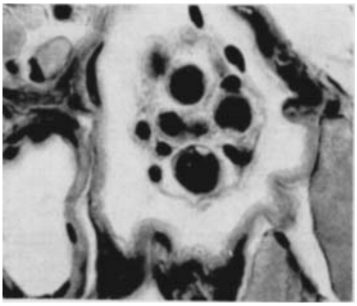

Fig. 11. Spindle with 3 bag fibres. Masseter, van Gieson stain. × 620.

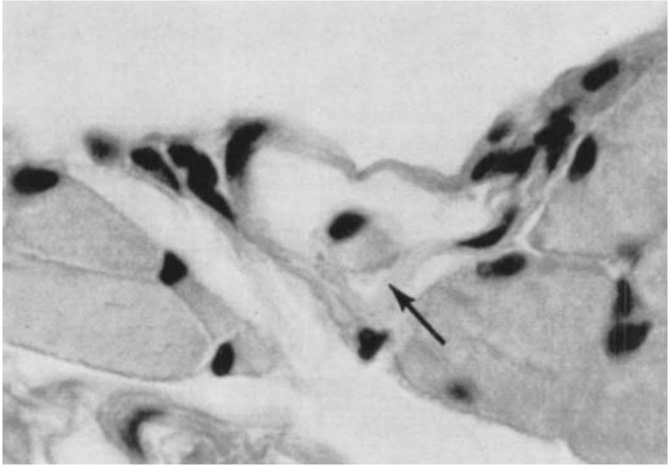

Fig. 12. Polar region of spindle which in this region has only one intrafusal muscle fibre. Masseter, van Gieson stain. × 900.

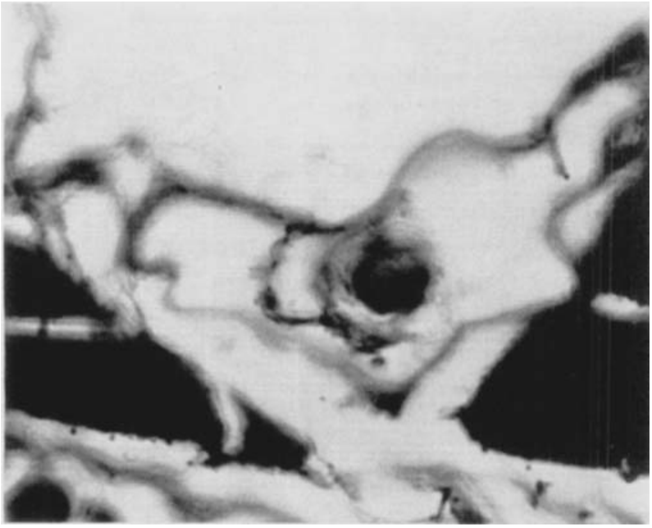

Fig. 13. Lymph space region of the spindle shown in Fig. 12 stained according to Bodian's method. The intrafusal muscle fibre is surrounded by nerve fibres. × 900.

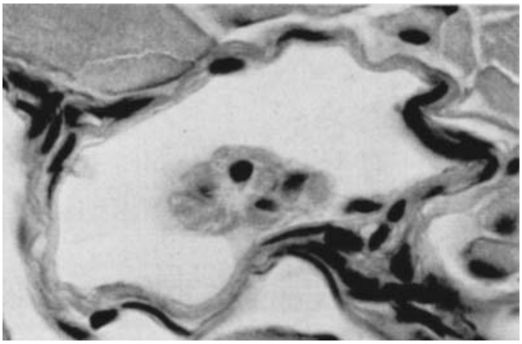

Fig. 14. The spindle shown in Figs. 12 and 13 from the other polar region. Here the spindle has three — possibly four — fibres, one of which is assumed to be of the bag type. van Gieson stain. × 900.

dles. In the first case one fibre is of the bag type, in the second case there are 4 bag fibres. Upon the whole, when studying serial sections one gains the impression that the chain fibres represent the most variable type, both with respect to number and length. While the bag fibres as a rule taper and extend beyond the spindle capsule at both ends, joining extrafusal fibres or other structures, the chain fibres often seem to join the bag fibres in the polar region within the capsule, or become attached to the capsule wall itself. On the other hand, spindles are found in which the chain fibres approximate the length of the bag fibres. In these spindles both fibre types penetrate the capsule. It should

