A study of single and tandem types of muscle-spindle in the cat

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A tandem spindle is defined as one in which several encapsulated sensory regions are linked together by some degree of muscle fibre continuity. Generally only one or two muscle fibres are continuous from capsule to capsule, while the rest taper off and partake of only one encapsulation. In the most common type, two capsules occur in linear succession (double tandem); triple and quintuple arrangements were also observed but not quadruple ones. Of 64 complete tandem spindles from cat rectus femoris cut in transverse section, 88% were double, 9% triple, and 3% quintuple. As measured in sectioned adult rectus femoris, the length of tandem spindles was 8.45 to 22.30 mm, mean 13.9 ± 3.24 mm (s.d.); by contrast, the length of 144 single spindles was 2.40 to 13.68 mm, mean 7.02 ± 2.45 mm (s.d.).

A study of the afferent innervation of 27 tandem spindles from the mesial flexor digitorum longus, semitendinosus, soleus, and rectus femoris muscles showed that the typical pattern was for a complex or intermediate capsule to be linked with one or two simple capsules. A quarter of the double tandems had complex or intermediate/intermediate capsule combinations; combinations in which all the capsules were simple, or all complex, did not occur. The primary ending in the simple capsules is invariably either wholly or predominantly irregular, and the intramuscular diameter of the fibre supplying it is usually less than that of fibres supplying other primary endings.

On the basis of a study of serial transverse sections of a pair of kitten recti, and of twelve blocks sampled from the recti of six cats, it is concluded that 16 to 20% of the spindles in the cat's rectus femoris are of the tandem type. Access to quantitative data gathered in connexion with other work suggests that, as compared with rectus femoris, the proportion of tandem spindles in semitendinosus and mesial flexor digitorum longus is slightly higher; in soleus, about the same; and in the pes interossei, considerably lower.

An analysis of the results of teasing seven entire adult rectus femoris muscles indicates the following conclusions with regard to the proprioceptive equipment: (a) the intermediate type of single spindle occurs, on the average, with about double the frequency of either simple or complex types; (b) primary and secondary endings are present in about equal proportion in the muscle; (c) there are usually fewer tendon-organ endings than primary endings (average 80%), but the proportion varies widely (41 to 139%) in different muscles; (d) paciniform corpuscles are relatively scarce and there appears to be no correlation between their frequency of occurrence as compared with other proprioceptors. The soleus, semitendinosus, and mesial flexor digitorum longus muscles appear to resemble rectus femoris with respect to (a) and (b), but in the fourth internal intercostal muscle complex spindles appear to be most frequent and secondary endings more abundant.

The position and measurements of 144 single spindles in rectus femoris indicate that the lengths of the poles are related to the position of the spindle in the extrafusal muscle bundles and its orientation with respect to nerve supply.

A re-appraisal of Rufin's classic paper (1898) on muscle-spindles suggests that in several respects the description was based on incomplete spindles cut in teasing gold chloride preparations. It is also evident that, owing to the methods employed, counts of muscle spindles made by most previous workers should probably be regarded as counts of spindle capsules. Failure to distinguish between single and tandem types of spindle also vitiates many of the measurements made of spindle length. Some discussion is offered on whether there is any functional significance in the tandem type of spindle and the proportional distribution of spindle types in a muscle.

Introduction

The tandem type of spindle has two or more encapsulated sensory regions spaced along the length of the intrafusal bundle, in contrast to the single spindle, which has one such region situated equatorially between two poles. While the term
polar regions are coupled together side by side, or spliced together by interdigitation, or so placed that there is only a short distance between the end of one spindle and the beginning of the next. It is convenient to restrict the morphological definition of a tandem spindle to those instances where the continuity of individual muscle fibres links successive capsular regions together. This is, in fact, the most common tandem condition in rectus femoris; in a sample of 119 spindles studied in sections of this muscle, there were 26 tandem spindles as defined above as against 9 instances of end-to-end arrangement. Double primary innervation rarely occurs; only 10 out of 689 spindle capsules teased from the 7 recti showed this condition, and the highest yield from an individual muscle was no greater than 3.6%.

The typical arrangement of the muscle fibres in a tandem spindle is for only one or two to be continuous from capsule to capsule while the rest taper off and partake of only one encapsulation. The continuous fibres are always of large diameter and usually bear nuclear bags in each successive capsule, while the others are mostly of small diameter and seldom interdigitate in the intercapsular regions. The most common type of tandem is that in which two encapsulated sensory regions occur in linear succession (double tandem spindle). We have also observed spindles with three and five successive capsular regions (triple and quintuple tandem spindles) but have not encountered a quadruple arrangement. Of 32 complete tandem spindles found in the adult rectus femoris sample, 28 were double and 4 triple. The kitten recti also yielded 32 tandem spindles of which 28 were double, 2 triple, and 2 quintuple. Hence of 64 complete tandem spindles studied in transverse section, 88% were double, 9% triple, and 3% quintuple. One of the quintuple tandem spindles from the kitten had four successive capsular regions while the fifth was located on a few intrafusal muscle fibres which left the main axial bundle to run alongside it as a side branch. This was the nearest approach to the compound tandem arrangement that occurs in the frog (Barker et al. 1960).

One of the capsular regions of a tandem spindle is generally considerably larger than the other(s) and contains 10 to 12 muscle fibres as compared with 3 or 4 found in the smaller capsule(s). In the large capsules there are usually from 3 to 6 muscle fibres with nuclear bags, as compared with only 0 to 2 in the smaller capsules. The other muscle fibres, in both large and small capsules, are smaller in diameter and possess simple chains of nuclei in place of nuclear bags. When present, the nuclear bag regions of the muscle fibres in the small capsules are always smaller and less pronounced than those in the large capsules.

Measurements of the total, polar, capsular, and intercapsular lengths of 32 tandem spindles from rectus femoris are shown in table 1. In designating a pole as ‘proximal’ or ‘distal’, the terms are used as advocated by Barker (1948) and denote polar orientation with regard to the origin or insertion of the muscle fibres respectively; capsule length is interpreted as described above (p. 379). The intercapsular regions are usually more than twice as long as the poles; in only one eighth of the tandem spindles studied were they of the same length or shorter. In these spindles the number of muscle fibres maintaining continuity between successive capsules is greater than when the intercapsular regions are longer.
Approximately one quarter \((25 \pm 6\% \text{ s.d.})\) of the total length consists of encapsulated sensory regions.

