ON A LAW DETERMINING THE NUMBER OF
MEDULLATED NERVE FIBERS INNERVATING
THE THIGH, SHANK AND FOOT OF THE
FROG—*RANA VIRESCENS*.

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During the past three years, while following the studies of Dr. DUNN (1900 and 1902) on the innervation of the frog's leg, it has been my endeavor to discover whether there was any law determining the distribution of the medullated nerve fibers to the segments of the leg. This law has been found and is expressed as follows :

The nerve fibers entering the leg of the frog (Rana virescens) by the sciatic and crural nerves, are distributed to the thigh, shank and foot in numbers which, for each of these segments are equal to the sum of the efferent fibers,—taken in proportion to the weight of the muscles,—and of the afferent fibers,—taken in proportion to the area of the skin.

The data discussed in the following pages are intended to furnish the evidence for the law just stated.

To make this investigation it was necessary to know:

- (1) The relative number of medullated ventral and dorsal root fibers in the nerves supplied to the frog's leg.
- (2) The relative weight of the muscles of the thigh, shank and foot.
- (3) The relative areas of the skin for the thigh, shank and foot.
- (4) The number of medullated nerve fibers entering the leg and also the number distributed to each segment.
- (5) The number of medullated fibers distributed as muscular and cutaneous nerves to each segment of the leg.

With the exception of the data called for under (3), the facts needed were to be found in papers already published from this laboratory. We shall take up the points in the order just given.

(1) *The relative number of medullated ventral and dorsal root fibers in the nerves supplied to the leg.*

The nerves sending fibers to the leg are the VII, VIII and IX spinal nerves as usually numbered, or, according to the recent numbering of GAUPP (1897), the VIII, IX and X.

According to the enumeration of the medullated nerve fibers in the dorsal and ventral roots of these nerves by HARDESTY (1899, p. 84), the proportion is.

TABLE I.
Relative number of fibers in roots,
Ventral. Dorsal.

Frog weighing 48 grams	100	177
" " 59 grams	100	175

The average of these two observations gives therefore 100 ventral root fibers to 176 dorsal root fibers, and this is the ratio here employed. Such being the relation found in the spinal roots, it is assumed to be the same in the sciatic and crural nerves at the point where they enter the leg. Whatever the number entering of fibers the leg, they are then to be divided, as motor and sensory, in the above proportion.

In this calculation no correction for possible efferent fibers in the dorsal roots is attempted, for we have no data with which to work. When efferent fibers appear in the dorsal roots of the frog, there is indirect evidence that the number must be quite small, and they are here neglected (HORTON-SMITH 1897, WANA 1898, DALE 1901). The ventral root is assumed, therefore, to contain only motor or efferent fibers and the dorsal root only afferent or sensory fibers.

Having determined the proportional numbers of the afferent and efferent fibers, the next step is to present the measurements according to which these fibers are to be distributed, namely, the relative weights of the muscles and the relative areas of the skin in the several segments of the leg.

(2) *The relative weight of the muscles of the thigh, shank and foot.*

In an earlier study, made in collaboration with Mr. SCHOE-MAKER (1900) it was determined in *Rana virescens* that the relative development of the muscles of the frog's leg, as indicated by the weight of the muscles of the thigh compared with those of the remainder of the leg, was nearly constant for all groups above five grams in body-weight (see DONALDSON and SCHOE-MAKER, 1900, pp. 124-125).

TABLE II.

Giving in grams the weights of the muscles in the thigh, shank and foot of the Frog—*R. virescens*. (From Table VII, DONALDSON and SCHOE-MAKER, 1900.)

No.	Body			Weight of Muscles		
	Sex	Weight	Lgth.	Thigh	Shank	Foot
18	F	29.40	185	3.105 3.097	1.141 1.201	.533 .538
19	F	30.45	179	3.330 3.232	1.240 1.195	.659 .603
20	F	33.96	172	3.480 3.681	1.393 1.354	.603 .631
22	M	38.16	200	3.637 3.536	1.563 1.456	.715 .653
23	F	42.54	215	4.455 4.369	1.562 1.535	.822 .843
25	M	45.37	205	4.383 4.278	1.496 1.493	.869 .816
26	F	46.00	216	4.797 4.830	1.844 1.828	.926 .926
27	F	47.58	206	4.713 4.616	1.741 1.813	.824 .871
28	F	48.33	220	5.402 5.430	1.906 1.949	1.006 1.019
29	F	52.55	206	5.404 5.456	2.450 2.400	.835 .850

From Table VII, in that paper is taken the following series of records comprising numbers 18-29, inclusive, (excluding numbers 21 and 24 for which the muscle weights were not determined). This is the series just as it stands in the original table, and these same records have also been employed in my paper "On a Formula for Determining the Weight of the Central Nervous System of the Frog from the Weight and Length of its Entire Body," 1902.

For a description of the method by which the weights of the muscles were determined, the reader is referred to the original paper (p. 118).

For the first five frogs entered in the table, calculation gives the following proportional values for the weights of the muscles of the thigh, shank and foot:

TABLE III.

Segment of Leg	Percentage Value of Weight of Muscles.
Thigh	63.9%
Shank	24.3%
Foot	11.8%

In the case of the second five frogs in this same table, the proportional values are as follows:

TABLE IV.

Segment of Leg.	Percentage Value of Weight of Muscles.
Thigh	63.9%
Shank	24.5%
Foot	11.6%

It will be seen that these two series differ only by some tenths of a percent. in the case of the shank and foot, so that the relative values may be considered fairly constant.

For use in the present investigation we take the average of the two series which gives:

TABLE V.

Segment of Leg.	Percentage Value of Weight of Muscles.
Thigh	63.9%
Shank	24.4%
Foot	11.7%

Having obtained the data according to which the motor fibers entering the leg should be distributed, we need next to

obtain the corresponding data for the areas of skin,—in accordance with which the afferent fibers are to be distributed.

