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C. S. Sherrington

THE TENDON ACTION AND LEVERAGE OF TWO-JOINT MUSCLES OF THE HIND LEG OF THE FROG WITH SPECIAL REFERENCE TO THE SPRING MOVEMENT.

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If a man had invented an apparatus for propelling a vehicle on the lines of the leg of a frog, I fear that he would be greatly criticised. It is not, at first sight, a very promising contrivance. The skeleton consists of fragile bones, loosely connected at their extremities by ligaments—a chain of levers, moved by muscles which are elastic structures, capable of shortening and pulling on the bones to which they are attached, but when at rest, extensible, flexible, and flaccid. Not only does this apparatus differ in respect to stability from most of those devised by man, but it has a remarkable arrangement, viz., the presence of many muscles which pass over two joints. Most of these two-joint muscles flex one joint by one end and extend an adjacent joint by the other end. For example, the gastrocnemius, the most powerful extensor of the lower leg, and one which evidently plays a very important part in the leap, not only extends the ankle but flexes the knee. Excite its nerve so that it contracts alone—it is seen to produce both of these effects at the same time. Since all the joints of the leg must be violently extended when the frog leaps, how can it fail to be a decided disadvantage for the strongest muscles of the leg, those which manifestly act as extensors to propel the body, to be attached so as to act at the same time as flexors?

A. Fick[1] points out many advantages which come from the presence of these muscles:—the lessening of the total mass of muscle substance which is required for movements of the different segments of the limb; the consequent economy in the expenditure of energy; the fact, shown by Borelli,[2] that the movement of one of the joints crossed may increase the tension of a muscle and so help it to work on the other joint; the fact that a contracted two-joint muscle may act merely as an elastic band, and transmit part of the energy developed by a one-joint muscle which passes over one of the joints, to the other joint, for example, when a man rises from the squatting position, a one-joint extensor of the hip, as the glutæus, may act through the rectus to

[1] Hermann's Handb. d. Physiol., 1879, Bd. I, II, S. 284; also Fick, Untersuch. u. Muskelarbeit, S. 39, Basel, 1867.

[2] De Motu animalium, first edition, 1680.

extend the knee.[1] Other examples are the action of the gastrocnemius at the end of a step, to continue the plantar flexion of the foot, and at the same time to flex the knee; the closing of the claws of a bird when it squats on its perch or raises the foot; extension of the claws of the lion when the fore leg is thrust out.

In the case of the frog, all the largest and strongest muscles of the hind leg are two-joint muscles; no one, therefore, can work on any problem involving the co-ordination of the action of the muscles of the leg without considering the method of action of these muscles. In an article on the "Centers and Paths of Transmission in the Spinal Cord of the Frog," Gad[2] refers to the passive action of the two-joint muscles of the leg of the frog, and shows how it may play an important part in locomotion. While working under Professor Ludwig in the Physiological Laboratory in Leipzig, in 1883 and 1884, on the spread of reflex impulses in the spinal cord of the frog, I found, like Gad and his students, that it was necessary to consider the effect of the passive action of two-joint muscles upon the movements of the leg. In publishing the results of these experiments[3] I called attention to the important part

Fig. 1.—*Diagrammatic representation of the tendon action of the two-joint muscles of the hind leg of the frog.* When the leg is extended, active contraction of a one-joint flexor muscle of the hip (a), and the passive tendon action of the two-joint muscles on the median side of the thigh (b) and on the lateral side of the lower leg (d) will cause complete flexion of the hip and knee, and partial flexion of the ankle. When the leg is flexed, active contraction of a one-joint extensor muscle of the hip, (f) and the passive action of the two-joint muscles on the lateral side of the thigh (c) and the median side of the lower leg (e) will cause the hip, knee, and ankle to be extended.

[1] Eugene Fick; Arch. f. Anat. u. Physiol., Anat. Abthl., 1879, S. 201.

[2] Verhl. d. physik.-med. Ges. in Würzburg, 1884, N. F., Bd. 18, S. 129.

[3] Die räumliche und zeitliche Aufeinanderfolge reflectorisch contrahirter Muskln; Arch. f. Anat. u. Physiol. 1885, S. 408.

which these muscles must play in the movement of the leg, illustrating their action by the diagram shown in Fig. 1.

Since that time, on several occasions, I have made a study of the anatomical relations of these muscles to the parts to be moved, and the effect of their peculiar method of attachment upon their functional activity. In the autumn of 1886, at the suggestion of Professor H. P. Bowditch, a series of experiments were made in order to ascertain, à propos of the Ritter-Rollet[1] phenomenon, whether the irritability of the muscles which flex and those which extend the leg is the same.

These experiments failed to give a satisfactory answer to the question. The fact stood out prominently that the largest and strongest of the muscles of the hind leg of the frog are two-joint muscles, and produce opposite types of action at their two extremities, flexing the joint at one end, and extending the joint at the other; they are, in short, both flexors and extensors. It seemed hardly possible that, when functionally active by locomotion, they should produce these two antagonistic types of movement at the same time, but it did not seem safe to class them either as flexors or extensors until their normal action had been investigated. In a letter to Dr. Bowditch in November, 1886, in which the double action of two-joint muscles was described and their method of action was speculated upon, I ended by saying: "I have reached a point where I have shown that it is possible for an extensor of the knee to flex the knee, and it is, perhaps, as well that I should stop my theorizing. The mechanics of the muscles of the leg of the frog is not the less a tempting subject for research and speculation because it offers an excellent opportunity for reasoning in a circle."

The following spring a careful study of the anatomy of the muscles and joints of the hind leg of the bull-frog was made by me at Johns Hopkins University. The results obtained added greatly to my admiration and respect for these wonderful mechanisms, but I was only led back to the apparent paradox, that a two-joint muscle, because of the tendon action of a muscle on the opposite side of the leg, may flex a joint of which it is an extensor or extend a joint of which it is a flexor. Which of these it would do by a given movement would seem to depend on the relative leverage of the two extremities of the muscle by the position of the joints at the time. During the past year the method of action of two-joint muscles of the hind leg of the frog has been again the subject of serious study, and especial attention has been given to the leverage of these muscles by different positions of the joints which they cross. This work is still in progress, but enough data have been gathered to justify the view expressed above with reference to the action of the two-joint muscles, and to remove one of the chief obstacles to an understanding of the action of these muscles by the leap.

[1] Sitzungsbr. d. k. Akad. d. Wissensch., Wien, 1876, Bd. VI, Abth. 3.

The Tendon Action of Two-Joint Muscles.

In the passage of the leg from the flexed to the extended position, as Hering[1] has shown, important rotation and adduction movements occur. The consideration of these will be deferred till another time, and in this paper attention will be paid only to the extension of the leg by the two-joint muscles. The terms flexion and extension are used differently by different authors, and so that there shall be no misunderstanding, I will state that in this paper the movements of the leg of the frog will be assumed to occur in a plane approximately parallel to that of the earth, and that the term *flexion* will be employed for movements in this plane of a type to cause the two bones entering into a joint to approach each other, and *extension*, for movements of a type to cause the bones to separate. In the case of the knee, the term *over-flexion* will be used to describe the position taken by the lower leg when it is carried by the flexing act past the thigh.

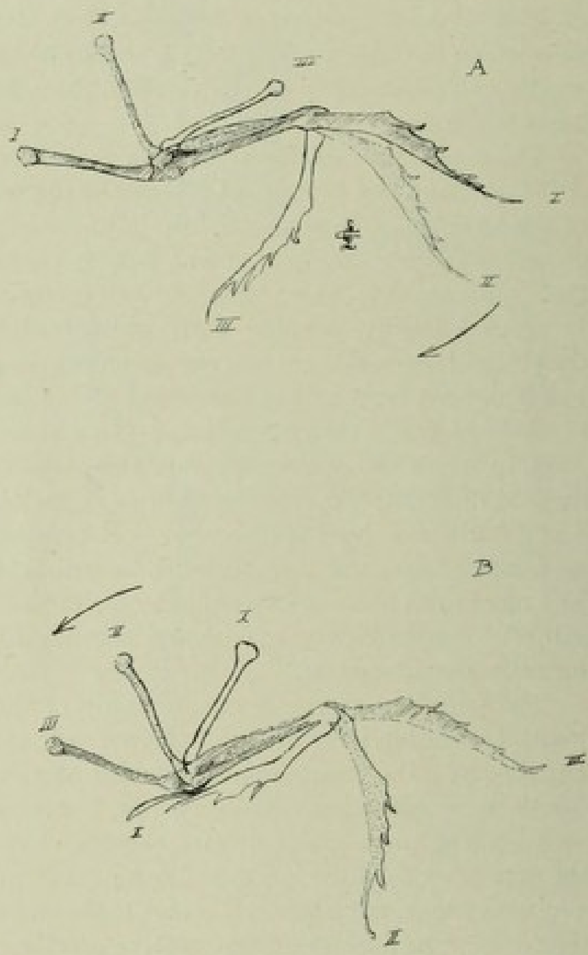


Fig. 2.—A, the effect of passive flexion of the foot to flex the femur; B, the effect of passive extension of the femur to extend the foot.