**Table 1. Length Measurements (mm) of 32 Tandem Spindles from Adult Cat Rectus Femoris**

<table>
<thead>
<tr>
<th>Region</th>
<th>Range</th>
<th>Mean and SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>Proximal pole</td>
<td>0-25-6-10</td>
<td>2.07 ± 1.44</td>
</tr>
<tr>
<td>Large capsule</td>
<td>1-08-3-20</td>
<td>2.15 ± 0.68</td>
</tr>
<tr>
<td>Small capsule</td>
<td>0.46-1.69</td>
<td>0.98 ± 0.41</td>
</tr>
<tr>
<td>Intercapsular region</td>
<td>1.09-7.39</td>
<td>4.79 ± 1.67</td>
</tr>
<tr>
<td>Distal pole</td>
<td>0.11-6.16</td>
<td>2.24 ± 1.38</td>
</tr>
<tr>
<td>Total length</td>
<td>8.43-22.30</td>
<td>13.00 ± 3.24</td>
</tr>
</tbody>
</table>

**Innervation**

It is convenient, in description, to use Ruffini’s (1898) categories of afferent innervation (simple, intermediate, and complex), with the complex category extended to include spindle capsules in which more than two secondary endings occur. We shall also use the symbols \(P, p, S,\) and \(s\) to denote primary and secondary endings and their degree of regularity (see Barker & Ip 1960), i.e. *primary endings*: \(P,\) wholly regular; \(p,\) wholly irregular; \(Pp,\) predominantly regular; \(pP,\) predominantly irregular; \(P-p,\) about half and half; *secondary endings*: \(S,\) chiefly rings and spirals; \(s,\) chiefly sprays. Since the two terminations vary in form over a range that is without clear discontinuity, it is necessary to summarize the histological criteria by which they may be distinguished. A primary ending is present in all capsules as the sole termination found in association with nuclear bags, and is supplied by the largest nerve fibre innervating the spindle. Its ramifications occupy a central position in the area of equatorial nucleation, and are never flower-spray in form. A secondary ending is present in intermediate and complex capsules only, and is located mainly to one side of the primary ending, sometimes extending into the juxta-equatorial region to produce ramifications of the flower-spray type on polar-form muscle fibres. The diameter of the nerve fibre supplying the secondary is smaller than that of the primary, and the width of the terminal ramifications is narrower.

In teased gold chloride preparations it is sometimes difficult to distinguish between a true tandem spindle, in which there is continuity of individual muscle fibres between capsules, and end-to-end arrangements of single spindles. In this respect, however, the study of sectioned rectus femoris material serves as a guide for it indicates that the chances of encountering end-to-end arrangements as opposed to true tandems are about one in four in this muscle (see p. 380). We have nevertheless excluded from our analysis of the innervation those preparations in which there was the slightest doubt about the true tandem condition. Our observations are based on the examination of ten tandem spindles from semitendinosus, eight from mesial flexor digitorum longus, seven from rectus femoris, and two from soleus. Only a few of these were teased out with their extremities intact, but in view of the high proportion of double tandems in rectus femoris,
Figure 1. Double tandem spindle with intermediate and simple capsules from cat flexor digitorum longus (gold chloride preparation). In the small-scale drawing the motor innervation is omitted. Primary and secondary endings indicated by symbols as used in the text.

it is probably safe to assume that the majority of those with one or both extremities cut were of the double type.

A double tandem spindle typically consists of a capsule with complex or intermediate afferent innervation linked to a capsule with simple innervation. In other
words, a secondary innervation is usually borne by only one of the two capsules, and since size of capsule is directly related to degree of secondary innervation, this is the largest. While two intermediate capsules may be linked together to form a tandem, we have never observed a tandem consisting of two complex capsules, and have only found simple capsules linked together to form part of triple tandems. In the preparations examined, 74% consisted of complex or intermediate/simple combinations, while the rest of the double tandems were complex or intermediate/intermediate combinations. The frequency of an intermediate or complex innervation of one of the capsules is about 50% each.

The primary ending in simple capsules belonging to tandem spindles is invariably either wholly or predominantly irregular. For example, a triple tandem teased from rectus femoris had a large capsule with complex innervation of S Pp s s, succeeded by two small capsules with a simple innervation of p and pP. In 18 simple capsules belonging to tandems, the ending was of the p type in 8 cases, pP in a further 8, P-p in one, and Pp in one. The intramuscular diameter of the fibres supplying these endings is usually less than that of fibres supplying other primary endings. The number of secondary endings in the complex capsules is usually two, but we have observed two such capsules with three secondaries, and two with four. There were only two instances of more than one primary ending occurring in a capsule, and one of these belonged to a tandem of exceptionally rich afferent innervation teased from flexor digitorum longus which consisted of a large capsule with three primary and four secondary endings succeeded by a smaller capsule with intermediate innervation.

The motor innervation of tandem spindles is distributed throughout the muscle bundle in the polar and intercapsular regions. A detailed analysis of it has not been made, but it is worth noting that in three tandems there were terminations which appear to conform with those described by Boyd (1958, 1959) and since demonstrated by him, in ganglionectomy and recording experiments, to be conclusively motor (personal communication). Three endings presumed to be of this type were seen, located on polar regions and adjacent to secondary endings of the s type. It is not unusual for secondary endings to overlap with the motor innervation in the juxta-equatorial region; this probably accounts for the appearance of the phosphatase preparations of Coërs & Durand (1956).

Figure 1 illustrates most of the features of a typical tandem spindle; the drawings are based on a photographic montage of the teased gold chloride preparation.