(3) *On the relative areas of the skin of the thigh, shank, and foot.*

Since the relative weights of the muscles in the several segments of the frog's leg remain unaffected by the size of the frog (DONALDSON, 1898, and DONALDSON and SCHOEMAKER, 1900), and since the conformation of the leg is similar in large and small frogs, it follows that the relative areas of the skin covering the different segments of the leg are unaffected by the absolute size of the frog examined. This removes the necessity of always working with frogs of the same size.

My acknowledgments are due to Dr. DUNN for working out the area of the skin in the several segments of the frog's leg. As the method used was somewhat novel, it will be necessary to describe it in detail.

The frogs examined had the following body measurements:

TABLE VI.
Frogs examined for area of skin.

Frog No.	Body Weight, grams.	Length from tip of nose to end of longest toe.
1	34.76	190 mm.
2	36.75	195 mm.
3	28.17	187 mm.

The procedure was as follows: The frog was killed with chloroform and pinned out on a sheet of cork with the ventral aspect uppermost. One leg was extended and abducted so that it made an angle of about forty-five degrees with the longitudinal axis of the body. A strip of glass about 3 cm. wide and a few centimeters longer than the frog's leg, was then passed beneath it. The leg thus rested on this strip of glass and was in turn covered by a similar strip of the same size. On the upper surface of the latter a layer of tracing paper had been fastened by a drop of paste at each of the four corners. Rubber bands were next passed over the two strips of glass and the leg lightly compressed between them. Before putting on the covering strip, however, the foot was stretched so as to

exhibit the full extent of the web. For this purpose, threads were tied to the first, third and fifth toes, pulled taut and fastened by pins. The web was stretched until the second toe showed a tendency to curl up, and this reaction was regarded as indicating the normal extension of the web. When so extended, the general outline of the foot is that of a quadrilateral.

These adjustments having been made, it was determined by measurements taken between the two plates of glass, that their faces were approximately parallel. Next an outline, just outside the contact line of the upper plate with the skin of the leg, was made with a pencil on the tracing paper, starting from the uppermost part of the thigh on one side, and following around the entire outline of the leg to the uppermost part of the thigh on the opposite side. The upper limit between the skin of the body and that of the thigh was marked by the adjustment of the glass strips, and the levels of the knee and ankle joints respectively, were fixed by passing needles through these joints when preparing the leg for this examination. By drawing, therefore, a line across the tracing paper at these several levels, the outlines for the thigh, shank and foot were obtained. It was assumed that the outline on the dorsal aspect of the leg would be similar to the one found on the ventral aspect. To obtain the areas for the sides of the leg, the distance between the two glasses at the hip, knee and ankle was measured and the length of the curved line (the "coast line") forming the lateral boundary in the case of the thigh and shank, taken on each side, by means of a waxed thread applied to the outline. This gave the initial measurements for the calculation of the area of the skin of the thigh and shank. Concerning the foot we shall speak later.

To illustrate the determination of the area for a given segment, let us take the thigh. In this case we have the area marked on the tracing paper between the boundary separating the thigh from the body and that separating it from the shank. The content of this area was determined in square millimeters by means of a planimeter and then doubled so as to include the

corresponding area on the opposite side; to this sum was added the areas obtained by multiplying the length of each curved side (the "coast-line"), by a number equal to half the sum of the height of the side at the hip plus its height at the knee.

The sum of the four areas thus obtained was considered as the total area of the skin of the thigh. By following the same steps, the total area of the skin of the shank was found. On coming to the foot, however, the method of determining the area required to be modified in order to include the additional surface represented by the toes. The original outline on the tracing paper gave the area of one side of the foot projected on a plane surface, to which, when doubled, should be added the amount represented by the elevation of the toes and that due to the thickness of the tarsus.

To illustrate the method used, the following figure is given:

Figure 1. Outline of Frog's leg, showing the outline of the ventral aspect of right leg. *Hip*—marks the junction line of the body with the thigh. *Knee*—the junction line of the thigh with the shank. *Ankle*—the junction line of the shank with the foot. *D¹-D*.—length of tarsus plus second toe. *M-A*—length of fifth toe. *M¹-B*.—length of fourth toe. *M²-C*.—length of third toe. (Second toe measured with tarsus). *M³-E*.—length of first toe.

The length of the line $D'-D$ was first taken, then the thickness of the foot at D' and at D . Half the sum of these last two measurements multiplied into the length $D'-D$ gave the lateral areas of the foot, considering these as extending from the ankle joint to the tip of the longest toe, and twice this gave the areas for both sides. The length of the lines MA , $M'B$, $M''C$ and $M'''E$ were then taken, and the thickness of the foot at M , M' , M'' , M''' and at each of the toes A , B , C and E (D being omitted, as it had been already measured). Half the sum of these two thicknesses was taken in each case as the average thickness of the toe, and the product of these numbers into the length of the respective toes, gave the area of the skin on one side of the toe considered as a plane surface. The surface is so rounded, however, that about one-half of the area thus calculated has already appeared in the surface projection of the foot, and has been counted in the area included within the original outline; therefore, instead of taking this area for the side of the toes twice, it was taken only once.

Thus to get the total area for the foot, there are added together: the two areas from the tracing—the number of square millimeters being determined by the planimeter—the area for the longest toe including that for the sides of the tarsus and finally the additional areas for the four remaining toes.

The areas thus obtained for the three frogs measured are given in the accompanying table, the records for the two legs being entered separately.

TABLE VII.

Giving the areas in square millimeters of the skin covering the thighs, shanks and feet of three frogs—*R. virescens*. The method of measurement is given in the text.

Areas in Square Millimeters.