The power of the spring of the frog is largely due to the method of attachment of the two-joint muscles and their resulting tendon action. *Because of the peculiar relation of the two-joint muscles to the joints which they cross, any force which extends or flexes either hip, knee, or ankle, tends to cause like movement of all the rest.* Fig. 2, A, shows the effect of the tendon action of

[1] Arch. f. d. Ges. Physiol., Bd. LXVIII, p. 9.

the gastrocnemius to flex the femur as the foot is flexed; and B, its effect to extend the foot as the femur is extended.

Gad[1] observed, that when the frog is suspended vertically, passive flexion of the thigh on the belly will cause complete flexion on the knee, and draw the lower leg up to the thigh, but that the flexion of the knee will not cause complete flexion of the ankle, the foot being raised only so as to form something less than a right angle with the lower leg (see Fig. 2, A).

Hering[2] states that the foot can be flexed by the passive action of the two-joint muscles, in the case of a pithed frog, only about ninety degrees, and that the active contraction of flexor muscles is essential to the completion of the act. He emphasizes the fact, however, that under normal conditions the muscles are in reflex tonus, and that through this their tension is considerably increased. That one of the one-joint flexors of the ankle must act, is shown by the fact that if the peroneal nerve be cut, it is only occasionally that the foot flies into the sitting position by recovery from the spring. The passive flexion of the foot he finds to be largely the result of the tension brought on the tibialis anticus longus where it draws across the extensor side of the knee. If the tendon of this muscle is cut, the passive flexion of the foot is much less.

Gaupp,[3] when describing the movements of the knee, refers to the passive action of the tibialis anticus longus and peroneus to extend the knee when the ankle is extended.

Extension of the hip causes the triceps to be pulled on, and the knee to be extended; extension of the ankle causes the tibialis anticus longus to be pulled on, and the knee to be extended; extension of the knee causes the semi-membranosus, gracilis magnus, and semitendinosus to be pulled on, and the hip to be extended; extension of the knee also causes the gastrocnemius to be pulled on, and the ankle to be extended. In certain positions of the joints, the ilio-fibularis and peroneus may also take part in producing these effects. In a similar manner, flexion effects are transmitted from joint to joint. This tendon action of the two-joint muscles can be readily seen in Fig. 1, and is well illustrated by a model, such as is roughly represented in Fig. 3.

Since the extension of the hip will extend the knee, and extension of the knee the ankle, a one-joint extensor muscle of the hip can cause extension of the knee and ankle; since extension of the ankle will extend the knee, and extension of the knee will extend the hip, a one-joint muscle of the ankle can extend the knee and the hip; finally, a one-joint extensor muscle of the knee can extend both hip and ankle. The same is true of the one-joint flexors

[1] Verh. d. physik.-med. Ges. in Würzburg; N. F., Bd. XVIII, 1884, p. 171.

[2] Arch. f. d. Ges. Physiol., Bd. LXVIII, S. 11.

[3] Ecker's and Wiedersheim's Anat. des Frosches, neu bearbeitet von Dr. Ernst Gaupp, 1896, p. 90.

of the hip and ankle; there are none of the knee. The one-joint flexor muscles of both ankle and hip can flex the ankle, knee, and hip. These effects are all the result of the passive, tendon-like action of the two-joint muscles, and the amount that distant joints are acted upon depends on the resting length of these muscles.

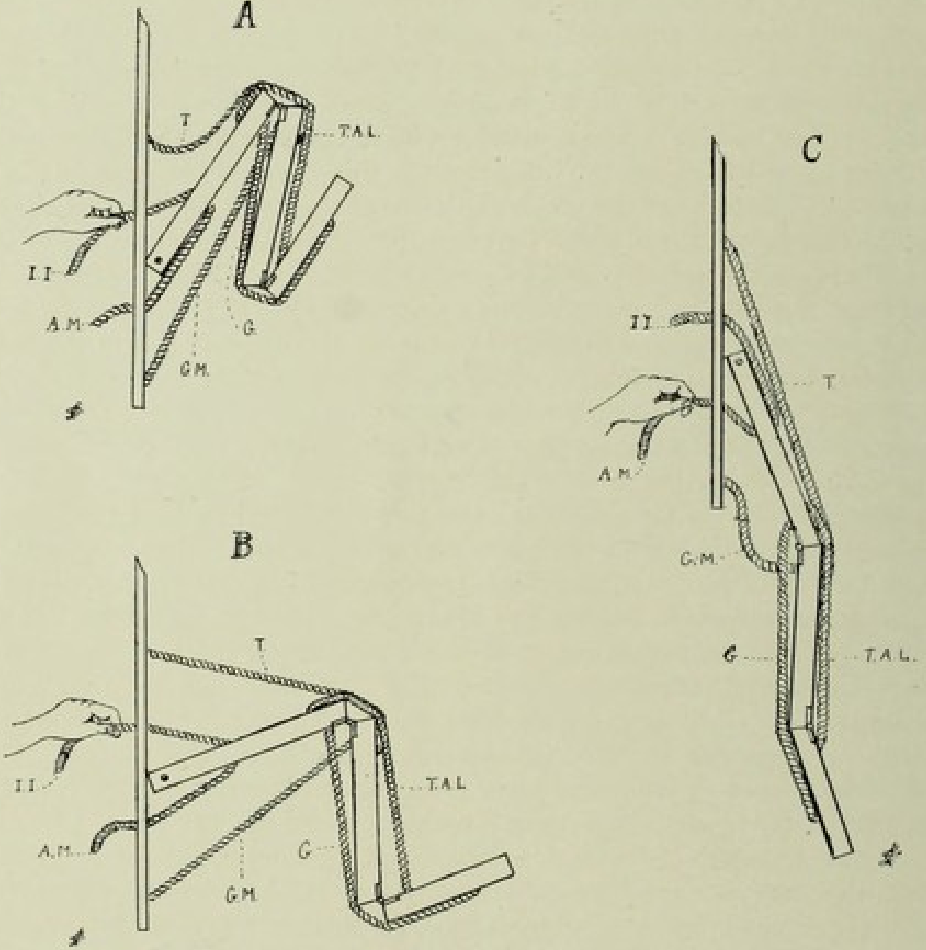


FIG. 3.—Model showing tendon action of two-joint muscles. II, one-joint flexor of hip, e. g., iliacus internus; A M, one-joint extensor of hip, e. g., adductor magnus; T, two-joint flexor of hip and extensor of knee, e. g., triceps; G M, two-joint extensor of hip and flexor of knee, e. g., gracilis magnus; T A L, two-joint extensor of knee and flexor of ankle, e. g., tibialis anticus longus; G, two-joint flexor of knee and extensor of ankle, e. g., gastrocnemius. If the one-joint iliacus internus is pulled on and it flexes the hip, the two-joint gracilis magnus flexes the knee and the tibialis anticus longus the ankle. If the one-joint adductor magnus is pulled on and it extends the hip, the two-joint triceps extends the knee and the gastrocnemius the ankle.

Not only the tendon action of muscles but the effects of inertia favor the simultaneous production of flexion and extension in adjacent joints. Otto Fischer[1] found that muscles can act on a joint over which they do not pass. He writes: "It appears in general, that a one-joint muscle calls forth, as a rule, in an adjacent joint, a rotation the opposite to that in the joint which lies between its points of insertion." Thus, a one-joint flexor of the elbow, which causes the lower arm to move forward, will act on the shoulder joint and cause the upper arm to move backward.

In a like manner a one-joint flexor of the ankle of a frog, which causes the foot of a frog to move in the lateral direction, will cause the lower leg to move in the median direction and produce flexion of the knee. A flexor movement of the knee, which carries the lower leg in the median direction, will carry the thigh in the lateral direction, *i. e.*, cause flexion of the hip. Similarly a one-joint extensor of the ankle will extend the knee and a one-joint extensor of the knee will extend the ankle.