**Proportion of tandem spindles in rectus femoris**

Examination of the serial transverse sections of each rectus femoris muscle of the kitten showed that there were 17 tandem spindles and 79 single spindles present in the left rectus, and 15 tandem and 75 single spindles present in the right rectus. The proportion of tandems among all spindles present (hereafter referred to as the tandem fraction) was thus 17.7% in the left rectus and 16.7% in the right.

The sample of 12 blocks of adult rectus muscle had 19 complete and 7 incomplete tandem spindles, as against 93 complete single spindles and 25 incomplete spindles in which only capsule was present. That some spindles should be incomplete is
inevitable owing to damage caused in the regions of the cuts made on removing each block from the muscles sampled. Considered in terms of complete spindles only, the tandem fraction is thus 17%. However, we must allow for the possibility that some of the 25 incomplete and apparently single spindles may have been cut portions of tandem spindles. Assuming all tandems involved to be of the double variety, the most common kind (88%), each one will thus have been recorded as two cut single spindles. If \( x \) is the number of tandem spindles so recorded, the total number of single spindles present may be represented as \( 93 + (25 - 2x) \), and the total number of tandems as \( 19 + (7 + x) \). Since the average length of a double tandem spindle is 1.74 times that of a single spindle, it follows that it has 1.74 times more chance of being cut. Further, the percentage of tandem spindles which were cut may be regarded as 1.74 times the percentage of single spindles cut. This allows the following equation to be derived:

\[
\frac{100 (7 + x)}{26 + x} = 1.74 \frac{100 (25 - 2x)}{118 - 2x}
\]

from which it may be calculated that \( x = 1.98 \). Taking all the spindles recorded into account, and allowing for the correction of an additional 2 double tandem spindles, the tandem fraction thus becomes

\[
\frac{19 + 7 + 2}{93 + (25 - 4) + 19 + (7 + 2)} \times 100 = 19.7%.
\]

If one of the two additional tandems is regarded as being of the triple kind, a rare contingency in view of their scarcity (9%), the tandem fraction would be increased by 0.14%. If we assume, on the other hand, that the cut portions of tandem spindles involved were of the triple variety, the value for \( x \) would be 3.48, increasing the tandem fraction to 21.5%. The chances of this being so, however, are 9% as against 88%, and the addition of two double tandem spindles is probably an adequate corrective to apply.

These results suggest that the proportion of tandem spindles present in the cat’s rectus femoris is fairly constant, and that we may regard it as being from 16 to 20% of the total spindle content of the muscle. In view of the fact that the figure of 19.7% was derived from the block sample in which six cats were used, as opposed to the slightly lower values obtained from the single pair of kitten recti, the tandem fraction should probably be regarded as lying nearer 20 than 16%.

**Distribution of tandem spindles in rectus femoris**

In the block sample of adult recti, and in the kitten recti, there was a tendency for the lateral half of the muscle to have more tandem spindles distributed within it than the mesial half. If the density of tandem spindles present in either half is expressed as a percentage of the total number of tandems present in the whole muscle, and if the symbols \( R, L, l, \) and \( m \) are used as above (p. 378), the density of tandem spindle distribution in the pair of kitten recti may be expressed as: \( Rl 25\%; Rm 22\%; Ll 34\%; Lm 19\% \). Similarly, the density distribution in the
block sample of adult recti may be expressed as: \( Rl \ 23\%; \ Rm \ 23\%; \ Ll \ 31\%; \ Lm \ 23\% \). The combined density in right and left lateral halves of the kitten recti compared with the combined density of the right and left mesial halves was thus 59 and 41\% respectively. A similar comparison of the combined density of tandem spindles in all lateral and all mesial adult rectus blocks gives 54 and 46\% respectively.

The distribution may alternatively be expressed in terms of the density of tandem spindles present in the muscle, which is regarded as divided into four equal quarters numbered first to fourth from origin to insertion. In this way the density of tandems in those blocks of adult recti taken from the first quarter is 30.8\%, from the second 38.5\%, the third 11.5\%, and the fourth 19.2\%. The combined figures for the pair of kitten recti are 25\%, 31.3\%, 28.1\% and 15.6\% for the first to the fourth quarters respectively.

![Figure 2](http://rspb.royalsocietypublishing.org/) Distribution of single (□) and tandem (■) spindles in a pair of kitten rectus femoris muscles. The histograms illustrate the combined data for both muscles in terms of muscle width and depth.

These results are what might be expected from the counts made of the spindle capsules in the cat's rectus femoris by Barker & Chin (1960). Their counts show there to be consistently more spindle capsules located in the lateral than in the mesial half of the muscle, and more in the proximal than in the distal half of the muscle, the distribution being related to nerve entry and the distribution of the major intramuscular nerve-trunks. It is evident that the distribution of tandem spindles forms part of this overall pattern, and this is clearly shown in the histograms of the distribution of single and tandem spindles in the pair of kitten recti (figure 2). There appears to be no constant feature regarding the location of tandem spindles in relation to the extrafusal muscle bundles; tandems may occur in any region of the muscle-bundles, and may sometimes even occupy their entire length.
SINGLE SPINDLES

Polar and capsular measurements

The sample of 12 blocks of rectus femoris taken from 6 cats for the tandem spindle study, together with the further 7 blocks taken for general study, gave 144 complete single spindles for measurement. It soon became obvious that polar length was related to the position of the spindle within the muscle. To facilitate description, we have regarded the extrafusal muscle bundles of rectus femoris as occupying three areas in their course from the tendon of origin, or from the central tendon, to their insertion on to the enveloping aponeurosis, or the tendon of insertion. These areas are designated the proximal, middle, and distal thirds of the muscle bundles (figure 3). Those bundles comprising the slip on the mesial side of rectus do not fall into this scheme, but their number is relatively so few that they may be ignored, and, as it happens, none of the spindles measured was located in this area.

Measurements of the polar, capsular, and total lengths of the 144 single spindles are shown in table 2, and in figure 4 the polar lengths are plotted against each other.