Frog.	Thigh.	Shank.	Foot.
1 Right	1584.1	1136.8	1695.3
1 Left	1675.5	1059.0	1793.6
2 Right	1519.2	1071.5	1539.1
2 Left	1506.3	1035.0	1538.7
3 Right	1377.0	1010.9	1396.5
3 Left	1356.2	972.4	1434.1
Totals	9018.3	6285.6	9397.3

When the percentage values of these numbers are found, they give the following:

TABLE VIII

Segment.	Average for first 3 entries	Average for second 3 entries	Average for all, 6 entries.
Thigh	36.5%	36.5%	36.5%
Shank	25.0%	25.8%	25.4%
Foot	38.5%	37.7%	38.1%

On attempting to apply these percentages in the calculation for the supply to the leg, it was found that the numbers obtained were somewhat larger than we expected them to be in the case of the thigh. It appeared that the area for the thigh had been over-estimated. Dr. DUNN therefore undertook a reinvestigation of the innervation of the skin of the thigh. This showed that the area was over-estimated in this sense, that in addition to the fibers entering the leg by the sciatic and crural nerves, there was a small independent bundle of nerves which entered through the anus and was distributed to a small triangle of skin just behind the anus and on the mesal surface of the leg. The area of this piece of skin thus innervated, was found to be 2.5 % of the area of the entire thigh. For the details of this determination the reader is referred to a forthcoming paper by Dr. DUNN.

To control these results, other measurements were made by an entirely different method. A plaster mould of the frog's leg was taken and the leg then cast in Woods metal. On this cast the thigh and shank were examined for their respective areas by winding them carefully with fine copper wire—of a uniform diameter. The diameter being constant, the areas covered by the wire would be directly proportional to the length or weight of the wire used. The relations were tested by weighing the wire. The weight of the wire needed to envelop the thigh, was to that needed to envelop the shank as 1.43:1.

On comparing this ratio with that from the areas for the thigh and shank, as shown in Table 7, it appears that this ratio is also 1.43:1.

Thus the proportional areas for the thigh as determined

by these two methods are identical. It would follow from this that the first method was probably accurate. On account of its shape the foot cannot be tested by this latter method.

When the area of skin for the thigh is reduced by the amount which is not innervated by fibers entering the leg in the sciatic and crural nerves, the following percentages are obtained as a general average from the three frogs measured :

TABLE IX.

Area of Skin.	
Thigh	35.9%
Shank	25.7%
Foot	38.4%

The above percentages are those used in the calculations which follow.

(4). *The number of medullated nerve fibers entering the leg and also the number distributed to each segment.*

Having thus determined the proportion in which the ventral root fibers and the dorsal root fibers entering the leg should be distributed to the several segments, it becomes desirable to estimate by means of the preceding tables, the total number of fibers going to each segment.

To show how this is done, let us assume that 100 ventral root fibers and 176 dorsal root fibers enter the leg—these numbers are in the proportion which has been determined. Then 63.9% of the 100 ventral root fibers go to the thigh and 35.9% of the 176 dorsal root fibers also go to the thigh. Now, in order to determine what percentage of the total 276, the sum of these two numbers is, we should divide their sum, namely, 63.9 fibers+63.2 fibers = 127 fibers by the total number of entering fibers, namely, 276. We then find that 46% of all the entering fibers go to the thigh when they are distributed in the above manner.

Extending the calculation in the same way to the shank and foot, we may tabulate the results as follows :

TABLE X.

Hereafter designated as the "formula".

$$\begin{array}{l} 46\% \text{ go to the thigh} \\ 25.3\% \text{ go to the shank} \\ 28.7\% \text{ go to the foot} \end{array} \} = 100\% \quad \left\{ \begin{array}{l} \text{shank } 46.8\% \\ \text{foot } 53.2\% \end{array} \right.$$

100.0% go to the leg.

If 46% go to the thigh, then 54% go to the remainder of the leg, i.e., shank and foot combined. Further, if we consider alone the fibers which go to the shank and foot and express the number as 100%, then of this 100% going to the shank and foot, 46.8% go to the shank and 53.2% to the foot. These calculations of the fibers distributed to the shank and foot are introduced here as they will be used later on.

The values in the above Table X are those with which all the subsequent calculations are made. It remains now to present the data concerning the number of nerve fibers observed to enter the leg of the frog and then to see in how far the estimated numbers for the segments of the leg correspond with the numbers which have been observed.

These observed numbers have been obtained by Dr. DUNN. The designation of the frog and the segment or segments for which the enumerations have been made, together with the date of publication, are given in the following Table XI in chronological order:

TABLE XI.

Frog B	Thigh	DUNN	1900
Frog C	Thigh	DUNN	1900
Frog B II	Thigh, Shank and Foot	DUNN	1902
Frog C II	Thigh, Shank and Foot	DUNN	unpublished

Below are given the details of the data for each frog so far as they will be required in this study.

The accompanying Figure 2, taken from Dr. DUNN's paper (1902), shows the levels at which the nerves for the frog's leg were sectioned and where the number of fibers was counted.

Figure 2. Diagram of the innervation of the Frog's Leg, showing the levels at which the number of nerve fibers was counted. *C*=level of Crural nerve just above branches to thigh. *S₁*=level of Sciatic nerve just above branches to thigh. *S₂*=level of Sciatic nerve just below branches to thigh. *P*=level of Peroneal nerve just above branches to shank. *T*=level of Tibial nerve just above branches to shank. *P₁*, *P₂*=level of Peroneal nerve just above branches to foot. *T₁*, *T₂*=level of Tibial nerve just above branches to foot.

Thus all the fibers entering the leg were in the sections at the levels $C+S_1$. All the fibers entering the shank were in the sections at $P+T$, and all the fibers entering the foot at P_1+P_2 and T_1+T_2 .

In the Tables XII–XVI which follow, these designations are used to indicate the levels at which all the fibers for a given segment were to be found. Below the entry for the number of fibers to each of the segments, stands “To Thigh” and “To Shank,” which means that all the branches to the thigh or to the shank contained the numbers there entered, under “observed.” The number of fibers immediately below the branches to the thigh is also given after S_2 .

In the column headed “muscular and cutaneous,” are the observed numbers found in the muscular and cutaneous branches and their sum is equal to the “observed number” in each case.

In the column headed “calculated,” we have the number determined by Dr. DUNN by taking the difference between the number just above the branches to the thigh ($C+S_1$), or shank ($P+T$), and the number just below at S_2 or at P_1+P_2 and T_1+T_2 .