Fischer[2] also found that a one-joint flexor or extensor of the shoulder of a man could produce an opposite rotation in the elbow. In a like manner a one-joint extensor of the hip of a frog would cause extension of the knee, and a one-joint flexor of the hip, flexion of the knee.

Nor is this transfer of action from joint to joint confined to the one-joint muscles. H. E. Hering[3] ascertained by experiments on frogs in which all the muscles of the thigh and lower leg, except the gastrocnemius or tibialis anticus were cut away, if the gastrocnemius, which extends the foot on the lower leg and flexes the lower leg on the thigh, was excited by electricity, it at the same time flexed the thigh on the pelvis, and the tibialis anticus longus, which flexes the foot on the lower leg and extends the lower leg on the thigh, if excited, also extended the thigh on the pelvis. "Several-joint muscles work also on joints over which they do not draw, and in such a way that they call out an opposite rotation in a proximal joint."[4]

I have repeated this experiment with success and, as Fischer has shown, it can be demonstrated on a model; he writes: "By the several-joint muscles, pulling across the elbow and shoulder joints, the relations lie not so simply. For these, also, indeed, it has proved, that as the contraction of the muscles follows the period of rest, with an arbitrary tension for every special point of departure of the arm, there belongs a special relation of the degrees of rotation in the shoulder and elbow joints."

A two-joint muscle of the leg of the frog, therefore, like a one-joint muscle, by causing the extension of a joint, may produce extension in neighboring

[1] Abhandl. d. k. Sächs. Ges. d. Wiss., math.-phys. Classe, 1895, Bd. XXII, No. 2, S. 193.

[2] Abhandl. d. k. Sächs. Ges. d. Wiss., math.-phys., Cl., 1897, Bd. XXIII, No. 6, S. 556.

[3] Arch. f. d. Ges. Physiol., 1897, Bd. LXV, S. 629.

[4] *Ibid.*, S. 630.

joints. These effects of inertia are in harmony with the effect produced by the tendon action of the muscles of the leg; they co-operate to cause all the joints to extend simultaneously by the leap.

If the joints are bound together by the tendon action of two-joint muscles, how can independent movement of the separate joints be made? All the two-joint muscles of the hind leg of the frog are attached under very slight tension, varying, of course, with the amount of reflex tonus present, and are all extensible. When they are not contracting, they readily yield to any stretching force sufficiently to permit of wide excursions of the joints. The one-joint flexors and extensors may, therefore, produce independent movements of any of the joints, if the corresponding movements of the other joints are prevented by the action of other muscles. There are one-joint flexors and one-joint extensors for the ankle and for the hip, and there is a one-joint extensor for the knee and another muscle, which, although having some action on the ankle, is principally a one-joint extensor of the knee. There are, strange to say, no one-joint flexors of the knee, and if the joint has to be flexed independently, it must be flexed by the two-joint muscles.

If a two-joint muscle contracts alone and unopposed, it produces (the sartorius is an exception) two opposite effects by its two extremities: it extends one joint by one end, and flexes the other joint by the other end. If the action of one end is prevented by some opposing force, as by the contraction of antagonistic one-joint muscles, the principal effect of the contraction is observed at the other end. Thus, the two-joint flexors of the knee which lie on the median and under surface of the thigh, and which tend as well to extend the hip, if the extension of the hip is opposed by one-joint flexors of the hip, will act chiefly as flexors of the knee. The same is true, to give another example, of the gastrocnemius which extends the ankle, as well as flexes the knee; if the extension of the ankle is opposed by the one-joint flexors of the ankle, its contraction will be manifested principally in a flexion of the knee.

What is the effect of the simultaneous contraction of all of the two-joint muscles of the leg?

Independent movements of separate joints can only occur when the two-joint muscles, as a whole, are at rest, because most of these muscles are more powerful than the one-joint muscles, and when they contract they become tense-like cords, and as has been described, compel like movements to occur in all the joints. Most of these muscles tend to flex one joint and to extend the next. Nor does a two-joint muscle merely extend the joint of which it is an extensor, it makes use of the tendon action of the other two-joint muscles to extend the other joints. The triceps, by extending the knee, pulls on the gastrocnemius and extends the ankle; the gastrocnemius, by extending the ankle, pulls on the tibialis anticus longus and extends the knee; the tibialis anticus longus, by extending the knee, pulls on the semimembranosus, gracilis magnus, and semitendinosus and extends the hip; and finally, the semimembranosus, gracilis magnus, and semitendinosus, by extending the hip, pull on the triceps and extend the knee.

Hering,[1] when studying the action of the muscles by which the leg is drawn to the sitting position, was compelled to ask himself, how it is that a muscle, like the tibialis anticus longus, which extends the knee as well as flexes the foot, can be used with economy at a time when all the joints of the leg must be flexed? I, long ago, found myself confronted by like questions when studying the action of the muscles of the frog by the spring movement. How can the tibialis anticus longus, which flexes the ankle as well as extends the knee, be of use in the leap, when the ankle, like the knee, must be vigorously extended? It is hard to believe that the muscle cannot be economically used, either when the leg, as a whole, is to be flexed or to be extended. One is the less ready to accept such a conclusion because it would apply equally well to the rest of the two joint muscles of the leg, which make up the bulk of the muscle substance.

Nevertheless, the question has to be answered: *Why, by the leap, when all the joints must be vigorously extended, does not the flexion action of these muscles interfere with the extension of the leg?* This question leads to a paradox. *A two-joint muscle may act as an extensor of the joint of which it is a flexor.*

The following conditions are essential for the production of this effect with completeness:

a. The muscle in question, A, must have a better leverage at the end by which it extends than at the end by which it flexes.

b. There must be on the opposite side of the leg a two-joint muscle, B, which flexes the joint which A extends, and extends the joint which A flexes.

c. The extensor leverage and strength of A must be sufficient to enable it to make use of the tendon action of B.

d. B must be sufficiently contracted to act as a tendon.

For example, the gastrocnemius, if all the other muscles of the leg be cut away, will, if it be excited, extend the ankle and flex the knee. Now, if a thread be fastened to the two ends of the tibialis anticus longus, on the opposite side of the leg, and be made sufficiently tense to produce the tendon action of this muscle, excitation of the gastrocnemius results in the extension of the knee, as well as of the ankle.

This can be readily shown by a model in which a spring is used to represent the contracting gastrocnemius, and a string, the tendon action of the tibialis anticus longus. I of Fig. 4 shows the foot flexed and femur extended, and II the extension of the foot and flexion of the femur which occur when the parts are released, and the spring, which represents the contracting gastroc-

[1] Arch. f. d. Ges. Physiol., Bd. LXVIII, S. 13.

nemius, is allowed to act. III shows the foot flexed and femur flexed, and IV the extension of both foot and femur, which occurs when the parts are released, and the spring, by extending the foot, pulls on the string, which represents the tense tibialis anticus longus, and through it extends the knee.