Figure 3. Schematic diagram showing a portion of the lateral half of the cat's rectus femoris as if cut in horizontal longitudinal section, and illustrating the proximal, middle, and distal-third regions of the extrafusal muscle bundles. A single spindle is shown in each region drawn in proportion to the average polar and capsular measurements of single spindles located in that region. The main intramuscular nerve trunk is shown in its characteristic position, and the spindles are shown diagrammatically as receiving a primary nerve fibre only.
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Figure 4. Proximal polar length plotted against distal polar length for 43, 51, and 50 single spindles from the proximal, middle, and distal-third regions respectively of the muscle bundles of the cat’s rectus femoris. Points on the hypotenuse in each graph represent spindles with poles of equal length.

Table 2. Length Measurements (mm) of 144 Single Spindles from Adult Cat Rectus Femoris

<table>
<thead>
<tr>
<th>Muscle-Bundle Region</th>
<th>Proximal Third</th>
<th>Middle Third</th>
<th>Distal Third</th>
</tr>
</thead>
<tbody>
<tr>
<td>Proximal Pole</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Range &amp; S.D.</td>
<td>0.47 ± 1.64</td>
<td>1.47 ± 3.64</td>
<td>1.31 ± 3.12</td>
</tr>
<tr>
<td>Distal Pole</td>
<td>1.28 ± 2.89</td>
<td>0.95 ± 3.24</td>
<td>0.08 ± 1.86</td>
</tr>
<tr>
<td>Capsule</td>
<td>0.42 ± 1.30</td>
<td>0.50 ± 1.83</td>
<td>0.45 ± 1.35</td>
</tr>
<tr>
<td>Total Length</td>
<td>2.40 ± 5.82</td>
<td>3.24 ± 8.71</td>
<td>2.90 ± 6.33</td>
</tr>
</tbody>
</table>

Total length of all spindles: range, 2.40–13.68; mean, 7.02 ± 2.45 s.d.

in the case of 43, 51, and 50 single spindles located in the proximal, middle, and distal thirds of the muscle-bundles respectively. Two conclusions may be drawn from the data thus presented: (a) With few exceptions, those spindles situated in the proximal third have longer distal poles than proximal; those in the middle third have poles more or less equal in length; and those in the distal third have longer proximal poles than distal. (b) The longest spindles are those located in the middle-third region, and these tend to have the longest equatorial encapsulation.

The relationship between polar length and spindle position is further reflected if the mean polar lengths for each region are expressed as percentages of the mean.
total spindle length for each region. Thus for spindles in the proximal-third region
the mean proximal polar length is 28% of the mean total spindle length, as com­
pared with 50% in the case of the distal pole. In the middle-third region the
proportions are 42 and 37%, and in the distal-third region 49 and 29%, for the
proximal and distal poles respectively.

It very seldom happens that a spindle is virtually unipolar as shown in Denny-
Brown’s schema of end-organs in mammalian muscle (in Creed, Denny-Brown,
Eccles, Liddell & Sherrington 1932, figure 71). In this series there was one such
spindle with polar lengths of 2·7 and 0·08 mm, and another of 4·7 and 0·45 mm
(proximal pole longest in both cases), but polar lengths of less than 0·5 mm are
rare.

In this sample of single spindles, the length of the intrafusal bundle encapsulated
in the equatorial region varied from 9 to 44% of the total length, the mean lying
at 21 ± 7%. Hence we may conclude that usually about one fifth of the length of
a single spindle in the cat’s rectus femoris is occupied by an encapsulated sensory
area in fixed material of this kind, a slightly lower proportion than for tandem
spindles (25 ± 6%). Swett & Eldred (1960b), taking points of measurement which
appear to coincide with our own and applying a correction of 15% to compensate
for shrinkage, found capsule length to be 30 to 50% of the total length of single
spindles in the cat’s soleus and mesial gastrocnemius muscles. However, there is
reason to suppose that their spindle length measurements may be on the low side
owing to deliberate omission of sections from the series examined (see Discussion).

Measurements of nuclear bag regions

Typically, the nuclear bags do not all lie at the same level in the intrafusal
bundle, so that the length of the region in which they occur is slightly longer than
the length of individual bags. In a sample of 94 single spindles from adult rectus
femoris, the length of the nuclear bag regions varied from 0·07 to 0·42 mm, with
73·4% measuring between 0·1 and 0·2 mm. Barker (1948) found the nuclear bag
region of the intrafusal bundle usually lying towards one end of the capsule. In
the above sample it occurred towards the proximal end in approximately 50% of
the spindles; towards the distal end in 40%; and in the middle in 10%. Where
there is a difference in length between the polar regions of a single spindle, there
is a tendency for the nuclear bag region to lie nearest to the longer pole. In the
sample studied, 91 of the spindles had poles of unequal lengths, and the nuclear
bag region lay nearest to the longer pole in 62%, as compared with 38% in which
it lay nearest to the shorter pole.

Proprioceptive equipment of rectus femoris

An analysis of the proprioceptive equipment of the cat’s rectus femoris is
presented on the basis of the results of teasing seven entire adult recti treated by
the gold chloride method. It was undertaken in order to determine whether, in
addition to the fairly constant tandem fraction, there was any constancy in the
proportional distribution within the muscle of simple, intermediate, and complex
types of single spindle; and whether there was any characteristic pattern in the
proportional distribution of nerve endings belonging to fibres of Group Ia (primary), Ib (tendon-organ), II (secondary), and paciniform corpuscles. A brief note summarizing the preliminary results of this work has already appeared (Barker 1959).

Muscle-spindles

It is necessary, in the first instance, to examine the results of teasing each muscle in terms of the number of spindle capsules obtained, classified according to their type of afferent innervation. These data are presented in table 3 together with the results of the spindle capsule count obtained from sectioning the rectus of the contralateral limb. Also shown are the control estimates, made from these counts, of the spindle capsule content of the muscles teased, as derived from the prediction formulae of Barker & Chin (1960). It will be seen that in the five cases where this control was applied, the approximation between the predicted number of spindle capsules in the teased muscle and the number actually obtained by teasing is very close. We may assume, therefore, that virtually no spindle capsules are lost in the teasing technique. However, cutting damage, or poor reduction, renders it impossible to identify the afferent innervation of some of the spindle capsules, and in this series 85, or 12·3%, were so affected. In terms of the variation in afferent innervation of spindle capsules present, it is evident that the order of frequency is intermediate, simple, complex.