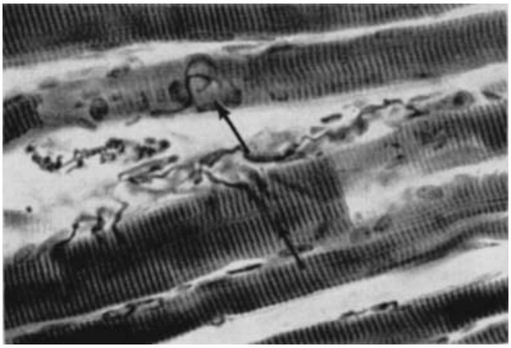

Fig. 15. Terminal arborizations of motor axon (arrow) in the middle region of an extrafusal fibre of the external pterygoid muscle. Bodian's method. × 620.

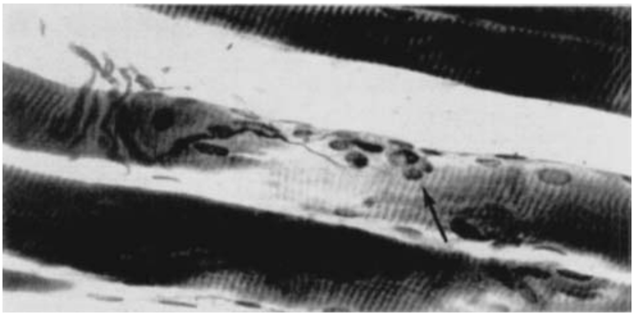

Fig. 16. Terminal arborization from the masseter. Note the accumulation of nuclei (arrow) in the terminal region. Bodian's method. × 620.

be emphasized, however, that studies of serial transverse sections revealed considerable variations with respect to the relative fibre length in a spindle.

In a very few cases, especially related to spindle units, one conspicuously long fibre was found to be enclosed in a separate sheath. This fibre (Figs. 12 and 13) is of the same diameter as the large bag fibres, and is at both ends attached to extrafusal fibres. It contains central and peripheral nuclei as well as a nuclear bag, and resembles a bag fibre. Beyond the lymph space, however, and through parts of one of the polar regions the cap-

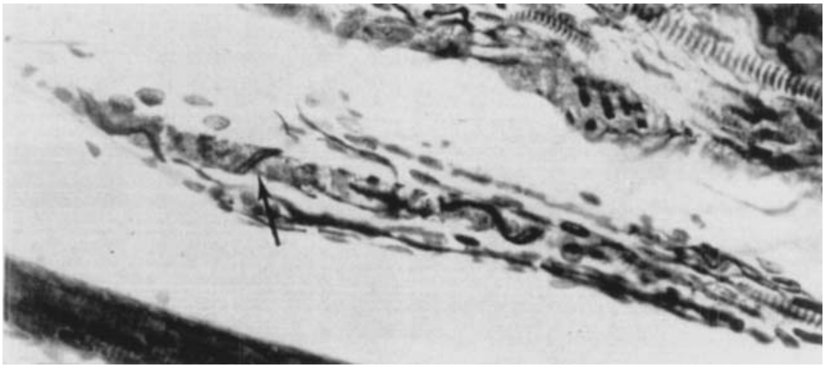

Fig. 17. Longitudinal section illustrating transitional zone at the end of the equatorial region. Note the two nerve fibres (arrow) at the left in the spindle. Bodian's method. × 620.

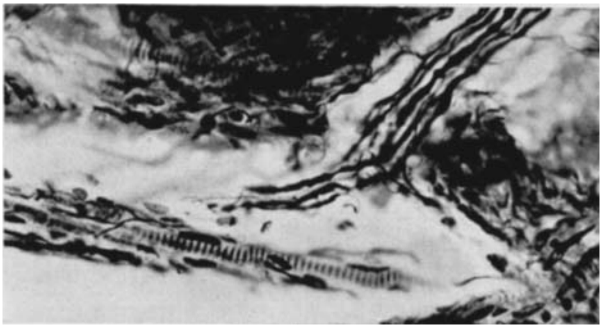

Fig. 18. Nerve bundle entering the lymph space region of a spindle. Bodian's method. × 620.

sule contains additional fibres (Fig. 14). These are much shorter and thinner than the long fibre and probably of the chain type. Whether they result from splitting of the long fibre or are separate fibres cannot be ascertained. The first assumption probably is correct.