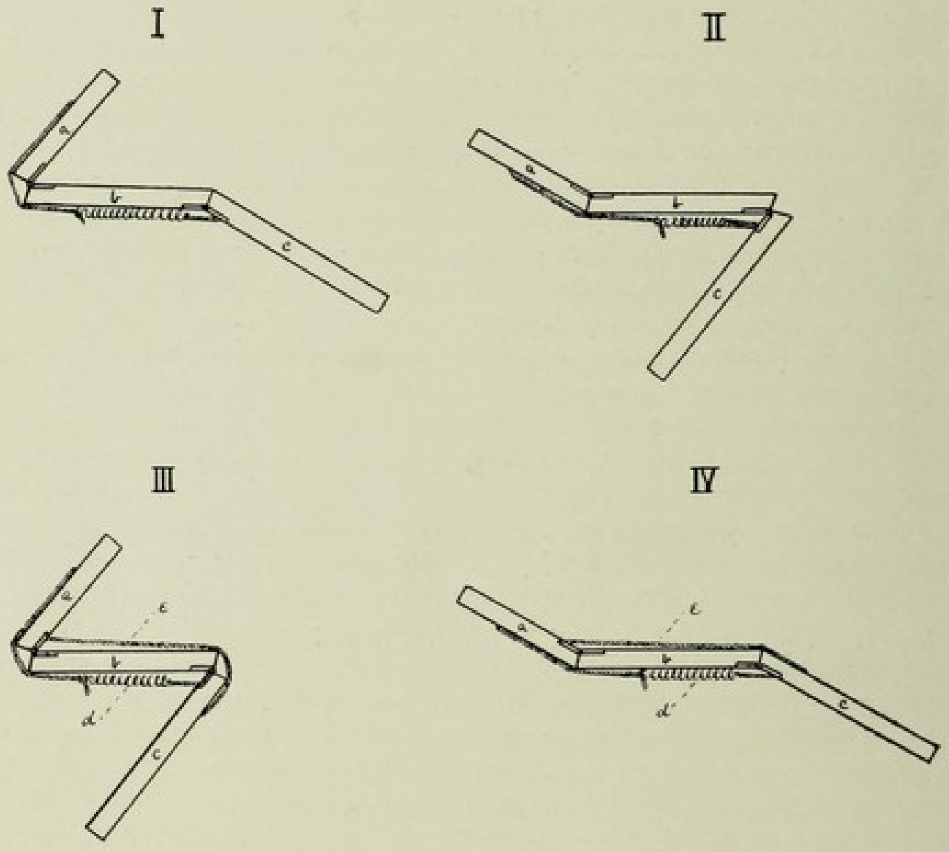


FIG. 4.—*a* represents the foot; *b*, the crus; *c*, the femur; *d*, the gastrocnemius, and *e*, the tibialis anticus longus. I, foot flexed and femur extended; II, extension of foot and flexion of femur caused by gastrocnemius; III, foot flexed and femur flexed; IV, exten, sion of femur, as well as foot, caused by strain brought by contracting gastrocnemius- through tibialis anticus longus on extensor side of knee.

The gastrocnemius has a better leverage on the tarsus than on the femur, and hence its contraction will act more strongly to extend the ankle than to flex the knee. Moreover, the leverage of the gastrocnemius on the tarsus is better than that of the tibialis anticus longus, hence, when the gastrocnemius contracts, it extends the ankle and exerts a vigorous pull on the tibialis anticus longus; this pull is transmitted through the muscle across the extensor side of the knee to the femur, and the knee is extended because the strength of the pull transmitted from the distal end of the gastrocnemius to the extensor side of the knee is greater than that applied by the muscle to the flexor side of the knee. The effect is still further increased by the fact that, when the leg is flexed, the extensor leverage of the tibialis anticus longus on the femur is stronger than the flexor leverage of the gastrocnemius.

Inasmuch as the tibialis anticus longus is extensible, it would be necessary that it should be contracting if its full tendon action is to be obtained. The contraction of the muscle would not oppose the extension effects produced by the gastrocnemius, but on the contrary, favor them. If all the muscles are cut away from the leg excepting the tibialis anticus longus, and that be excited, it will extend the knee and flex the ankle. If a string be substituted for the gastrocnemius, and this be made tense enough to produce its tendon action, excitation of the tibialis anticus longus will produce extension of the ankle, as well as of the knee. These two apparently antagonistic muscles, therefore, work in the same sense, each helping the other to produce extension of the ankle and knee.

We can sum up the process by saying: The energy of the two-joint muscles of the lower leg of the frog is transmitted in a circle in the direction of the greatest leverage. The same principle would be effective in the production of extension by two-joint muscles of the thigh.

As has been said, extension of the knee acts through the tendon action of the two-joint semimembranosus, gracilis magnus, and semitendinosus on the median and under surface of the thigh, to cause extension of the hip. So the gastrocnemius and tibialis anticus longus, muscles of the lower leg, can extend the hip. Moreover, since extension of the hip causes through the triceps extension of the knee, the energy of contraction of the gastrocnemius, for example, would be transmitted all the way around, through ankle, knee, hip, and knee to the muscle where it was developed. The same is true of any of these muscles; the energy is imparted to the bones through the end having the better leverage, and is transmitted thence through all the joints back to the point of origin.

The energy of the two-joint muscles of the hind leg of the frog is transmitted as by an endless chain, having the form of a figure eight with the crossing at the knee, and the effect progresses in the direction of the better leverage.

H. E. Hering,[1] in his study of the voluntary movements of the hand and fore-arm, observed that by flexion or extension of the fingers there is a movement of the middle hand in the opposite direction, caused by the simultaneous contraction of the hand extensors or flexors, as the case may be. Hering[2] gives the rule, that, "In general, one can say that a muscle which draws freely

[1] Zeitschr. f. Heilkunde, 1895, XVI, S. 129.

[2] Arch. f. d. Ges. Physiol., 1897, Bd. LXV, S. 631.

across two joints will always move the bone lying between these two joints, in the same sense as that on which it is inserted and on which it acts."

As Duchehene pointed out in the case of the hand, so with the foot, to get the strongest flexion or extension, the simultaneous movement of the lower leg in the same direction must be prevented, or better yet, the lower leg must be caused to make a movement of the opposite direction by the simultaneous action of the muscles. Hering calls these muscles pseudo-antagonists. "While the antagonistic muscles are inserted on the same bones, which they are able to move in an opposite direction, the pseudo-antagonists are inserted on two different bones. The pseudo-antagonists are antagonists in so far as they tend to move the bone in the opposite direction; but while the one muscle, namely, that inserted on this bone, rotates the same directly, the other rotates the same bone indirectly, in that, pulling across the bone it moves it only by means of a neighboring bone to which it is inserted. Thus, while the flexors and extensors of the hand are antagonists, the flexors of the hand and extensors of the fingers are pseudo-antagonists." Hering does not state in so many words in what light we shall regard two-joint muscles, like the gastrocnemius and the tibialis anticus longus, which lie on opposite sides of a bone, and which, when acting alone, move each of the two bones adjacent to this, in opposite directions; but to judge from the sentence last quoted, they are to be considered antagonist. I have shown, however, that these muscles, if contracting together, would help each other to move the bones to which they are attached, in the same direction, because they are capable each of employing the tendon action of the other. Hering[1] writes: "The view prevails that antagonists are simultaneously innervated when a movement results in the direction of one of the two antagonists. This, however, cannot be proved." "Antagonists are synergetic only by the fixation of a bone; pseudo-antagonists are, also, synergetic by the movement of a bone."

It seems to me that in the light of my observations Hering's statement will have to be modified. I admit that, as yet, there is no direct proof that the tibialis anticus longus, for example, contracts by the spring movement synchronously with the gastrocnemius, but the value of a co-operation on the part of these muscles is so evident, that the probabilities are decidedly in favor of the supposition. There is no more reason for doubting the action of the tibialis anticus longus by the spring, than that the triceps, which appears to be the chief extensor of the knee and is also an opponent of the gastrocnemius, fails to contract by the spring. Apparently muscles which may be regarded as antagonistic, because of the opposite effects which they produce when acting under certain conditions, may act together; and further, that when acting together, they may so alter the effects which either would have produced when acting alone, that their ordinary antagonistic action may be temporarily

[1] Loc. cit., S. 632.

converted into one which is mutually helpful. In short, muscles like the tibialis anticus longus and gastrocnemius, which, on account of the opposite effects which they ordinarily produce, are to be regarded as antagonists, may, under certain conditions, when acting together, become temporarily co-operators.

The Leverage of Two-Joint Muscles.

It is evident that the effect of the contraction of a muscle depends largely on the leverage which it exerts on the bones to which it is attached. The leverage of each of the one-joint muscles of the leg changes with each new position of the joint which it controls, and the leverage of each of the ends of each of the two-joint muscles changes with each position of each of the joints on which it acts. As this is the case, a knowledge of the leverage of each of the muscles of the leg, by every position possible to it, is indispensable to a complete understanding of the functional activity of these muscles. At present I am engaged in an attempt to determine the flexor and extensor leverage of each of the one-joint muscles of the hind leg of the frog at every ten degrees, at 10°, 20°, 30°, etc., as the joints are moved from extreme flexion to extreme tension. This work is very laborious, and is only partially completed, but the results which have been arrived at are very satisfactory, and a preliminary set of curves have been obtained, showing the change in leverage of all the one-joint muscles of the ankle and knee, and of each end of each of the larger two-joint muscles of the hind leg.