Table 3. Spindle capsule content of rectus femoris

<table>
<thead>
<tr>
<th>afferent innervation</th>
<th>teased muscles</th>
<th>sectioned contralateral muscles</th>
</tr>
</thead>
<tbody>
<tr>
<td>cat</td>
<td>(1)</td>
<td>(2)</td>
</tr>
<tr>
<td></td>
<td>simple</td>
<td>intermediate</td>
</tr>
<tr>
<td>C4</td>
<td>41</td>
<td>31</td>
</tr>
<tr>
<td>C5</td>
<td>17</td>
<td>41</td>
</tr>
<tr>
<td>C35</td>
<td>21</td>
<td>30</td>
</tr>
<tr>
<td>C41</td>
<td>28</td>
<td>33</td>
</tr>
<tr>
<td>C42</td>
<td>34</td>
<td>37</td>
</tr>
<tr>
<td>J12</td>
<td>27</td>
<td>34</td>
</tr>
<tr>
<td>J18</td>
<td>37</td>
<td>36</td>
</tr>
<tr>
<td>total</td>
<td>205</td>
<td>242</td>
</tr>
</tbody>
</table>

* Diagnosis of afferent innervation prevented by cutting damage or reduction quality.

In order to demonstrate how these results may be used to calculate the proportional distribution of spindle types, we will take the data of the teased rectus femoris from cat C41. The number of tandem spindles teased out from this muscle was four (three double and one triple). However, since the tandem fraction of the muscle is 16 to 20%, and since approximately 70% of the spindles suffer one or both poles being cut in teasing, we may assume that more tandem spindles were present than found, and that they have appeared in the preparations as incomplete single spindles. From the study of sectioned material it was found (p. 380) that the
double type of tandem most frequently occurred (88%), and the quintuple type occurred so seldom (3%) that our calculations will not be unduly affected if we regard the tandems present as being 88% double and 12% triple. If we assume the tandem fraction to be 20%, and regard the number of tandem spindles that this represents as x, it follows that the number of single spindles present is 4x. The maximum number of apparently single spindles that could be produced by cutting tandems may be expressed as $2\left(\frac{88}{100}x\right) + 3\left(\frac{12}{100}x\right)$, and since the total number of capsules teased from the muscle was 100, we may derive the equation $1.76x + 0.36x + 4x = 100$, which gives a value for x of 16.3. Hence we may conclude that there were 16 tandem spindles present in this rectus, and allowing for the nature of the four obtained, and for the frequency of the different types, we may suppose that of the 12 tandems cut in teasing, 11 were double and 1 triple. The actual number of single spindles present is accordingly $100 - 9 - 22 - 3 = 66$, and the spindle content of the muscle may be expressed in terms of spindle types and spindle capsules as follows:

<table>
<thead>
<tr>
<th>spindle types</th>
<th>no. of spindles</th>
<th>no. of capsules</th>
</tr>
</thead>
<tbody>
<tr>
<td>single</td>
<td>66 (80%)</td>
<td>66</td>
</tr>
<tr>
<td>double tandem</td>
<td>28</td>
<td>28</td>
</tr>
<tr>
<td>triple tandem</td>
<td>6</td>
<td>6</td>
</tr>
<tr>
<td>total</td>
<td>82</td>
<td>100</td>
</tr>
</tbody>
</table>

It now remains to allocate an appropriate number of simple, intermediate, and complex capsules to the 16 tandems from the totals of capsule types found in teasing (columns 1 to 3, table 3). The 4 tandem spindles obtained account for 5 simple, 2 intermediate, and 2 complex capsules. The capsules belonging to the further 12 tandems calculated to be present may be allocated in accordance with the quantitative findings regarding afferent tandem innervation (see p. 383). On this basis we may suppose (a) that one of the capsules in each of the 12 tandems was either intermediate or complex in equal proportion; (b) that in 74% of the 11 double tandems the combination was with a simple capsule, and in 26% with an intermediate capsule; and (c) that the triple tandem included two simple capsules. This entails a total allocation of 15 simple, 11 intermediate, and 8 complex capsules to the tandem fraction. These capsules may either be deducted from the totals of simple, intermediate, and complex capsules found in teasing, or allowance can be made for including the damaged capsules (column 4, table 3) in the calculations. We have found, however, that inclusion of the damaged capsules does not materially affect the results of the final analysis, either in the case of cat C41, or in any of the others. The final analysis of the C41 rectus may therefore be expressed as follows: tandem spindles: 16; single spindles: intermediate, 22; complex, 18; simple, 13; damaged capsules: 13.

The proportional distribution of spindle types, calculated in this way for each of the seven recti studied, is shown in table 4. Apart from cat C4, the intermediate type of single spindle predominates, while the simple and complex types, though approximately of the same order in quantity, fluctuate in ascendancy from muscle to muscle. The high proportion of simple types in cat C4 produces their slight
excess over the complex type in the overall analysis, but if C 4 is excluded the position is reversed. In final assessment of the spindle population of rectus femoris, we may summarize the overall average percentage distribution of spindle types that emerges from this study as follows: single spindles: 80 to 84; intermediate, 46; simple, 28; complex, 26; tandem spindles: 16 to 20; double, 88; triple, 9; quintuple, 3.