In the column marked “splitting fibers,” we have the *difference* between the observed—the larger number—and the calculated—the smaller number—which difference is due to fibers that have split in their course so that they are represented either by two divisions having the same distribution (i. e., both run in the branches supplying the segment), or by one division running in the branches to the segment, and by the other in the main trunk of the nerve to some point below the level of the branches. It is the presence of these splitting fibers which renders complicated the application of the test which it is proposed to make, since the formula based on the law of distribution does not take account of the additional fibers which appear as the result of splitting.

TABLE XII.

Data taken from Dr. DUNN's paper, 1900; Tables III, IV, V and VI.

Frog B. *Right Leg.*

Locality	Number of Fibers		
	Observed	Calculated	Splitting Fibers
	Total	{ Cutaneous = C Muscular = M	
C + S ₁	5273	-----	-----
To thigh	2623	C { 876 M { 1747	2405 218
S ₂	2868	-----	-----

Left Leg.

C + S ₁	5385	-----	-----
To thigh	2600	C { 871 M { 1729	2411 189
S ₂	2974	-----	-----

TABLE XIII.

Data taken from Dr. DUNN's paper, 1900; Tables III, IV, V and VI.

Frog C. *Right Leg.*

Locality	Number of Fibers		
	Observed	Calculated	Splitting Fibers
	Total	{ Cutaneous = C Muscular = M	
C + S ₁	6011	-----	-----
To thigh	2814	C { 1279 M { 1535	2643 171
S ₂	3368	-----	-----

Left Leg.

C + S ₁	5987	-----	-----
To thigh	2777	C { 1219 M { 1558	2586 191
S ₂	3401	-----	-----

TABLE XIV.

Data taken from Dr. DUNN's paper, 1902; Tables V to XIV inclusive.

Frog B II. *Right Leg.*

Locality	Number of Fibers		
	Observed	Calculated	Splitting Fibers
	Total	$\begin{cases} \text{Cutaneous} = C \\ \text{Muscular} = M \end{cases}$	
C + S ₁	7107	-----	-----
To thigh	3508	$\begin{cases} C \ 1678 \\ M \ 1830 \end{cases}$	3165 343
S ₂	3942	-----	-----
P + T	4152	-----	-----
To Shank	2130	$\begin{cases} C \ 1003 \\ M \ 1127 \end{cases}$	1665 465
P1 + P2 and T1 + T2	2497	-----	-----

TABLE XV.

Data taken from Dr. DUNN's paper, 1902; Tables V to XIV inclusive.

Frog B II. *Left Leg.*

Locality	Number of Fibers		
	Observed	Calculated	Splitting Fibers
	Total	$\begin{cases} \text{Cutaneous} = C \\ \text{Muscular} = M \end{cases}$	
C + S ₁	7129	-----	-----
To thigh	3481	$\begin{cases} C \ 1676 \\ M \ 1805 \end{cases}$	3167 314
S ₂	3962	-----	-----
P + T	4146	-----	-----
To shank	2108	$\begin{cases} C \ 903 \\ M \ 1205 \end{cases}$	1660 448
P1 + P2 and T1 + T2	2486	-----	-----

TABLE XVI.

Data from specimen of *R. virescens*. Body-weight 51 grms. Observations by Dr. DUNN not previously published. The section at S_1 of the left leg was unfortunately too imperfect to be counted.

Frog C II.		Right Leg		
		Number of Fibers		
Locality		Observed	Calculated	Splitting Fibers
	Total	$\left\{ \begin{array}{l} \text{Cutaneous} = C \\ \text{Muscular} = M \end{array} \right.$		
$C + S_1$	$\left\{ \begin{array}{l} 1301 \text{ C} \\ 4610 \text{ S}_1 \\ \hline 5911 \end{array} \right.$	-----	-----	-----
S_2	3313	-----	-----	-----
$P_1 + P_2 \text{ and } T_1 + T_2$	2026	-----	-----	-----
<i>Left Leg</i>				
$C + S_1$	$\left\{ \begin{array}{l} 1323 \text{ C} \\ \text{----- } S_1 \text{ (Section lost)} \end{array} \right.$	-----	-----	-----
S_2	3389	-----	-----	-----
$P_1 + P_2 \text{ and } T_1 + T_2$	1969	-----	-----	-----

To illustrate the use of the data in the foregoing tables, we will take the right leg of Frog B II (Table XIV), and determine how far the observed numbers there given agree with those estimated by the aid of my own formula. Table XIV shows 7107 fibers entering the leg. When the proportional numbers are calculated according to the formula (Table X), we obtain the following:

TABLE XVII.

Entering right leg of Frog B II—		7107 fibers
To thigh—	46.0% =	3269 fibers
To shank—	25.3% =	1796 fibers
To foot—	28.7% =	2042 fibers

The above numbers of fibers are the *numbers of single pathways between each segment of the leg and the entering nerve.*

When the observed numbers of fibers to the several segments of the leg (see Table XIV) are compared with those here estimated, we obtain the following:

TABLE XVIII.

Number of fibers to the several segments of the right leg of Frog B II.

	Estimated (DONALDSON)	Observed (DUNN)
To thigh	3269	3508
To shank	1796	2130
To foot	2042	2497

Thus in every case the numbers estimated by the formula are less than those observed by Dr. DUNN. But as Table XIV shows, Dr. DUNN's count includes a large number of fibers which have split (see "splitting fibers" in tables), and which, therefore, are not taken into account by the formula, which applies to single pathways only.

The next step, therefore, in the comparison is to bring the two series of numbers to the same standard. There are two ways of doing this, namely, either by removing the additional fibers due to splitting from the number observed by Dr. DUNN, or by adding the additional fibers to the number as determined by the formula. The latter method was followed; first, because it was desirable to consider the *observed* number as the fixed standard, not to be altered in any way, and second, because it seems probable that the most direct utilization of this formula will be for determining the number of fibers which a direct count would show to be supplied to a given segment.