The method of measuring the leverage can be best described by taking a special case, e. g., the measurement of the leverage of the gastrocnemius on the ankle joint (See Fig. 5; Plate II). All the muscles going to the ankle, except the gastrocnemius, were cut away; the crus was cut in halves, and the lower half was fastened in a clamp, so that the bone and the foot were horizontal; and the toes were cut off. The gastrocnemius itself was divided, and a strong, flexible silk thread was tied to the tendo Achillis. This thread was led over a vertical, easily moving pulley, and weighted with 50 grams. This weight was arbitrarily chosen to represent the contraction force of the muscle. The leverage was then measured by fastening one end of a thread to the end of the tarsus, 2 cm. from the ankle joint, and connecting the other end of the thread to a spring-balance devised to measure slight changes in tension and mounted on a movable iron standard. This balance was constructed by Mr. Miller, instrument-maker, of the University of Michigan. The construction of the spring-balance is shown in Fig. 6. It consists of a spiral watch-spring, *a,* fastened by its outer end to a pin driven into a brass plate, *b,* and by its central end to a steel axis which supports the hard rubber disk, *c,* which carries the scale. The steel axis has a fine point at each end, and the inner point is pivoted in the brass plate, and the outer point in a screw which passes through a strip of brass, *d*, which is fastened to the top of the base plate, and extends forward a short distance and then downward in front of the hard rubber disk. The circumference of the disk is grooved to receive a thread which is attached to the preparation. The strip *d* is prolonged as a pointer, and enables the number of grams, representing the leverage of the muscle, to be read off on the scale. This balance gives accurate readings to two-tenths of a gram.

When the leverage was to be measured, the standard carrying the spring-balance was placed in such a position that the thread to the spring-balance

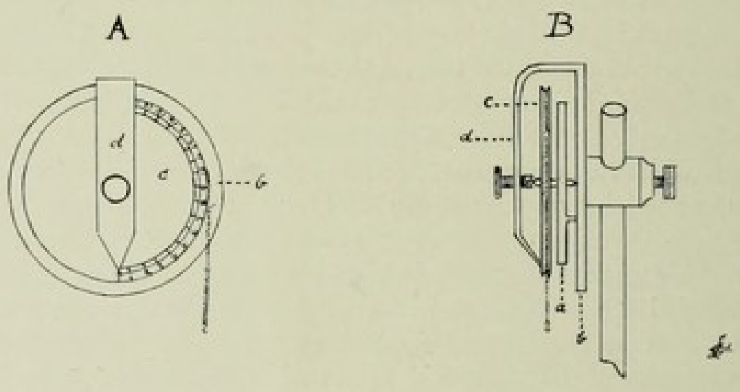


Fig. 6.—Spring-balance which measures the leverage of the muscle. A, front view; B, side view.

pulled at a right angle to the long axis of the tarsus, and then the standard carrying the balance was gradually moved away from the tarsus, until the strain exerted by the weight through the tendon on the tarsus was exactly balanced by the resistance of the spring. To facilitate the establishment of the angles to be measured and to insure that the thread leading off from the tarsus should always form a right angle with its long axis, pieces of wire were bent to give each of the angles from 10° to 170°, and the wire at the end of one leg of each angle was bent to form a right angle. One of these wires was held directly above the preparation, and the position of the joint and of the thread, with respect to the balance, was adjusted to correspond. The amount of the tension produced by the muscle was read off on the scale of the spring-balance, this having been previously graduated to show, in grams, the tension put upon it. The strain exerted by the muscle was thus ascertained for every angle of ten degrees, 0°, 10°, 20°, 30°, etc., from complete flexion to complete extension, and the results plotted in the form of a curve, in which distances on the abscissa represented degrees of extension, and the distances on the ordinates represented in grams the strain exerted by the muscle at a point on the tarsus

2 cm. from the joint. In measuring the leverage of the two-joint muscles acting on the hip, the femur was fastened horizontally and the pelvis suspended at an angle of about 30° to the earth. The amount of adduction and abduction of the femur has a marked effect on the leverage, a question which will be referred to at another time.

The same method was followed in the measurement of all the muscles, in each case the pull of the muscle being assumed to be 50 grams. This assumption is, of course, incorrect, but makes it possible to compare the leverage of the different muscles, and the relative leverage of the two extremities of the two-joint muscles, for each of the positions possible to the joints. Errors are bound to creep into such measurements, and one ought to have enough measurements to be able to offer average curves. This failing, it would seem best to give for comparison only curves of like date. As a matter of fact, the time required for making the measurements is so long that it has not been possible to obtain a complete set from any one frog. Inasmuch as the curves which have been obtained from the muscles of different frogs have been found to resemble each other very closely, and as the number is not large (2 to 5 for each form of preparation), I have decided to present at this time only those curves which appear the most reliable and most characteristic.

These curves (See Plates I and II) show the greatest differences. No two muscles give exactly the same curves, and the curves obtained from the two ends of the two-joint muscles differ greatly. Moreover, the curves show that we must be cautious of how we speak of the flexors and extensors of a limb until we have carefully studied the action of the muscles. Not only can most of the two-joint muscles produce opposite effects (flexion and extension) by their two extremities, the intensity of these effects changing with different positions of the joints, but they may produce opposite effects by the same extremity, at some position of the joint a reversal of the action of the muscle occurring, so that it may change from being a flexor to being an extensor. This reversal of action has been seen also in the case of one of the one-joint muscles. Some examples of the inconsistency of the action of muscles are the following:

Ilio-fibularis (flexor of knee)	flexes hip, 0°–70° extension. extends hip, 80°–170° extension.
Semitendinosus (flexor of knee)	flexes hip, 0°–40° extension. extends hip, 50°–170° extension.
Glutæus magnus (extends knee)	extends hip, 0°–20° extension. flexes hip, 30°–170° extension.
Peroneus (flexes ankle a short distance)	extends knee, 30° over-flexion to 10° over flexion. flexes slightly knee, 0°–40° extension. extends knee, 50°–170° extension.
Gracilis magnus (extends hip)	flexes knee, 40° over-flexion to 110° extension. extends knee, 120°–140° extension. flexes knee, 150°–170° extension.

Semimembranosus (extends hip)	flexes knee, 40° over-flexion to 90° extension. extends knee, 100°–130° extension. flexes knee, 140°–170° extension.
Tibialis posticus (one-joint muscle, lower leg)	extends ankle, 10°–60° extension. no action, 70°–110° extension. flexes ankle, 120°–170° extension.

The Leap.

The only attempt to explain the great force with which the body of the frog is propelled through the air when he leaps, that the writer has come across, is that of Gad.[1] "If the leg is brought into the position ready for the spring, and the muscles named [the ilio-psoas (the iliacus internus), tibialis anticus (the longus is referred to) and peroneus] remain strongly contracted, the innervation of all the other muscles of the leg can increase very markedly without its coming to a spring movement. If the extension of the foot is hindered more strongly (by the tibialis and peroneus) than the flexion of the knee, the gastrocnemius will act as knee flexor, as will also the two-joint muscles on the inner side of the thigh (semimembranosus, rectus internus, [the gracilis magnus,] semitendinosus, biceps [ilio-fibularis]), so long as their action on the hip joint is held in equilibrium by the ilio-psoas and triceps. As soon as the ilio-psoas relaxes, the muscles on the inner side of the thigh overweigh as hip extensors, wherefore they, in their knee-flexing action, will be overcome by the triceps the more easily, if their thus far 'Cumpan,' the gastrocnemius, as a result of the simultaneous relaxation of the foot flexors, can transmit its principal effect from the knee to the ankle. The change from flexion to extension is further thereby favored, that a part of the thigh muscles, as already stated (vastus externus and the adductors), from a given position of the thigh on, from hip flexors become hip extensors."

"The process by the ordinary locomotion of the frog consists, therefore, therein, that first, when the legs are extended, the position ready for the spring is produced through an out-weighing or separate action of the ilio-psoas and the foot flexors, that then the innervation of all the leg muscles rises uniformly, until a condition of considerable tension is reached, and that, finally, the giving out of the tension which had developed in flexion, to produce the extension of the spring, is caused by the sudden relaxation of the ilio-psoas and the foot flexors."