Table 4. Proportional distribution of spindle types in rectus femoris

<table>
<thead>
<tr>
<th>Type</th>
<th>Single Spindles</th>
<th>Total Plus Damaged Capsules</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cat</td>
<td>Simple Intermediate Complex</td>
<td></td>
</tr>
<tr>
<td>C4</td>
<td>16</td>
<td>27 20 6</td>
</tr>
<tr>
<td>C5</td>
<td>14</td>
<td>4   32 10</td>
</tr>
<tr>
<td>C35</td>
<td>12</td>
<td>11 22 6</td>
</tr>
<tr>
<td>C41</td>
<td>16</td>
<td>13 22 18</td>
</tr>
<tr>
<td>C42</td>
<td>20</td>
<td>16 25 25</td>
</tr>
<tr>
<td>J12</td>
<td>16</td>
<td>13 23 7</td>
</tr>
<tr>
<td>J18</td>
<td>18</td>
<td>21 24 22</td>
</tr>
<tr>
<td>Total</td>
<td>112</td>
<td>105 168 94</td>
</tr>
</tbody>
</table>

Table 5. Proportional distribution of afferent endings in rectus femoris

<table>
<thead>
<tr>
<th>Type</th>
<th>Primary</th>
<th>Secondary</th>
<th>Tendon-Organ</th>
<th>Paciniform Corpuscle</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cat</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C4</td>
<td>98</td>
<td>67</td>
<td>58</td>
<td>23</td>
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<tr>
<td>C5</td>
<td>84</td>
<td>87</td>
<td>56</td>
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<tr>
<td>C35</td>
<td>75</td>
<td>64</td>
<td>104</td>
<td>2</td>
</tr>
<tr>
<td>C41</td>
<td>102</td>
<td>109</td>
<td>102</td>
<td>18</td>
</tr>
<tr>
<td>C42</td>
<td>127</td>
<td>140</td>
<td>104</td>
<td>16</td>
</tr>
<tr>
<td>J12</td>
<td>99</td>
<td>89</td>
<td>85</td>
<td>2</td>
</tr>
<tr>
<td>J18</td>
<td>114</td>
<td>112</td>
<td>47</td>
<td>5</td>
</tr>
<tr>
<td>Total</td>
<td>699</td>
<td>668</td>
<td>556</td>
<td>76</td>
</tr>
</tbody>
</table>

In order to assess the number of primary and secondary endings present in each of the muscles teased, it is necessary to allocate a quota to the damaged capsules and add this to number of endings observed. Since duplication of the primary ending within a capsule is rare (see p. 380), we may assume that there was one such ending in each damaged capsule, and we may allocate secondary endings on the assumption that intermediate and complex capsules occur in the same proportion among the damaged capsules as among the rest of the capsules in the particular muscle teased. This will fail to account for complex capsules innervated by more than two secondary endings, but this seldom occurs and the contingency may be ignored. Within these limits, the totals of primary and secondary endings present in each of the seven recti are presented in table 5. The results suggest that the two types of afferent termination are present in about equal proportion in the muscle. In terms of percentages of primary as to secondary endings, the widest divergence is 59:41 (cat C4), the nearest equivalence 50:4:49:6 (cat J18), and the overall proportion 51:49. These results are probably more accurate than those published.
for five recti at a preliminary stage of the investigation (Barker 1959), for these omitted consideration of some of the damaged capsules; moreover, all the preparations concerned have since been thoroughly re-checked.

Tendon-organs

It is not possible to observe tendon-organs in sectioned material with sufficient ease and certainty to enable a reliable count to be undertaken of the total number present in a muscle. Estimates of the number present in a teased muscle, based on a count of the sectioned muscle of the contralateral limb, cannot, therefore, be usefully undertaken. However, in teased gold chloride material the tendon-organ is more readily apparent than the muscle-spindle, and in view of the close approximations obtained between the estimated and actual numbers of spindle capsules, it is unlikely that many tendon-organs were missed in teasing the seven recti. The total number of tendon-organs found in each muscle is shown in table 5. While the nerve fibre innervating a tendon-organ may branch to supply several areas of termination in elaborations of the simple fusiform type of receptor, we may regard each tendon-organ as receiving one Ib afferent ending.

Since the primary ending of the spindle, and the tendon-organ ending, are both supplied by Group I fibres, it is interesting to determine whether there is any degree of constancy in their proportional distribution in the muscle. The results indicate that though there are usually fewer tendon-organ than primary endings (80% as many in the overall total), there is wide variation in proportion in individual muscles, the lowest being 41%, the highest 139%.

Tendon-organs are distributed throughout the muscle wherever tendon and muscle fibres unite. As in the case of spindle capsules (Barker & Chin 1960), the greatest concentration tends to occur in the proximal half of the muscle. In two muscles, tendon-organs were plentiful in the distal extremity, but in all other cases they were few in number in the regions of origin and insertion. A separate paper on tendon-organs is in preparation.

Paciniform corpuscles

The occurrence in muscle of small encapsulated end-bulbs, similar in structure to the much larger Pacinian corpuscles, has been known for many years (see Regaud 1907 for review of earlier literature). They have recently been the subject of electrophysiological study by Paintal (1960) who concludes that they are pressure receptors innervated mostly by Group III fibres, some by Group II fibres, and very few by Group I fibres. In rectus femoris, the diameter of the fibres, as measured in teased gold chloride preparations in the region of intramuscular nerve trunks, is 3.0 to 8.5 μ with the majority measuring 3.0 to 3.5 μ (Adal & Barker, unpublished). It is characteristic for the receptors to occur in groups, and for several to be innervated by one nerve fibre, which otherwise remains unbranched so far as it can be traced; they are sometimes located in intimate association with tendon-organs. The most common type consists of an undivided axis-cylinder lying in a central core, which is encapsulated by a few concentric lamellae; this type was also found to be the most frequent by Hromada & Poláček (1958) in joint
capsules and periarticular tissue mainly of rats. The numbers of these paciniform corpuscles found in teasing the seven recti varied from 2 to 23 per muscle (see table 5). The total number of these receptors in a muscle is considerably less than the number of muscle-spindles or tendon-organs, and there appears to be no correlation between their frequency of occurrence as compared with the other proprioceptors. Pacinian corpuscles were not encountered.