Thus in the further work, the observed number is in each case taken as the standard, and the calculations are directed to determining the number which must be added to that estimated by the formula in order to make it comparable with the standard. To illustrate the steps taken for this purpose, we shall do best to examine the innervation of the thigh in the case chosen, namely, the right leg of Frog B II. My estimation gives for the thigh 3269 fibers and Dr. DUNN's observation 3508. When, however, in this instance the number of fibers observed *above* the branches to the thigh at (C+S₁) was diminished by the number observed just *below* the branches at (S₂), the difference was found by Dr. DUNN to be 343 (see Table XIV). Thus her observed number exceeded her number calculated in this manner by 343 fibers. This excess is explained as the

result of splitting fibers and means—if dichotomous splitting be the form assumed—that 343 of the fibers counted at C+S₁ have split later into two divisions each. Just where this splitting occurs, we are obliged to guess. The numerical results indicating the number of splitting fibers would be the same, whether it occurred in the main stem, C+S₁, just where the branches to the thigh are given off, or within the branches after these had been given off, but before the levels at which they were individually sectioned. For the further development of our idea of the innervation of the leg, however, these two possible arrangements leading to like numerical results, have very different values. In the latter instance, where the splitting occurs within the branches, the splitting fiber is in no wise represented in the main trunk of the nerve below the level of the branches, whereas in the former instance, where splitting occurs in the main trunk, one division can appear in the branches and the other continue in the trunk, the original fiber being therefore still represented in the trunk, below the point at which it has split.

It was necessary to assume that some of the fibers that split did so in the trunk, and thus were represented both in the branches and in the trunk below the branches, while others split in the branches themselves; both divisions in this case having a similar distribution.

After several tests, it was found that the most accordant results were obtained when it was assumed that one-third of the splitting fibers split in the branches. Fibers splitting in this way form Class a. Since the total number of splitting fibers was in this case 343, one-third would be 114.3 fibers. These are to be added to the number estimated by me (see Table XVII): $3269 + 114.3 = 3383.3$.

‡The number of fibers that pass to the shank and foot is not affected by this process, since each one of these fibers splitting in the branches is without representation in the trunk below the level of the branches.

By this step 114.3 of the splitting fibers have been with-

drawn from the original 343, leaving 228.7 to be still considered.

These remaining fibers are assumed to be of the second class of splitting fibers (Class b), i. e., those, one division of which passes into the branches, while the other continues in the trunk below the branches.

Since by the formula we have taken 46% of the total number of the fibers entering the leg (see Table XVII), we must assume that we took 46% of the fibers with double representation (Class b). It follows, therefore, that in the original 46% or 3269 fibers, there are already included 46% of the fibers with double representation, or 46% of the 228.7 fibers which constitute Class b at this level. Therefore, to bring the estimated up to the observed number in this respect, there are still to be added to the estimated number $100\% - 46\% = 54\%$ of 228.7, which equals 123.5 fibers. In general, therefore, to make the estimated number comparable with that observed by Dr. DUNN, we should add one number representing the fibers splitting in the branches (Class a), and also a second number representing the splitting fibers with double representation (Class b), in so far as they have not been included in the original 46%.

TABLE XIX.

Showing the number of fibers to be added to the original 46% in the case of Frog B II—Thigh.

	Calculated numbers.	Observed number
Original 46%	= 3269	
Fibers splitting in branches (Class a)	= 114.3	
Splitting fibers with double representation (Class b)	= 123.5	
	<u>3506.8</u>	
	or 3507	3508
Difference	= 1 fiber	

As the table shows, the estimate is almost identical with the observation, being but one fiber less. Without commenting on this result at this place, we shall pass on to the consideration of the nerve supply to the shank of this same leg.

It must be kept clearly in mind that our calculation for the

percentage distribution of the fibers to the segments of the leg applies to the number of *single medullated fibers found entering the leg at C+S_i*; in this case, 7107 fibers. Having removed 46% of this number for the innervation of the thigh, there remain 54% to be distributed to the shank and foot.

Thus: $7107 - 3269 = 3838$ fibers.

The law calls for a distribution of this 54% of the initial number in the proportion of 25.3% to the shank and 28.7% to the foot. When, however, we attempt to deal with the splitting fibers belonging to the shank and foot in making the estimated comparable with the observed results, it is necessary to distribute these splitting fibers in the same proportions in the branches to the shank as they were distributed in the branches to the thigh, and in order to make the distribution in a like manner, it is necessary to treat the number of fibers going to the shank and foot, 3838, as 100% of all the fibers concerned, and then designate those to the shank as 46.8% of the same number,

Since 46.8% of $3838 = 25.3\%$ of $7107 = 1796$

53.2% of $3838 = 28.7\%$ of $7107 = 2042$

According to the formula, therefore, 1796 fibers (single pathways) are estimated as going to the shank. Dr. DUNN observed 2130 fibers to the shank, and further, by the same methods as were employed in the case of the thigh, she determined that there were 465 splitting fibers in the branches to ank. (See Table XIV.)

In adjusting the estimated number to that observed, these splitting fibers are treated in the same manner as those found in the supply to the thigh, i. e., one-third are taken as dividing in the branches, and of the remainder it is assumed that 46.8% are included in the original estimate, so that 53.2% only need to be added to bring the estimate to the same standard as that of the observed number. Thus, imitating Table XIX, for the thigh, we have the following:

TABLE XX.

Showing the number of fibers to be added to the original 25.3% in the case of Frog B II—Shank.

	Calculated numbers.	Observed number
Original 25.3% of 7107 or 46.8% of 3838	=	1796
Fibers splitting in branches (Class a)	=	155
Splitting fibers with double representation (Class b)	=	165
		<hr/>
		2116
Difference	=	—14 fibers or 0.6%
		<hr/> 2130

The approximation between the estimated and observed numbers is not so close here, but is still fair, being within less than one per cent.

The number of fibers to the foot has still to be considered. In the case of the foot, the observed numbers are taken from the enumeration at the levels P₁+P₂ and T₁+T₂. Figure 2. These levels would correspond to those just above the branches in the case of the thigh and shank. We have to assume, therefore, that in the number observed by Dr. DUNN at these levels as going to the foot, there are in addition to the single pathways represented by fibers that pass unsplit from their entrance into the leg, two other classes, those namely (a) that have split within the trunk, both divisions descending to the foot, and (b) all other split fibers, one division of which goes to either the thigh or shank, while the other goes to the foot.