There are several strong objections to be made to this theory. First, there is no proof that the one-joint flexors contract during the development of the early part of the spring movement; second, the muscles which are supposed to inhibit the extension of the leg are too feeble or have too slight a lev-

[1] After experiments in which ¦Dr. O. Wegele, Hirsch, and Fuhr had taken part; "Einiges über Centren und Leitungsbahnen im Rückenmark des Frosches,"—Verhandl. d. physik.-med. Ges. in Würzburg, 1884, N. F., Bd. XVIII, S. 173.

erage to do this. When the leg is in the sitting position, the two-joint tibialis anticus longus and peroneus have a good extensor leverage on the knee, and the tibialis anticus longus has little flexor leverage, and the peroneus a slight extensor leverage on the ankle. Moreover, the gastrocnemius has no flexor leverage on the knee in the squatting position. Experiment shows that even when all the flexor muscles are acting, the extensors are capable of extending the leg, as is seen when all the nerves of the pelvic plexus are simultaneously excited. Third, even if, as is quite possible, the flexor muscles contract at the beginning of the spring movement, there is no proof that they suddenly relax and so release the tensed extensor muscles. Fourth, the theory apparently includes the idea that for a muscle to act well at one end, its action at the other end must be hindered in some way, and that, if the checking force be removed, the effect of the contraction will be suddenly transferred from the end formerly acting to the other. It is hard to see how this could take place. The tension developed in a muscle must be equally felt by both of the extremities of the muscle, and in the case of a two-joint muscle, when the conditions of leverage are suitable, movement must result at both ends, unless the parts to be moved offer more resistance at one end than the other.

Relation of the Leverage of Two-Joint Muscles to the Action of these Muscles by the Leap.

One would expect to find that the leverage of both the one-joint and the two-joint muscles would be more favorable for extension than flexion when the leg was in the squatting position. This is, however, not universally the case.

The following table gives roughly in grams the leverage of the two-joint muscles when the leg is in the squatting position:

Muscle.	Hip.	Knee.	Ankle.
Gastrocnemius	....	Flexor — 0	Extensor—7
Tibialis anticus longus	....	Extensor— 3	Flexor —3
Peroneus	....	" — 3	" —0
Triceps	Flexor —0	" — 7	....
Semimembranosus	Extensor—2	Flexor — 8	....
Gracilis magnus	" —3	" —10	....
Semitendinosus	" —0	" —15	....
Ilio-fibularis	Flexor —2	" — 6	....

In the squatting position the gastrocnemius has a strong extension leverage on the ankle and no flexor leverage on the knee, so that the whole effect of the contraction would be expended in extending the ankle. The tibialis anticus has a comparatively small, but about equal leverage on the ankle and knee, a condition favorable to the use of the tendon action of this muscle by the gastrocnemius to extend the knee. The triceps closely resembles the gastrocnemius; just as the latter has a strong extensor leverage on the ankle and no flexion leverage on the knee, so the former has a strong extension leverage on the knee and almost no flexor leverage on the hip.

All this is favorable to extension. On the other hand, the strong group of muscles on the median and under side of the thigh, the semimembranosus, gracilis magnus, semitendinosus, and ilio-fibularis, has a stronger flexor leverage on the knee than extensor leverage on the hip. This would seem an unfavorable condition to a sudden and powerful extension of the leg. It must be remembered, however, that if the knee were extended before or at the same time with the hip and ankle, the leg would be thrown out laterally instead of backward, and the effect of the stroke would be lost. To judge from the leverage curves, it would appear that the ankle begins to extend first, the hip next, and the knee last. They also suggest that the resistance of the flexors of the knee at the beginning of the stroke has a further effect to put the extensors of the knee under tension, and to bring into full play the tendon action of these muscles, so that when they overcome the effect of the flexors of the knee, there would be a very sudden and powerful extension of the joint.

The energy liberated by a contracting muscle is transmitted in both directions throughout its length equally well. The fact that the leverage is better at one end of a two-joint muscle would not interfere with its action at the other end, and the fact that the gracilis magnus and semimembranosus and semitendinosus have, in the squatting position, a more powerful flexor leverage on the knee than extensor leverage at the hip would not prevent these muscles from acting at the hip. In the squatting position the knee is overflexed, and the strong flexor leverage of these muscles would tend to keep it flexed. The muscles are attached close to or in the knee joint and would practically act, as far as the hip is concerned, as one-joint extensors of the hip. The triceps does not have much flexor leverage on the hip in the squatting position, and would not greatly oppose the extensors of the hip. As the thigh was extended, the triceps would be put under more and more tension, and by its tendon action would transmit the strain brought upon it to the extensor side of the knee. At the same time, the tibialis anticus longus through its tendon action would be transmitting to the extensor side of the knee the strain brought upon it by the extension of the ankle by the gastrocnemius. The effect would be extension of the hip and ankle with ever-increasing tension on the extensor side of the knee.

There can be little doubt that sooner or later the flexor action of the muscles on the median and under side of the thigh would be overcome by the rapidly increasing tension being brought to bear on the extensor side of the knee, by the contraction of the triceps, tibialis anticus longus, peroneus, and extensor brevis, and the strain transmitted by the tendon action of the tibialis anticus longus from the gastrocnemius, and by the tendon action of the triceps from those muscles themselves which lie on the under and median side of the thigh. Of course, if this group of muscles on the inner and under side of the thigh continued, as the spring movement progressed, to exert a strong flexor effect on the knee and only a feeble extensor effect on the hip, they would impede rather than aid the leap. This is not the case, however. The leverage of all these muscles changes as the leg is extended. In the case of the powerful semimembranosus and gracilis magnus muscles, the flexor effect on the knee rapidly lessens as it is extended, and at about 100° extension there is an actual change of the leverage on the knee from flexion to extension. The leverage on the hip likewise undergoes a quick alteration; the leverage in favor of extension increases with great rapidity up to about 110° extension, when it reaches its maximum, and is very powerful, the semimembranosus having an extensor leverage on the hip represented by 17 grams, the gracilis magnus 17 grams, the semitendinosus 15 grams. The ilio-fibularis reversing its leverage at about 70° extension, from flexion to extension, has at an increasing extension leverage to about 150°, where it is 9 grams.

While the powerful group of muscles on the median surface of the thigh is gaining in extension power over the hip, the triceps group on the lateral surface is gaining in flexor leverage, but the gain is by no means as great, and probably acts not so much to impede the extension of the hip as to increase the tendon action of the muscle, and enable the muscles on the median side of the thigh, which extend the hip, to work through the triceps to help extend the knee.

Concerning the one-joint muscles, it may be remarked that the extensor leverage of the tarsalis posticus and tibialis posticus, in the squatting position is good, but decreases as the ankle extends until 60°, after which, in the case of the former, it is small but constant until near the end of the extension movement, while in the case of the latter it is nul at 60°, and for some distance beyond this point.

The flexor leverage of the tibialis anticus brevis and the tarsalis anticus on the ankle is weak when the ankle is flexed, but increases as it extends until 60°, when it is quite strong. From this point on, it remains quite constant, until near the end of the extension movement.

The extensor leverage of the extensor brevis on the knee, though not very strong, and also undergoing fluctuations, exists in all positions of the leg.

It has been said that the energy of the two-joint muscles of the hind leg of the frog is transmitted as by an endless chain having the form of a figure eight, with the crossing at the knee, and the effect progresses in the direction of the better leverage.

The leverage curves would seem to show that the condition thus formulated does not exist by the spring until the muscles which extend the knee have been put under high tension and have overcome the resistance of the thigh muscles which flex the knee. As the knee extends, the flexor leverage on the knee of the muscles on the median and under side of the thigh lessens, while at the same time, extension going on in the hip, the extensor leverage of these muscles on the hip increases. When extension has progressed to a certain point, therefore, all of the two-joint muscles will have a good extensor leverage, and the direction of the transmission of the energy will be from gastrocnemius, on the median side of the leg, around the ankle to the tibialis anticus on the lateral side of the lower leg, from this around the knee to the group of muscles on the median side of the thigh, thence around the hip to the triceps group on the lateral side of the thigh, and so back around the knee to the gastrocnemius.

Another point of interest revealed by the leverage curves is, that towards the end of the extension, the ends of the two-joint muscles which act as extensors begin to lose in extensor leverage, while those which act as flexors begin to gain in flexor leverage. Likewise, the energy of the one-joint flexors increases, and that of the one-joint extensors decreases.

The extension effect of the semimembranosus, gracilis magnus, semitendinosus, and ilio-fibularis on the hip begins to lessen beyond 110° to 130° extension, while the flexor effect of the triceps is maintained.

The extensor effect of the gastrocnemius on the ankle begins to lessen at 120°. On the other hand, the flexor effect of the tibialis anticus longus and the peroneus begins to increase at this point.