The regions of the muscles provided with spindles show a conspicuous abundancy of nerve bundles of different sizes. These bundles again divide when approaching the spindle region where nerve bundles of 4 to 30 fibres run direct to the spindles. The fibre diameters vary. The smaller nerve bundles provide a single spindle, while the greater bundles are concerned with the innervation of greater spindles and units.

The individual spindle nerve usually bends towards the spindle in the polar region and runs along the capsule to the equatorial region where it enters the spindle (Fig. 8) and splits.

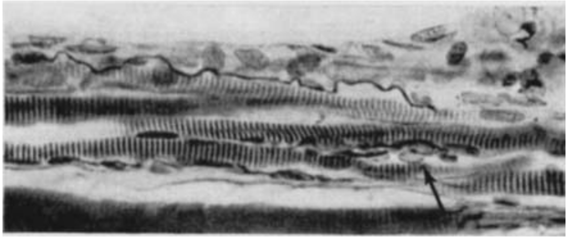

Fig. 19. Motor end plate (arrow) in the juxtaequatorial part of an intrafusal fibre. Bodian's method. × 620.

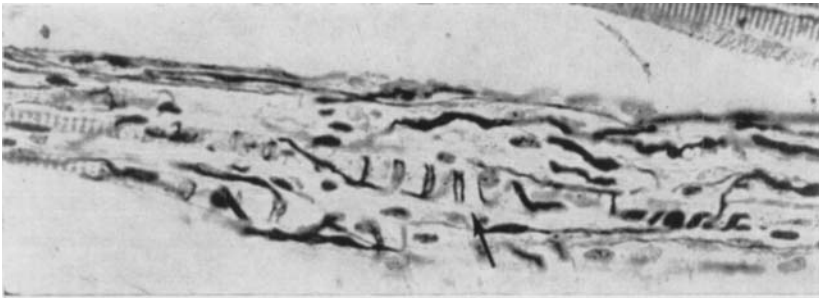

Fig. 20. The primary nerve ending of the muscle spindle is formed by two fine, parallel fibres which twine several times (arrow) around the intrafusal fibres. Bodian's method. × 620.

All the jaw muscles were also examined in longitudinal sections, which were stained according to the method of Bodian. Regarding the location of the motor end plates of extrafusal fibres the findings confirm those made with Miller's method. Additional information was, however, obtained as regards the mode of termination of the motor axon. While in the Miller stained sections only faintly indicated, it is in the Bodian sections clearly seen that the axon ends on the extrafusal muscle fibre with fine branches which split off immediately before the fibre is reached, thus forming a terminal arborization (Figs. 15 and 16).

Further details in the structure of the muscle spindles are also revealed in the Bodian sections. The findings substantiate those made in the transverse sections with regard to spindle distribution, formation of spindle units, and occurrence of bag and chain fibre nuclear arrangement in the equatorial region of the fibres. In addition, these sections reveal cross striation of the intrafusal fibres throughout their entire length, except for a restricted area in the equatorial zone where the nuclear concentration dominates the picture (Fig. 17).

Small bundles of nerve fibres enter into the spindle in the lymph space region (Fig. 18). In several cases it was possible to follow nerve fibres for some distance inside the capsule before they divided or were resolved into complex formations.

The nerve fibres entering the capsule are not of uniform diameter. On the other hand, for technical reasons it is very difficult in longitudinal sections to divide the fibres accurately into categories.

Inside and parallel with the capsule some nerve fibres are found which seem to be of a middle or small sized type. They run from the equatorial region in both directions and are seldom seen to divide before they terminate on the striated part of an intrafusal fibre. Here the nerve fibre branches and participates in the formation of a small motor end plate (Fig. 19).

Motor end plates are usually found within the capsule, but some fibres are also provided with a motor end plate in the extracapsular region. Not all the end plates are of the same appearance. While many of them are of an extensive, elaborate type, others appear as small, roundish dots and look simpler.

Motor end plates were found in all the spindles examined, and appear to occur most frequently on bag fibres.

From the relatively large nerve fibres entering the spindles, the so-called annulospiral or primary endings are formed within the area of the lymph space, both on bag and chain fibres. These nerve fibres apparently divide frequently, mostly inside the capsule.