Of the class (b), there are in the entire leg at least three groups: b₁, the fibers which split, one division passing to the thigh and the other to the foot; b₂, fibers which have split, one division going to the thigh and the other to the shank; b₃, splitting fibers which have one division going to the shank and one to the foot.

These several groups are all marked, Figure 3, as in b₁, b₂, b₃. At the level where the nerves enter the foot, it is necessary to make allowance for groups b₁ and b₃ of class (b), as well as for representatives of class (a).

According to formula, 2042 fibers pass into the foot. Dr. DUNN observed 2497. To make the estimated number comparable with that observed, the allowance for the splitting fibers

must be introduced. The principle involved in making the allowance is that the division of any splitting fiber which has already been counted as a fiber entering the leg is to be considered as additional, and hence added to my estimate of the number to the foot.

For example, the splitting fibers included in the original 46% of those entering the leg and sending one division to the thigh (b_1) are pictured as sending the other division to the foot.

This group (b_1) contributes 106 fibers to the foot. As the fibers representing these divisions have already been accounted for, they would not appear in my estimate, and hence must be added to it. In like manner, the long divisions of the splitting fibers which go to the shank come from fibers already counted and are therefore additional; thus these also should be added to my estimate. The latter group (b_3) represents 46.8% of the splitting fibers which pass to the shank and these amount to 145. To the original estimate of 2042, therefore, $106+145=254$ is to be added, making a total of 2293 fibers. This number is still 204 fibers less than the observed 2497. The difference may justly be credited to the splitting fibers of class (a), namely those, both divisions of which have a like distribution. That many such splitting fibers occur is shown by Dr. DUNN's observations (1902, p. 314).

The arrangement of the fibers as here imagined is exhibited in Figure 3, which is purely a schema. Here the largest column represents the fibers going to the thigh, the next largest those to the foot and the smallest those to the shank. The size of the columns is proportional to the number of fibers they contain.

Figure 3. The explanation of this schema intended to illustrate the arrangement of the splitting fibers distributed to the leg of the frog, is given on the following page.

All the fibers entering the leg by the crural and sciatic nerves are enclosed within the circle marked "Fibers entering the leg, 100%." At the next lower level, the small circles enclose all the fibers to each of the three segments of the leg marked respectively :

Thigh	46.0%
Shank	25.3%
Foot	28.7%

Within the last three columns the heavy black lines indicate the splitting fibers, which according to the description in the text, are distributed to the thigh, shank and foot. These splitting fibers are divided into two classes :

Class a—splitting fibers, both divisions of which are distributed to the same segment :

Class b—splitting fibers, the divisions of which are distributed to different segments.

This latter class is represented by three groups:

b₁, one division of which goes to the thigh and the other to the foot ;

b₂, one division of which goes to the thigh and the other to the shank ;

b₃, one division of which goes to the shank and the other to the foot.

C + S₁, indicates the level above the branches to the thigh; P + T, the level above the branches to the shank, and P₁ + P₂ and T₁ + T₂, the level above the branches to the foot.

Within each column is represented the several sorts of splitting fibers, each one bearing the designation used to indicate it in the text. The designation "a" always indicates the splitting fibers, both divisions of which have the same distribution. Class "b" is represented by the three groups, b₁, one division of which goes to the thigh, while the other goes to the foot ; b₂, one division of which goes to the thigh and the other to the shank, and finally, b₃, one division of which goes to the shank and the other to the foot. The splitting fibers are counted only once, and are credited to the column in which they appear above C+S₁ in the figure. The other divisions are in addition to the number of fibers called for by the formula.

The levels C+S₁, P+T, and P₁+P₂ and T₁+T₂ are all indicated. If there were no splitting fibers the schema would be made up of the outlines of the three columns alone.

Turning now to general results of this test, we find that in the case of the right leg of Frog B II, the estimated numbers agree very closely with those observed when an allowance, *according to a fixed procedure*, is made for the splitting fibers.

The significance of this result depends largely on the possibility of repeating it. Using exactly the same methods, the results for the left leg of this frog (data presented in Table XV) are almost as good as those for the right.

The following table presents the results for both legs Frog B II:

TABLE XXI.

	Estimation (DONALDSON) Corrected for splitting fibers	Observed (DUNN)	Difference in fibers	Percent- age
Thigh R	3507	3508	— 1	— .03%
Thigh L	3497	3481	+ 16	+ .40%
Shank R	2116	2130	— 14	— .65%
Shank L	2110	2108	+ 2	+ .09%
Foot R	2497 ¹	2497	----	-----
Foot L	2486 ¹	2486	----	-----

¹ 8% of the observed numbers being added to represent the splitting fibers with a similar distribution of both divisions—see text.

This is the only frog we have in which the enumeration at different levels has been complete enough to permit of this full test of the formula. In Frog C II, however, the endeavor was made to determine whether the proportional distribution of the fibers at different levels in the leg would correspond with those found in Frog B II, for it seemed very probable that if the two frogs corresponded in this respect, they would also correspond in the number of fibers supplied to each segment of the leg.

The data for Frog C II give the number of fibers entering the leg at C + S₁ the number at S₂, and the number entering the foot, at P₁ + P₂ + and T₁ + T₂, see Table XVI.

On adding these three numbers together and then taking the proportional value of each of them, we find the following :

TABLE XXII.

Level	Right Leg	Left Leg
C + S ₁	52.4%	-----
S ₂	29.4%	-----
P ₁ + P ₂ + T ₁ + T ₂	18.2%	-----

This calculation could not be repeated for the left leg, as the sections for S₁ were imperfect. The remaining sections were, however, counted at levels C, S₁ and P₁ + P₂ + T₁ + T₂ on the left leg, and gave numbers so closely similar to those from the right leg, that it is highly probable that the innervation of the two legs agreed closely.

The tabulation of these same numbers in Frog B II is given below :

TABLE XXIII.