**Discussion**

In tandem spindles, and in end-to-end arrangements of single spindles, the distance over which changes in extrafusal length can affect the discharge of the sensory endings involved is greatly increased. In pointing this out, Swett & Eldred (1960a) suggest that such arrangements may serve to collect information on extrafusal length of a more generalized nature than that provided by shorter, scattered single spindles. They found instances of end-to-end arrangements in the cat's mesial gastrocnemius muscle involving three spindles stretching from the dorsal to the ventral aponeurosis; this compares with instances of tandem spindles which we have observed in rectus femoris extending for the entire length of the extrafusal bundles. The relative scarcity of end-to-end arrangements of single spindles in rectus femoris as compared with tandem spindles (see p. 380), and the apparent constancy, within narrow limits, of the tandem fraction of this muscle, suggest that the continuity of a few muscle fibres between capsules may be functionally significant and not merely a morphological anomaly. Muscle fibre continuity between capsules is also a feature of the compound tandem spindles ('spindle systems' of Gray 1957) that extend throughout the length of the fourth extensor digitorum longus muscle of the frog. The presence of such spindles may be associated with the important role that this muscle plays in jumping; they appear to be absent in the sartorius and pectoral cutaneous muscles (Barker & Cope, unpublished). Other tandem spindles, with the more simple serial arrangement of capsules such as has been described in this paper, also occur in the frog, indicating that the tandem type may have been established early in tetrapod evolution. In mammals, they have so far been reported in the rabbit, cat, pig, and man.

In the only other quantitative assessment of the tandem fraction of a muscle that has been made, Swett & Eldred (1960a) studied serial transverse sections of a soleus and a mesial gastrocnemius muscle from a young adult cat. Their findings may be expressed as soleus: 42 single spindles, 5 tandem spindles (4 double, 1 triple); gastrocnemius: 41 single spindles, 13 tandem spindles (10 double, 3 triple). This gives tandem fractions of 11 and 24% respectively for the two muscles, and the results, both with regard to proportion of tandem spindles present, and frequency of doubles and triples, approximate closely with our own findings for rectus femoris. An examination of 78 spindles cut transversely and sampled from cat interosseeous and soleus muscles led Boyd (1960) to conclude that tandem spindles were rare, but this cannot be regarded as any more than an impression. As compared with rectus femoris, our impression of the tandem fraction in semitendinosus and mesial flexor digitorum longus muscles is that it is slightly
higher; in soleus, about the same; and in the interosseous muscles of the foot, considerably lower. In forming these impressions we have been able to take into account a considerable amount of quantitative data concerning the muscles which have accumulated in connexion with other work in progress in this laboratory.

We may suppose that the proportion of tandem as to single spindles is determined at that stage of muscle development when, as described by Tello (1922), the primary nerve fibres initiate spindle formation by associating here and there with bundles of developing myotubes. Whether a tandem or a single spindle is formed in the cat's rectus femoris would seem to depend on (a) a 16 to 20% chance that certain myotube bundles will receive two or more primary fibres at widely spaced intervals; (b) the operation of some other developmental factor; or (c) a combination of both. It might, for example, be the outcome of some myotube bundles being considerably longer than others and thus more exposed to multiple primary fibre connexions. The subsequent proportional distribution of the secondary fibres, which arrive later, is probably not a matter of chance since the addition of secondary endings to the large capsules of tandem spindles appears to be a constant feature.

Few quantitative observations have been made on the proportional distribution of spindle capsules in a muscle in accordance with their type of afferent innervation. In Ruffini's (1898) preparations (cat), the order of frequency was complex, simple, intermediate, but he does not state the number of spindles studied or the muscles used. In a sample of twenty-two spindles from mm. vastus intermedius, vastus lateralis, and pes interosseus of the rabbit, Barker (1948) found the intermediate type to be the most common; in eight spindles from mm. vastus medialis and suberureus of the cat, however, the complex type predominated. Cooper (1959) found an equivalent ratio of primary and secondary endings present in the cat's soleus, and the intermediate type of innervation most frequently occurred in her sample (personal communication). This agrees with our own experience, and we are of the opinion that in this respect the soleus, semitendinosus, and mesial flexor digitorum longus muscles of the cat resemble rectus femoris. In teasing two fourth internal intercostal muscles of the cat, however, we found the complex type of innervation to be most frequent and secondary endings to be more abundant than in the limb muscles studied. The rich proprioceptive innervation of the intercostal muscles was pointed out long ago by Huber (1902) who suggested that it might be correlated with their function in maintaining respiratory rhythm.

With regard to the primary and secondary afferent innervation of a muscle, it is a matter for speculation as to whether the functional significance lies in the overall ratio of the two endings, or in the proportional distribution of the two endings among the spindle capsules. In rectus femoris the two endings are present in about equal proportion; this could simply be the outcome of all spindle capsules receiving an intermediate afferent innervation, but it is, in fact, achieved as the result of the overall balance between simple, intermediate, and complex capsules. If, as Cooper (1959) suggests, the behaviour of the primary ending is modified by the presence of secondary endings in the same spindle, this is clearly significant, but the supposition rests on the claim (Boyd 1959) that the secondary endings are
almost exclusively confined to the small muscle fibres in the spindle. This remains
to be conclusively established: we doubt whether it is so in cat spindles.

Counts of the spindle capsule/tendon-organ population made by Swett & Eldred
(1960a) in the cat were 53/45 for a soleus muscle, and 70/44 for a mesial gastro-
cnemius muscle. In the mesial gastrocnemius of the mouse, Wohlfart & Henriksson
(1960) made a count of 12/7 in one muscle; counted 6 and 5 tendon-organs in two
other muscles; and 15 spindles in another. Counts of twenty pairs of cat soleus
muscles show the spindle capsule content to vary over the range of 40 to 70, with
the mean at 56 ± 7 s.d. (Chin, Cope & Pang, unpublished); spindle capsule/tendon-
organ counts for two soleus muscles made in connexion with other work were
54/29 and 49/28 (teased gold chloride material). As compared with these results,
the spindle capsule count for soleus made by Swett & Eldred (1960a) is typical,
but the tendon-organ count is much higher. This is probably attributable to
individual variation which, as our work on rectus femoris shows, can be con-
siderable. On the other hand, it should be noted that Swett & Eldred studied serial
transverse sections stained with haematoxylin and Van Gieson; while this is
wholly satisfactory for spindle counts, our experience, in common with that of
Wohlfart & Henriksson (1960), is that tendon-organs cannot be identified with
sufficient accuracy in such material to permit reliable counts to be made.