In the vast majority of the cases the primary ending seems to twine several times around the intrafusal fibre in its equatorial region. These loops appear as composed of two fine and parallel nerve fibres (Figs. 17 and 20), resulting from division of a single fibre. In other cases the loops have the appearance of one broad nerve fibre. Where double fibre loops appear, the latter seem to give off very delicate branches, the courses of which cannot be followed.

In some spindles secondary terminations are observed. Their distribution and number vary extensively. They occur on both fibre types, but most frequently on the chain fibres.

On some intrafusal fibres, especially in greater spindles, some larger and middle sized nerve fibres are found. These fibres mostly terminate in the juxtaequatorial region where they form wavy and highly irregular sprays of fine fibrils. In addition to the nerve fibres described here, every spindle contains a number of delicate nerve fibres forming a complete network.

DISCUSSION

The findings made in this study largely confirm what is known as regards the innervation pattern of striated muscles in mammals. Thus it appears that in all jaw muscles the extrafusal muscle fibres receive their motor innervation in one relatively restricted zone situated equidistantly from the ends of the muscle. The direction of this zone is approximately perpendicular to the muscle fibre direction. This is in agreement with the findings by *Coërs* (1959) and *Christensen* (1959), who from studies of different muscles in man, cat and rat indicate that motor innervation in striated mammalian muscles with few exceptions occurs in restricted zones at the midpoint of the single muscle fibres. In addition, *Coërs* (1959) and *Christensen* (1959) found that in muscles with a single innervation band the muscle fibres run continuously from origin to insertion. Also in this respect the findings made in this study are in accordance with their observations. Usually only one end plate is situated on each muscle fibre of the jaw muscles, but in a few places two separate plates are found on the same fibre. The two plates lie close together. This pattern was occasionally observed by *Coërs & Woolf* (1959) in the limb muscles of the rat. Even though it was difficult to follow the terminal axon the present author gained the impression that the two end plates in the jaw muscles resulted as a branching of one terminating axon. It is interesting that similar observations were made in other rat muscles by *Edds* (1950).

Regarding the number of nerve fibres in the nerve bundles at the level of the innervation zone, *Coërs* (1959) gives numbers from 5 to 50 in various muscles. In the case of the jaw muscles of the rat many bundles contain less than 10 fibres. In none of the bundles did the number exceed 30, however.

In the Miller stained sections it appears very clearly that a great number of delicate boutons participate in the formation of the end plate. The same finding was made by *Coërs & Woolf* (1959) in the various types of muscles in the rat examined by these authors. The Bodian sections reveal further details in the end plates of the jaw muscles. The plexiform nature of the end plate is clearly visible, and in addition it is seen that the boutons terminate in a region of the muscle fibre where there is a great concentration of nuclei. The morphology of the motor end plate in the jaw muscles thus offers great resemblance to that of end plates in various muscles of man and guinea pig as these appear in silver stained sections (*Couteaux,* 1960). It should be mentioned, however, that *Coërs* (1953) and *Woolf & Till* (1955), judging from vitally stained specimens and material treated for cholinesterase activity, found striking differences in the morphology of end plates of man and rat. The reason for this discrepancy is not known.

Another interesting detail should be mentioned. Despite the absence of muscle spindles in the external pterygoid muscle (see later), the motor innervation of this muscle corresponds in all respects to that of the other jaw muscles examined.

Counting of muscle spindles was made on transverse sections stained according to van Gieson's method. The total number of spindles in one of each of the four muscles was registered accurately, and comparison made with corresponding areas of the same muscle on the opposite side in the same animal. The countings show that there is a slight bilateral asymmetry in the number of muscle spindles. *Barker* (1962) found the same in other muscles in the cat.