A similar change is to be observed in the case of most of the one-joint muscles of the ankle. The extensor leverage of the tarsalis posticus lessens at 120°, and the leverage on the tibialis posticus, which is in favor of extension when the ankle is flexed, undergoes a reversal and becomes favorable to flexion at about 120°. The flexor leverage of the tibialis anticus brevis appears to be an exception, its flexor leverage lessening from 50° extension on.

The extensor leverage of the triceps, tibialis anticus longus, peroneus, and extensor brevis on the knee lessens slightly towards the end of the extension movement, while the leverage of the semimembranosus and the gracilis magnus on the knee undergoes, at 130° extension, a second reversal, these muscles again becoming flexors. The flexor leverage of the ilio-fibularis, which has been lessening to 110°, here begins to increase; that of the semitendinosus, though less than when the knee is flexed, remains high; finally, the flexor leverage of the gastrocnemius increases as the extension of the leg progresses, being strong at the close.

In short, *towards the end of the extension movement there is a decrease of extensor leverage and an increase of flexor leverage.* It is scarcely necessary to comment on the effect this alteration of leverage must have to protect the joints, and to favor a rapid recovery of the leg to the flexed position.

Summary.

In this paper only the flexing and extending action of the two-joint muscles of the hind leg of the frog has been considered.

Any force, whether acting upon the body from without or developed within the body by muscular contraction, which acts to extend or to flex either hip, knee, or ankle, because of the tendon-like action of the two-joint muscles, tends to cause a like movement of the two other joints. The one-joint extensors of the hip help in the spring movement to extend the knee and the ankle, and one-joint extensors of the knee and of the ankle also help to extend the whole leg.

The resting length and the extensibility of the two-joint muscles is such that it is possible for quite extensive independent movements of any of the joints to occur when the other joints are fixed by the action of one-joint muscles.

Nearly every one of the two-joint muscles, when acting alone, will flex one and extend the other of the joints which it crosses. If its action on one of these joints is prevented by any external force or by the contraction of one-joint muscles, the whole effect of its contraction will appear in a movement of the other joint.

The fact that a two-joint muscle can make use of the tendon action of another two-joint muscle on the opposite side of the leg accounts for the paradox that a two-joint muscle, when in a position to have a stronger extensor than flexor leverage, may extend a joint of which it is a flexor.

Two-joint muscles can make use of the tendon action of other two-joint muscles to move joints over which they do not pass.

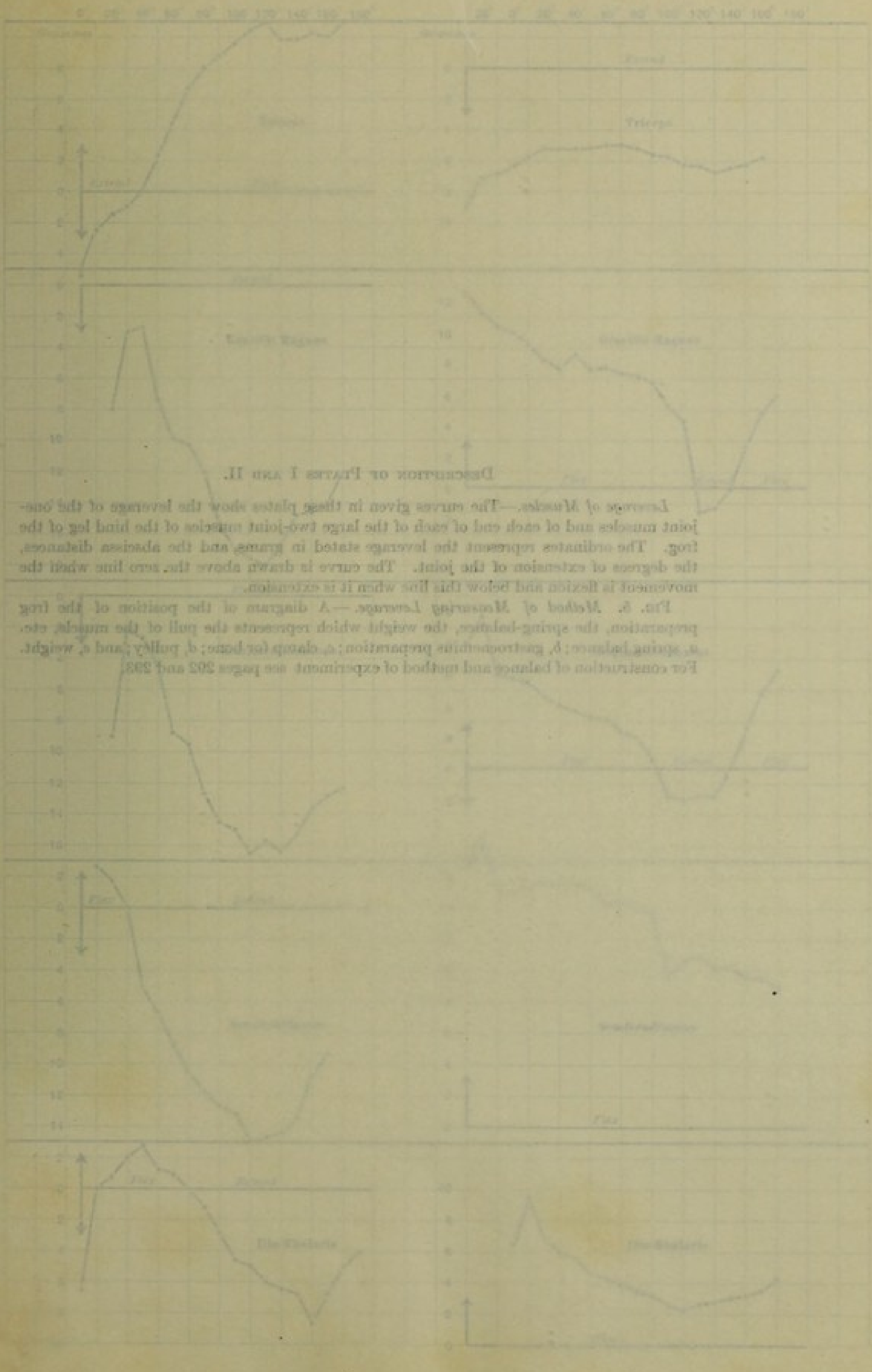
When all the largest two-joint muscles of the hind leg of the frog are contracting simultaneously, the energy which they develop may be transmitted, as by an endless chain, having the form of a figure eight with the crossing at the knee, and the effect progresses in the direction of the better leverage Thus, the total effect produced by a given two-joint muscle depends not only on what it individually might accomplish, but on the energy imparted to it from distant muscles, through the tendon action of two-joint muscles.

In the leap, the two-joint muscles, by their tension action, transfer the energy liberated by each of the muscles, which have a leverage in favor of extension, from the joint upon which it acts directly, to all the rest of the joints, thus enabling all the extending muscles to co-operate in the production of the extension of the whole leg.

As the leg of the frog is gradually extended, the curve of leverage of the one-joint muscles, and of each end of each of the two-joint muscles, continually changes. The change may be so great that there is a reversal of the action of a muscle, its effect on a joint changing from flexion to extension and in some cases back again.

Although the tendon action of the two-joint muscles, together with the leverage of the two extremities of these muscles by different positions of the joints which they cross, go far toward explaining the mechanics of the leap, these are, of course, not the only factors of importance that enter into the production of this remarkable phenomenon. The rotation effect exerted by adjacent members of a limb on each other, gravity and inertia, the relative strength and the shape of the different one-joint and two-joint muscles, their tension by different positions of the limb, their elasticity, the rapidity with which they contract and relax, and, above all, the order, strength, and duration of the nervous impulses reaching them from the spinal cord, must all be ascertained before we shall have a clear conception of the process.