	Right Leg	Left Leg
C + S ₁	51.6%	51.8%
S ₂	30.2%	30.1%
P ₁ + 2 P ₂ + T ₁ + T ₂	18.2%	18.1%

When we compare these percentages with the corresponding determinations for Frog B II, in which the two legs are quite similar, we find that C II has .8% more in the thigh, .8% less in the shank and that they exactly coincide as regards the foot.

If we may judge from this, then other frogs are similar to B II in the general arrangement of the nerve supply to their legs, and hence the formula would be applicable to them as a class.

In support of this view, we have the results of applying the formula to Frogs B and C. In these cases to be sure, both legs were examined, but the supply to the thigh alone was observed and therefore the comparison is limited to that segment of the limb.

As the data for these calculations is to be found in Tables XII and XIII, it will be necessary to give only the comparison of the estimated number of fibers in each case with those observed.

TABLE XXIV.

	Estimation (DONALDSON) Corrected for the Splitting fibers	Observed (DUNN)	Difference	Percent.
<i>Frog B</i>				
Thigh r.	2577	2623	— 46	—1.7%
Thigh l.	2608	2600	+ 8	+0.3%
<i>Frog C</i>				
Thigh r.	2884	2814	+ 70	+2.5
Thigh l.	2887	2777	+110	+4.0

If we take the differences between the estimated and observed number of fibers to the thigh in all three frogs, B, C and B II, we find that the total is 251 fibers, neglecting signs, or deducting the — fibers from the + fibers, an excess of + 189 fibers. In the first case the difference amounts to an average of 1.4%, neglecting signs, or +1.1% when the signs are taken into account.

This is a very satisfactory approximation of the estimate to the observed number.

In the case of the shank we have only the two observations on Frog B II, with which to make the test. Here the approximation is closer, being 16 fibers when the signs are neglected, or a difference of — 12 fibers regarding the signs. This gives the percentage values of .37% and —.28%. In the case of the foot, owing to the fact that we have not the data for controlling the splitting fibers, the divisions of which have a similar distribution, but credit the differences between the estimated and observed numbers to this class, the test of the approximation cannot be made, as it has been for the thigh and shank. However it will be well to point out the reasons in detail for thinking that in the nerves to the foot, this class of fibers will account for the differences which have been found.

In the first place, Dr. DUNN (1902, p. 315, Table XII) has shown in Frog B II, between S₂, just below the branches to the thigh and T and P just at the entrance of the trunk into the shank, an interval from which no branches are given off—, that at the lowest level on the right side there was a gain of 210 fibers and on the left, 184, or 5.3% on the right and 4.5% on the left, the percentage in each case being based on the number

at S₂. This is proof positive of the splitting of the fibers within the nerve trunks. Moreover, in our calculations which were made to get the estimated number of fibers going to the thigh, the average value of the splitting fibers of class "a" in these case was 2.9%. For the two shanks of Frog B II it was 9.2%, while that demanded for the foot was 9.9%, all these percentages being based on the calculated number of unbranched fibers to each segment.

The significance of the foregoing paragraph is the following: When we assume the splitting fibers of this class to this amount, the results of the estimation and observation agree closely, and that in the shank where good agreement is obtained, we have assumed 9.2% of these splitting fibers, whereas in the foot, at which level our results cannot be tested in the same way, but where we should expect a priori a somewhat greater number of splitting fibers of this class, we are compelled to assume only a slightly greater proportion, namely 9.9%.

The claim made, therefore, for the splitting fibers at this level of the foot has ample indirect evidence in its favor.

Just at this point it may be fitting to call attention to the fact that the law here enunciated is deduced from the results already presented in four different investigations: HARDESTY (1899), DONALDSON and SCHOEMAKER (1900), and DUNN (1900 and 1902), that these were all independent and undertaken without any thought of the present problem, and that the data taken from them have been here employed without any modification whatsoever. The only special investigation taken up after this problem was formulated was the study of the areas of skin in the several segments of the leg, and the observation by Dr. DUNN on the nerves in Frog C II, with a view to testing whether the results on Frog B II might be considered as generally applicable.

This examination of the data from which the deduction has been made goes a long way to protect it from the criticism of bias, either unconscious or otherwise.

It has then been possible to show that, allowing fo

splitting fibers, the number going to any segment of the leg, calculated on the basis of the proportional area of skin and the proportional weight of the muscles, agrees very closely with the number observed.

To generalize these results, it is desirable to know, not only what percentage of all the fibers which enter the leg goes to any segment, as given by the formula in Table X, but also the percentage of that number that should be added to the supply of a given segment, to make it equal to the observed number.

This can be obtained by tabulating in each case the estimated and observed numbers, finding the number of fibers by which they differ and the percentage value of this number on the basis of the number estimated.

The averages of the percentages in each case then show the proportion of fibers which should be added to the estimate in order to represent the number which would probably be observed.

TABLE XXV.

Showing the percentage of the estimated number of fibers to be added in order to make the estimate agree with the number observed.

Frog	<i>Thigh</i>		
	Estimate 46%	Added in calculation	Required to balance
B. r.	2426	151 = 6.2%	197
B. l.	2477	131 = 5.3%	138
C. r.	2765	119 = 4.3%	49
C. l.	2754	133 = 4.8%	23
B II. r.	3269	237 = 7.2%	239
B II. l.	3279	228 = 7.0%	212
Total	16970	999 = 5.9%	858 = 5.0% Difference = .9%
<i>Shank</i>			
	25.3%		
B II. r.	1796	320 = 17.8%	334
B II. l.	1802	308 = 17.1%	306
Total	3598	628 = 17.5%	640 = 18% Difference = 0.5%
<i>Foot</i>			
	28.7%		
B II. r.	2042	455 = 22.3%	455
B II. l.	2048	436 = 21.3%	436
Total	4090	891 = 21.8%	891 = 21.8% Difference = 0%

A glance at Table XXV shows (1) that to make the 46% of the fibers entering the leg equal the number that will probably be observed to the thigh, 5% of itself must be added to it.