The masseter is far more richly endowed with spindles than are the other muscles. The masseter contains 130, the temporal 46, and the internal pterygoid muscle only 16 spindles. These proportions may seem striking compared with the numbers for the same muscles in man. These are 160, 217 and 155, respectively (*Freiman,* 1954). Furthermore, it is noticeable that *Freiman* (1954) found the spindles distributed in the medial as well as in the lateral parts of the muscles. Moreover, in the masseter 118 spindles were located in the lateral (superficial) and 42 in the profound part of the muscle. In the jaw muscles of the rat spindles were only found in the medial part of the muscle with exception of a few spindles in the lateral (superficial) part of the masseter. Since to the author's knowledge a similar distribution pattern has not been found in other mammals, the strictly medial location of spindles in the jaw muscles in the rat should probably be considered to be due to species differences. However, a somewhat uneven spindle distribution in both planes with spindle-rich and spindle-poor zones is also well known from other mammalian species (*Boyd*, 1962 a). Recalling the total absence of spindles in the distal third of the internal pterygoid muscle in rat it is interesting to notice that *Cooper & Daniel* (1949) find 41 out of 47 spindles in the proximal end of the human musculus rectus oculi inferior.

While the masseter, temporal and internal pterygoid muscles are well provided with spindles, at least in their medial portions, the external pterygoid muscle seems completely devoid of spindles. This muscle, therefore, was especially well examined through serial transverse as well as longitudinal sections. Special attention was paid to the region of origin and insertion of the muscle, but no spindles or spindle-like structures were observed. *Freiman* (1954) reached the same conclusion in his studies of jaw muscles in man, and *Cooper* (1960) confirmed the absence of spindles in this muscle in goat and cat. In this connection it should be mentioned that also the eye muscles show some peculiarities regarding spindle occurrence. Thus, although their presence has been confirmed in man, primates and some ungulates, they are assumed to be lacking in dog, cat and rabbit (*Cooper & Daniel*, 1949). In the external pterygoid muscle, however, spindles have hitherto not been found in any species. On the other hand, *Cooper & Fillenz* (1955) suggest that in muscles where spindles probably are lacking, other receptors may be present. This suggestion is based on experiments where afferent discharges were recorded when stretching of such muscles was made. So far, similar experiments have not been made with the external pterygoid muscle.

The architecture of the spindles of jaw muscles in rat is largely the same as that of mammalian spindles in general. The well known two fibre types, bag and chain fibres, are also found in the spindles of jaw muscles. As is found for spindles of other muscles they diverge strikingly in their nuclear arrangement. However, long as well as short fibres belong to both types. Except for the equatorial region no clear-cut difference in fibre diameters was observed, nor could the two intrafusal muscle fibre types be distinguished from each other by different staining properties. These findings are in agreement with those made by *Barker* (1962) in cat.

Obviously the spindle content varies in different muscles in the same species. Thus *Barker & Hunt* (1964) on the basis of studies of rectus femoris and soleus state that the typical fibre content of rat spindles is 2 bag and 2 chain fibres. This is a rather rare finding in the jaw muscles where most spindles contain 5—7 fibres of which 1—3 are bag fibres. It should also be recalled that in the jaw muscles spindles of 10 and 12 fibres occur.

A special spindle type was found in a few cases, and always in close association with other spindles and spindle units. This type is of a considerable extension and contains in its entire length an intrafusal fibre of relatively large diameter. In its equatorial region it resembles a bag fibre (Fig. 13), and here also a nerve fibre surrounds the muscle fibre. In one of the polar regions this fibre is in a restricted part associated with a few, short fibres similar to the chain type. Possibly this large fibre is of the same category as that described by *Barker* (1962) as belonging to a third type of muscle fibre which occasionally branches. It is, however, difficult to ascertain whether the smaller fibres result from splitting of the large fibre, or if they represent separate structures. Splitting of intrafusal fibres has long been a matter of controversy. *Barker* (1948), judging from studies in rabbit, denied splitting. Also *Boyd* (1958), *Cooper* (1960) and *Swett & Eldred* (1960) questioned a splitting. Later *Barker* (1959, 1962) admits the splitting of at least some chain fibres, and *Boyd* (1962 a) demonstrates the splitting of a bag fibre. It should be stressed, however, that it is often difficult to distinguish a splitting of fibres from separate fibres when these are of different length. Therefore, the present author cannot give decisive statements on this matter.

Tandem spindles are rare in the jaw muscles of the rat. On the other hand, spindle units are frequent. A great number of the spindles belong to complex formations where several spindles at different levels in the transverse plane overlap each other and share a common, continuous capsule. They have the same structure as similar units in many other mammals (see, e.g. *Eldred et al.*, 1962; *Cooper & Daniel*, 1963).