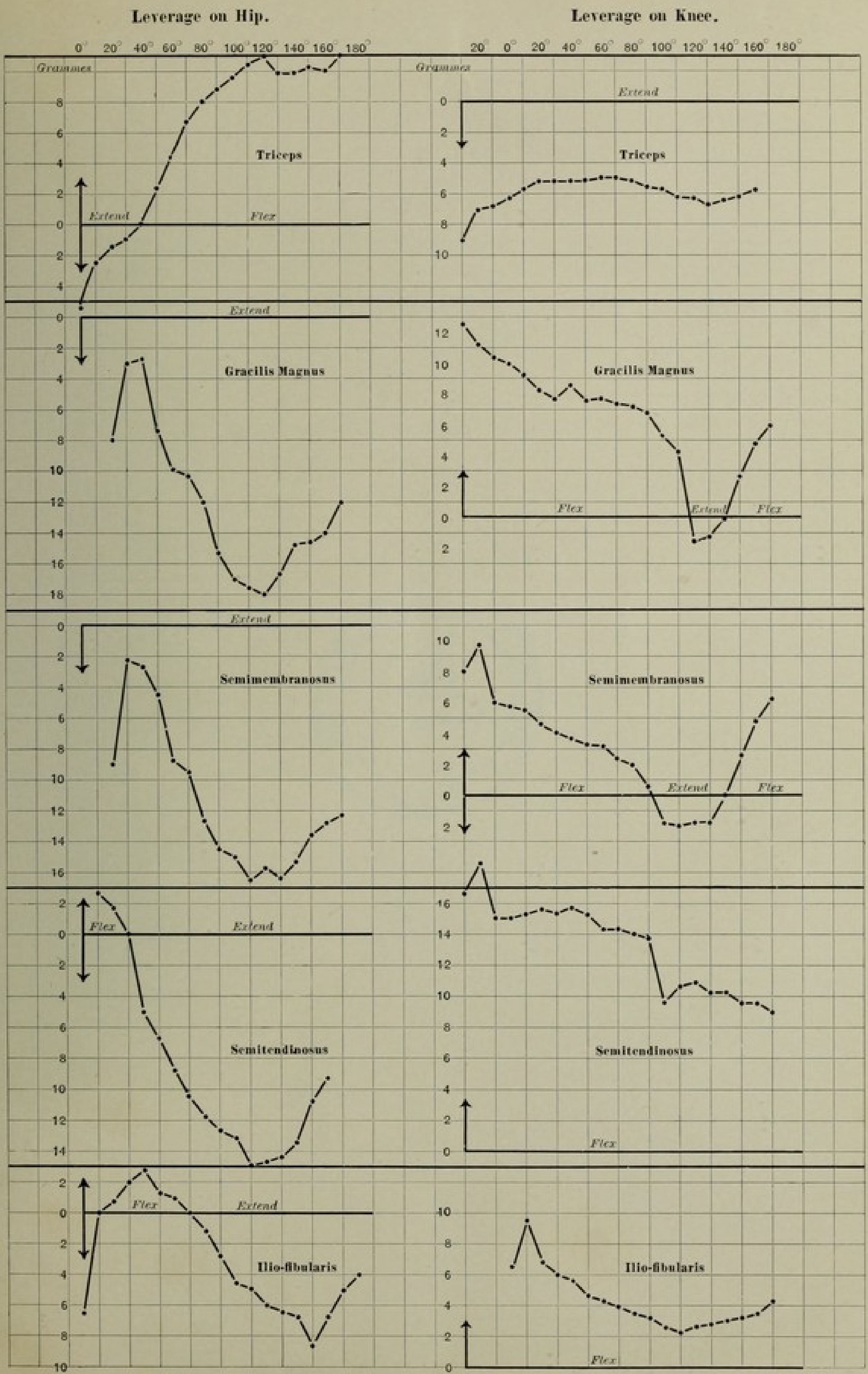
Leverage on Hip. Leverage on Knee.

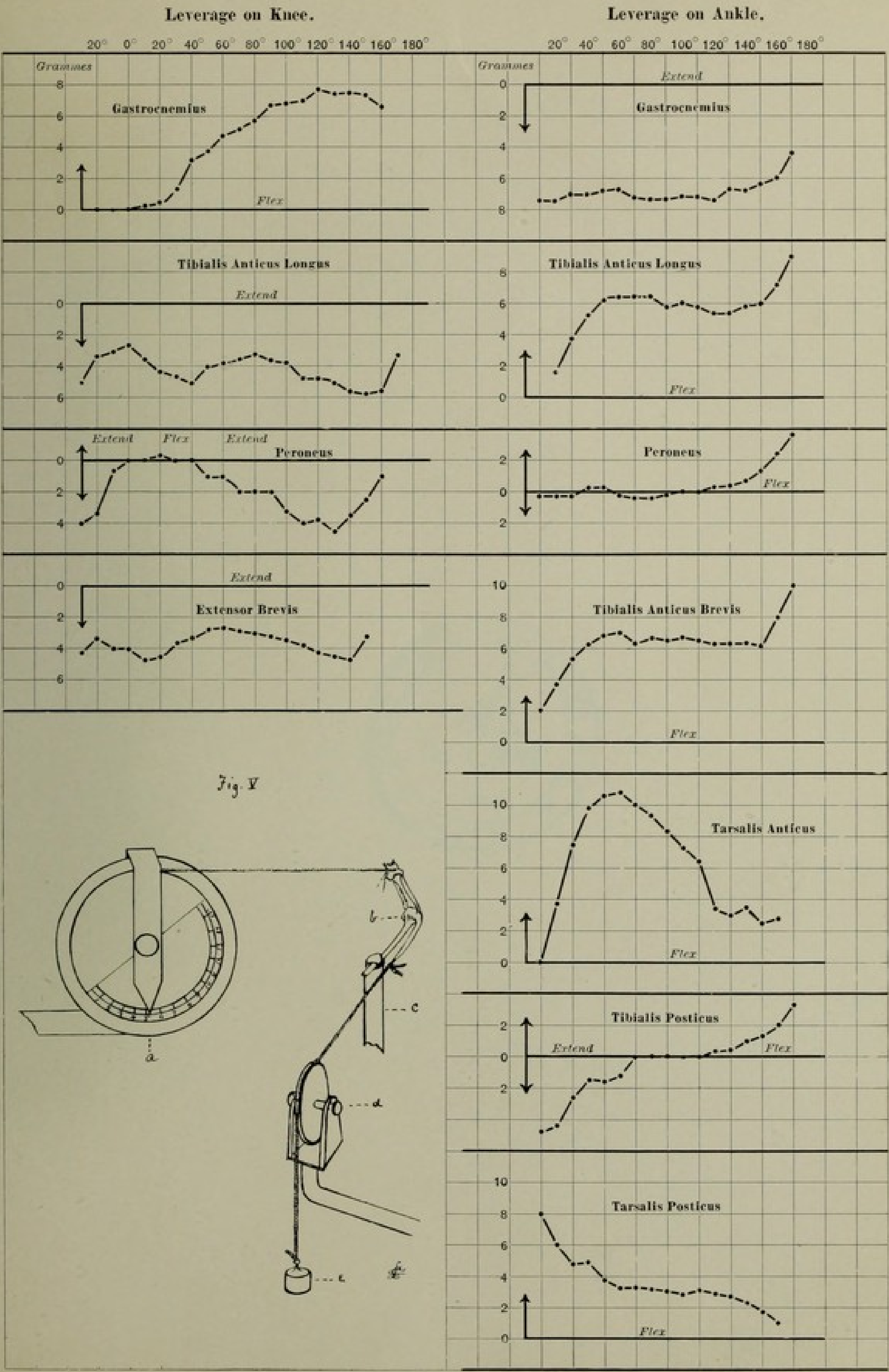


Description of Plates I and II.

Leverage of Muscles.—The curves given in these plates show the leverage of the one-joint muscles and of each end of each of the large two-joint muscles of the hind leg of the frog. The ordinates represent the leverage stated in grams, and the abscissa distances, the degrees of extension of the joint. The curve is drawn above the zero line when the movement is flexion and below this line when it is extension.

Fig. 5. *Method of Measuring Leverage.* — A diagram of the position of the frog preparation, the spring-balance, the weight which represents the pull of the muscle, etc. *a*, spring balance; *b*, gastrocnemius preparation; *c*, clamp for bone; *d*, pulley; and *e*, weight. For construction of balance and method of experiment see pages 292 and 293.


Leverage on Hip.
Leverage on Knee.
Grammes
Triceps
Extend
Flex
Gracilis Magnus
Semimembranosus
Semitendinosus
Ilio-fibularis


Leverage on Knee.
Leverage on Ankle.
20° 0° 20° 40° 60° 80° 100° 120° 140° 160° 180°
20° 40° 60° 80° 100° 120° 140° 160° 180°
Grammes
Gastrocnemius
Tibialis Anticus Longus
Peroneus
Extensor Brevis
Tibialis Anticus Brevis
Tarsalis Anticus
Tibialis Posticus
Tarsalis Posticus
Extend
Flex
Fig. V
a
b
c
d
e