(2) That to make the 25.3% of the fibers entering the leg equal the number that will probably be observed to the shank, 18% of itself must be added to it.

(3) That to make the 28.7% of the fibers entering the leg equal the number that will probably be observed to the foot, 21.8% of itself must be added to it.

By the aid of these results, therefore, if one is given the number of fibers entering the leg, it is possible to estimate with a high degree of accuracy, the number which will be found going to any segment.

(5) *The number of medullated fibers distributed as muscular and cutaneous nerves to each segment of the leg.*

The efferent nerve fibers in a given segment are present in numbers proportional to the weight of muscle and the afferent according to the area of skin. The muscular nerves must contain all the efferent or motor medullated fibers, but it would certainly be very unexpected to find that the cutaneous nerves contained all the afferent fibers.

The number of cutaneous and muscular fibers has been determined in every instance for both thigh and shank by Dr. DUNN, and with this we can compare the distribution, calculated on the assumption that all the afferent fibers have a cutaneous distribution.

In the following table, in each instance, the calculated sensory (afferent supply, Cal. S.), is compared with the observed cutaneous (Obs. Cut.) supply—the calculated number always being the *larger*. The absolute difference in number of fibers is noted and its percentage value given—the number forming the observed cutaneous supply, being taken as a standard in calculating the percentage. In like manner, the observed muscular (Obs. Mus.) supply is compared with the calculated motor (Cal. Mot.), the observed muscular supply always being the *larger*—the absolute difference in number of

fibers as well as their percentage values are also given, the observed number being taken as the standard.

The shank is tested in the same way. For the foot observations are lacking. A study of the table will show, first, that the afferent or sensory fibers going to the muscles of the thigh are from 45% to 3.8% of the number of the cutaneous nerve fibers, while the excess of the muscular nerves of the thigh over the calculated number of motor fibers, is from 25.1% to 3.1% of the muscular nerve fibers.

In the case of the shank, the calculations for afferent fibers going to the muscles gives from 52% to 37% and an excess of fibers in the muscular nerves of from 34.3% to 38.6%.

TABLE XXVI.

Comparing the calculated number of sensory fibers with the number observed in the cutaneous supply and the calculated number of motor fibers compared with the number observed in the muscular supply and giving in each case the number of fibers by which they differ as well as the percentage value of this number. The observed numbers being used as the standards.

Frog	Thigh	Difference			
		Cutaneous		Muscular	
			%	Abs.	%
B. r.	Cal. S. 1281	Obs. Cut. 876	405 = -45.0%	451 = +25.1%	
	Obs. Mus. 1747				
B. l.	Cal. S. 1297	Obs. Cut. 871	426 = -48.9%	418 = +24.2%	
	Obs. Mus. 1729				
C. r.	Cal. S. 1436	Obs. Cut. 1279	217 = -17.8%	107 = + 6.8%	
	Obs. Mus. 1535				
C. l.	Cal. S. 1434	Obs. Cut. 1219	145 = -11.3%	85 = + 5.5%	
	Obs. Mus. 1558				
B II r.	Cal. S. 1743	Obs. Cut. 1678	65 = - 3.8%	67 = + 3.6%	
	Obs. Mus. 1830				
B II l.	Cal. S. 1748	Obs. Cut. 1676	72 = - 4.3%	56 = + 3.1%	
	Obs. Mus. 1805				
Shank					
B II r.	Cal. S. 1376	Obs. Cut. 1003	373 = -37.0%	387 = +34.3%	
	Obs. Mus. 1127				
B II l.	Cal. S. 1371	Obs. Cut. 903	468 = -52.0%	466 = +38.6%	
	Obs. Mus. 1205				

From these data it appears probable that in all these frogs and in every segment of the leg, some afferent fibers are distributed, with the muscular nerves. Moreover, the proportion thus distributed is shown to be very variable in the case of the thigh.

On comparing the proportion of these afferent fibers going to the muscles in the case of the shank, we find that the number is relatively larger than to the thigh. The comparison in the case of the shank B II, should be made, not with the data for the thighs of all the frogs, but with the data for the thighs of frog B II. Thus, in round numbers, there are in this instance, 4% of these afferent fibers to the thigh and 45% to the shank.

The better supply of the muscles with afferent fibers as we pass to the more distal segments of the limb, is what we should expect a priori, though in this case the difference appears very large.

Conclusions.

The present study is concerned with the number of medullated nerve fibers going to the different segments of the frog's leg.

1. The nerve fibers entering the leg being considered as so many separate lines of connection with the several segments are found to be distributed in accordance with the law that the efferent fibers are present in proportion to the weight of the muscle, and the afferent in proportion to the area of skin.

2. When this statement is reduced to numerical terms, it is expressed by the following formula :

Of the fibers entering the leg of the frog,

46.0% go to the skin and muscles of the Thigh.
25.3% go to the skin and muscles of the Shank.
28.7% go to the skin and muscles of the Foot.

3. Since some of the fibers split after entering the leg, the numbers found in the nerve branches to the segments are larger than the number of single pathways assigned to the segment by the formula. Calculation shows that to determine the number which will probably be observed in each case, the

number given by the formula must be increased by a certain percentage of itself:

For the Thigh by 5.0%
For the Shank by 18.0%
For the Foot by 21.8%

4. When due allowance is made for the splitting fibers, it is found that the agreement between the estimated and observed numbers is close:

	Difference.
For the Thigh.....average of 6 cases =	+1.10%
For the Shank.....average of 2 cases =	-.28%
For the Foot.....average of 2 cases =	"

*The necessary observations for the foot are lacking, though the agreement would probably be close there also.

5. Some of the afferent fibers are distributed to the muscles. The proportion in the thigh is highly variable. The one case available shows a larger proportion of afferent fibers to the muscles of the shank than to those of the thigh, suggesting that in the foot the proportion would be still greater.

Thus, while the number of afferent fibers in a segment appears to be in proportion to the area of the skin, yet the distribution of these fibers is both to the skin and the muscles. The significance of this arrangement can only be determined by work on other forms, both higher and lower than the frog, in the zoological scale.

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