The fact that in a muscle such as the cat’s rectus femoris about one fifth of the
spindles are of the tandem type, raises the question as to whether the counts of
muscle-spindles made in the past by Gregor (1904), Voss (1937), and others, should
be regarded as counts of spindle capsules rather than counts of spindle receptors.
The identification of tandem spindles in serial transverse sections is only possible
if the muscle-bundle of each spindle encountered is followed through from section
to section in order to determine muscle fibre continuity between capsules.
Deliberate gaps in a series may only be made with safety if the investigator is
aware of the tandem type of spindle and thus ready to notice instances of muscle
fibre continuity, as in the case of Swett & Eldred (1960a). In determining the
spindle contents of a muscle it has been reasoned by many previous workers,
however, that the choice of sections for examination in a series could safely be
determined by adjusting the interval so as to cater for the minimum spindle length.
Hence Gregor (1904), assuming the minimum spindle length to be 180 μ in human
foetal material, cut transversely at 60 μ and mounted every third section. Voss
(1937) examined every fifth section in a transverse series cut at 30 to 40 μ; and
in studies by Merrillees, Sunderland & Hayhow (1950), and Hagbarth & Wohlfart
(1952), transverse sections were examined at 100 μ and 250 to 350 μ intervals
respectively. There is no doubt that such methods, while saving in labour, greatly
reduce the opportunities for establishing tandem linkages, and the spindle length
measurements given suggest that tandem spindles have, in fact, been overlooked.
The results of such investigations should, therefore, probably be reassessed in
terms of spindle capsule counts. An estimate of the number of muscle-spindles
present in any given muscle can only be made if its tandem fraction is known.
Barker & Chin (1960) acknowledge that their counts of spindles in three cat
muscles should more accurately be regarded as counts of the encapsulated sensory
regions of spindles, a proportion of which may be arranged in tandem. It is, perhaps, more useful to know how many spindle capsules there are in a muscle, than how many receptors the capsules belong to, since the former figure indicates approximately how many primary endings are present, each spindle capsule generally accounting for only one such ending.

It is clear from our results that measurements of spindle length should take into account not only the type of spindle (single or tandem), but also its position in the muscle bundles; muscle, age, and species are also significant. Length measurements are best made on serial transverse sections, but it is essential that the series should be complete, for otherwise not only may tandem linkages be overlooked, but the tenuous polar extremities may not be fully traced. Spindle lengths determined from sections mounted at intervals in a series should therefore be accepted with caution for the lengths obtained may be little more than an expression of the incompleteness of the spindles measured. Thus Hagbarth & Wohlfart (1952), mounting sections at 250 to 350 μ intervals, concluded that the average length of spindles in the cat’s soleus was 2-6 mm, and in gastrocnemius 1-8 mm, whereas Swett & Eldred (1960), mounting sections at 85 μ intervals give average values of 5-8 mm and 4-8 mm respectively for the two muscles. The maximum spindle lengths so far reported are those given by ourselves, i.e. 13-68 mm for single spindles, 22-30 mm for tandems. Compound tandem spindles in the frog have been observed to attain a length of 26-52 mm (Barker & Cope, unpublished).

The position of the encapsulated sensory region of a single spindle in relation to its total length is presumably determined in development by the location of the connexion of the primary nerve fibre with the myotube bundle. The orientation of the myotube bundles in relation to the nerve entry of the muscle should, therefore, be of significance. In the cat’s rectus femoris the nerve entry is proximal, and the intramuscular nerve trunks approach the muscle bundles obliquely at their proximal ends (see Barker & Chin 1960, figure 3A). The main nerve trunk runs within the muscle close to the central tendon, branching in its course so as to innervate the pennate bundles on either side. It follows that when this pattern of distribution is established during development, the spindles will typically receive their innervation from nerve fibres approaching obliquely from the proximal end, as is the case, and that their polar lengths will to a large extent be determined by their position in the muscle bundles, as demonstrated (pp. 386 to 388).

A reappraisal of Ruffini’s classic paper on muscle-spindles (1898) suggests that in several respects the description was based on incomplete spindles cut in teasing gold chloride preparations. Allowing for the maximum care and practice in teasing, the chances of obtaining complete, or virtually complete, spindles are no higher than about 30%. That many of Ruffini’s spindle preparations may have been incomplete is suggested, for example, by his assertion that the intrafusal muscle bundle ‘...need not itself be fusiform. Wide above in the muscular end of the spindle it gradually diminishes in width and becomes very slender at the tendinous end’ (1898, p. 196). In fact, there is no characteristic difference in width between the two polar regions of a complete spindle; the intrafusal bundle is of approximately the same diameter throughout except in the equatorial region, where it
tends to be narrower, and at its extremities where it tends to taper down chiefly because of the different lengths of the muscle fibres composing it. On the other hand, an incomplete spindle, in which one pole has been cut in teasing, conforms closely with Ruffini’s description. His semi-schematic figure of a spindle with complex afferent innervation (1898, figure 1), which has so often been reproduced, shows an incomplete spindle, which could be interpreted as a portion of a tandem spindle comprising a large capsule, and part of one pole and one intercapsular region. His conclusion that the primary ending is usually irregular in spindles where it is the sole afferent termination is open to doubt on the same grounds. The basis for this may well have been preparations consisting mainly of incomplete portions of tandem spindles comprising small capsules in which, as we have shown, the primary ending is usually either predominantly or wholly irregular.

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References

Barker, D. 1959 J. Physiol. 149, 7-9 P.
Barker, D. & Ip, M. C. 1960 J. Physiol. 153, 8-10 P.
Baum, J. 1900 Anat. Hefte, Abt. 1, 13 (42), 251-305.
Boyd, I. A. 1958 J. Physiol. 140, 14-15 P.
Boyd, I. A. 1959 J. Physiol. 145, 55-56 P.
Cooper, S. 1959 J. Physiol. 149, 27-28 P.
Cooper, S. & Daniel, P. M. 1956 J. Physiol. 133, 1-3 P.
Ruffini, A. 1898 J. Physiol. 23, 190-208.
Sherrington, C. S. 1894 J. Physiol. 17, 211-258.