Since the muscle spindles act as stretch receptors, special attention has long been paid to their innervation. As is known today, the innervation of the spindles is very complex, and despite extensive research there are still many controversies concerning details in the innervation pattern. As early as in 1898, *Ruffini* gave a relatively detailed description of the afferent innervation of spindles. Later his findings have largely been confirmed (see, e.g. *Barker,* 1948; *Boyd,* 1962 a; *Cooper & Daniel,* 1963). The findings made in the present study show that primary endings are present on bag as well as on chain fibres in the jaw muscles of rat. They are more distinct and have a more uniform appearance on the bag fibres. The endings are located in the equatorial region and are derived from axons of relatively large diameters. While *Barker* (1962) found that branching of the primary nerve is rare, it appears to occur extensively in the jaw muscles. The axon may divide both outside and inside the capsule. In addition, at least two branches are observed in opposite directions inside some spindles. These branches probably run to different intrafusal fibres. The same findings were made by *Cooper & Daniel* (1963). Secondary terminations are present in some spindles. They occur in both fibre types, especially in chain fibres.

Other details are also observed. When one of the primary nerve fibres reaches the intrafusal muscle fibre it very often is seen to branch once more. From this final branching two parallel nerve fibres sweep around the muscle fibre (Figs. 17 and 20). To the author's knowledge this final branching giving rise to the double nature of the nerve fibres which form the primary ending has not been described in other mammals. *Coërs* (1962), judging from studies with vital staining, mentions some special broad fibres. Also *Cooper & Daniel* (1963) mention "broad ribbons and blobs". In their opinion these phenomena are the results of staining of nerve fibres and adjacent structures. Such broad fibres are also seen in some preparations in the present study. However, in sections 10 μ thick treated according to Bodian's method, two delicate fibres are seen to emerge from thicker fibres and thereafter to surround the intrafusal fibre. They are therefore different from the broad fibres.

Motor end plates on intrafusal fibres were first described by *Hines & Tower* (1928). Structures similar to extrafusal motor end plates, and resembling those illustrated by *Cooper & Daniel*

(1963), are also observed towards the polar region on the intrafusal fibres of jaw muscles. They seem to arise from relatively small fibres which run straight from the equatorial zone to the end plate region probably without branching.

In addition to the nerve endings here mentioned, there are along almost the entire length of the muscle fibre small circular, irregularly distributed dots. These are not present in the equatorial region. As far as could be judged, they are related to small nerve fibres. They are, like similar structures described by *Coërs* (1959), considered to belong to the motor system. Recently *Barker & Ip* (1964) too have given evidence of two kinds of motor endings in spindles from cat and rabbit.

Finally, a complex network of nerve fibres of irregular course occupying the juxtaequatorial region, and extending somewhat in the polar direction, should be mentioned. These fine fibres seem to be derived from thicker fibres. They are probably identical to the flower spray endings described by *Coërs & Woolf* (1959), *Coërs* (1959), *Cooper & Daniel* (1963) and others. Whether in the jaw muscles they belong to the motor or sensory system cannot be decided from the present study. *Coërs* (1962) when comparing histological and histochemical findings recently suggests that flower spray endings probably are related both to the motor and to the sensory systems.

SUMMARY

The present study deals with the location of motor end plates and the distribution and histological structure of muscle spindles in jaw muscles of the rat.

White adult normal rats were used. The excised muscles were treated according to Miller's, van Gieson's or Bodian's staining methods. The masseter, the temporal and the internal and external pterygoid muscles were examined.

In all muscles, the fibres run continuously from origin to insertion. One motor plate is situated approximately at the midpoint of each fibre. Very few muscle fibres have two motor end plates close together. Thus a motor innervation band is located across the muscle equidistantly from both ends. The end plates are of a plexiform type.

Muscle spindles were found in the medial portions of the masseter, the temporal and the internal pterygoid muscles; in the latter only in the proximal two thirds. In the external pterygoid muscle no spindles were found.

The spindles of the examined muscles all have bag and chain fibres. In a few cases spindles were observed which contain one long fibre, probably of the bag type, and in its polar region a few short fibres, seemingly of the chain type. The spindles occur singly or in complex units. In a few cases an extension of the spindle capsule also surrounds a small bundle of extrafusal muscle fibres.

In some sections the primary endings consist of two parallel nerve fibres resulting from a terminal splitting of the nerve fibre as this reaches the intrafusal fibre. Intrafusal motor end plates are observed in all spindles.

RÉSUMÉ

LOCALISATION DES PLAQUES MOTRICES ET DISTRIBUTION ET STRUCTURE HISTOLOGIQUE DES FUSEAUX NEUROMUSCULAIRES DANS LES MUSCLES MASTICATEURS DU RAT

La présente étude a pour objet la localisation des plaques motrices et la distribution et la structure histologique des fuseaux neuromusculaires dans les muscles masticateurs du rat.

Des rats blancs adultes normaux ont été utilisés. Les muscles excisés ont été traité par les méthodes de coloration de Miller, de van Gieson et de Bodian. Les muscles masséter, temporal, ptérygoïdien interne et ptérygoïdien externe ont été examinés.

Dans tous les muscles, les fibres vont d'un trait de l'origine à l'insertion. Une plaque motrice est située à peu près au milieu de chaque fibre. Qualques fibres très peu nombreuses ont deux plaques motrices l'une près de l'autre. Il existe donc une zone d'innervation motrice en travers du muscle à égale distance des deux extrémités. Les plaques motrices sont du type "plexiforme".

Les fuseaux neuromusculaires ont été trouvés dans la partie médiane des muscles masséter, temporal et ptérygoïdien interne; dans ce dernier seulement dans les deux tiers proximaux. Dans le ptérygoïdien externe, aucun fuseau neuromusculaire n'a été trouvé.

Les fuseaux des muscles examinés avaient tous des fibres de type "bag" et de type "chain". Dans quelques cas, on a observé des fuseaux contenant une longue fibre, probablement de type "bag", et dans la région polaire quelques fibres très courtes, probablement de type "chain". Les fuseaux se présentent isolément et en associations. Dans quelques cas, une extension de la gaine du fuseau englobe un petit faisceau de fibres musculaires extérieures au fuseau.

Dans quelques coupes, les terminaisons primaires consistent en deux fibres nerveuses parallèles résultant d'une division terminale de la fibre nerveuse lorsqu'elle atteint la fibre musculaire du fuseau. Des plaques motrices à l'intérieur du fuseau ont été observées dans tous les fuseaux.

ZUSAMMENFASSUNG

DIE LOKALISIERUNG MOTORISCHER ENDPLATTEN UND DIE ANORDNUNG DER MUSKELSPINDELN IN DEN KAUMUSKELN DER RATTE

Die Untersuchung umfasst die Lokalisierung von motorischen Endplatten und die Anordnung und histologische Struktur der Muskelspindeln in den Kaumuskeln der Ratte.

Weisse, erwachsene, normale Ratten kamen zur Verwendung, und Millers, van Giesons oder Bodians Färbemethoden wurden benutzt. M. Masseter, M. Temporalis, M. Pterygoideus int. und ext. wurden untersucht.

In allen Muskeln verlaufen die Fasern kontinuierlich von Ursprung zu Ansatz. Eine motorische Endplatte liegt ungefähr in der Mitte von jeder Faser. Einige Fasern haben zwei benachbarte Endplatten. Es entsteht also eine Innervationszone quer über den Muskel, gleichweit von Ursprung und Ansatz. Die Endplatten sind alle "plexiformer" Natur.

Die Muskelspindeln befinden sich in den medialen Gebieten des Masseters, Temporalis und Pterygoideus int., in dem letzteren doch nur in den proximalen zwei Dritteln. In Pterygoideus ext. wurden keine Muskelspindeln gefunden.

Die Spindeln der untersuchten Muskeln haben sowohl "Bag" als "Chain" Fasern. In einigen Spindeln befindet sich eine lange, intrafusale Faser, wahrscheinlich eine "Bagfaser", und in dem einen Endgebiet der Spindel befinden sich ein paar sehr kurze

Fasern, wahrscheinlich "Chainfasern". Es kommen sowohl einzelne Spindeln als grosse Spindelnkomplexe vor.

In einigen Fällen besteht "the primary ending" von zwei parallellaufenden Spiralen, da sich die Nervenfaser, indem sie die intrafusale Muskelfaser erreicht, teilt. Intrafusale, motorische Endplatten befinden sich in allen Spindeln.

In einigen Fällen schliesst die Spindelkapsel ein kleineres, extrafusales Faserbund ein.

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