ON THE NATURE OF THE KNEE-JERK. By WARREN PLIMPTON LOMBARD, M.D., *Assistant in Physiology at the College of Physicians and Surgeons of New York.*

IT has long been known that if the ligamentum patellae of a normal individual be struck when the leg is hanging freely in a position of partial flexion, the quadriceps muscle is irritated and contracts, causing a sudden extension of the knee, which we call a knee-jerk. The process by which the muscle is stimulated, however, is still a subject of discussion.

Some authors claim that the muscle fibres are directly stimulated by the sudden twitch to which they are subjected, the method of excitation being similar to that resulting from a direct blow on the muscle, and these writers think that the time which elapses between the moment of the blow on the ligament and the resulting muscular contraction is far too short to admit of any other interpretation.

Other authors call attention to the fact that the phenomenon cannot be obtained if the nerve connecting the muscle with the spinal cord first be severed, or if the corresponding reflex mechanisms of the cord have been injured by disease, and conclude that since the integrity of the reflex arc is essential to the phenomenon the knee-jerk must be a reflex act. They admit that the time involved in the process is very short, but say that the time required by such a reflex action, as they suppose this to be, is not known, and that it may well be as short as the interval found.

Those who regard the process to be wholly peripheral, answer the objection that it is lost if the reflex arc be destroyed, by suggesting that the ability of a muscle to respond to such a slight mechanical stimulus as that caused by a blow on its tendon may depend upon its having a certain amount of tension, and that this necessary tension is dependent on the tonus of the muscle, which is lost, when, upon division of the nerve or destruction of the cord, tonus impulses cease to come to the muscle.

Thus we find two distinct parties; the one regards the phenomenon reflex, the other considers it a wholly peripheral process. Both admit that the integrity of the reflex arc is essential to the knee-jerk, and that the time involved in the process is much shorter than that required by the few reflex acts of which the time has been studied.

Undoubtedly the reflex theory offers the simplest and most satisfactory explanation of the intimate dependence of the phenomenon upon the spinal cord. Indeed the time argument would have but little weight if those who doubt the reflex nature of the process were unable to explain this connection. It is worth while, therefore, to consider the soundness of their explanation.

As has been said, they assume that the ability of the muscle to respond to the twitch transmitted to it from its ligament is dependent on the tension of the muscle, and that this is dependent on tonus impulses coming to it from the spinal cord.

One cannot help feeling that this explanation has been manufactured to meet the emergency and is somewhat forced, both because of the uncertain basis on which the tonus theory rests, and because there is no proof that the irritability of a muscle to mechanical stimuli is dependent on its tension.

The knee-jerk, though it varies greatly in amount, can almost always be obtained, while there is reason to doubt that muscles are kept continuously in tonus by impulses either of automatic or of reflex origin. It is most probable that there are times when they receive slight motor impulses of reflex nature, and that they respond by the feeble increase in tension which we call tonus, but there is no reason to suppose that they are continually in receipt of tonus impulses.

Suppose, however, for the sake of argument, that tonus is continuous, there is no surety that it is essential to the knee-jerk. It is true that for purely mechanical reasons, tension of the muscle not only favors but is necessary to the phenomenon. If the blow be struck when the ligament and muscle are loose, there is no twitch transmitted to the muscle and consequently no knee-jerk developed. On the other hand, if the slack has been taken up, the sudden strain caused by the blow on the ligament is transmitted through the whole muscle. Moreover, when the muscle is under tension the smallest contraction will reveal itself. By giving the leg a proper position, one can secure to the muscle any desired degree of tension, this, however, does not enable one to get a knee-jerk when the spinal cord is diseased.

If tonus be essential to the phenomenon it would seem to be for some other reason than because it supplies a required tension. One might conceive that in some unknown way it increases the irritability of muscle tissue. If this be true, however, it would seem as if the knee-jerk which disappears when the tonus of the muscle is lost, upon division of its nerve, would be obtained again, when, by electrical stimulation of the cut-nerve, the tension of the muscle is restored. This experiment has been made upon a rabbit but failed to recall the knee-jerk.

This last winter I examined a man who was young, vigorous and showed no sign of disease. His legs were well developed, and his muscles firm and elastic. There was no sign of lack of tension of the muscles. He claimed to be the equal of his fellows in all manly sports. I could not prove that he had or had not tonus of the muscles, but I saw no reason to doubt that he had as much as most men. This man gave no knee-jerk and no reenforcement of the knee-jerk.

It is not uncommon to find a person in good health with no knee-jerk, though it is exceptional to find one from whom a reenforced knee-jerk cannot be obtained. If the absence of the knee-jerk in these cases be due to a lack of tonus, and if muscle tonus plays the important rôle attributed to it, it is strange that these men should show no disturbance of muscular co-ordination. Indeed, such cases tend to show that something more than a suitable condition of the muscles is essential to the production of the knee-jerk.

Any theory of the nature of the knee-jerk, to be acceptable, must likewise explain the reenforcements of the knee-jerk. It occurred to me, therefore, that a study of the reenforcements of the knee-jerk might throw much light on the nature of the phenomenon. If the processes on which the knee-jerk depends are wholly peripheral, the increase of the contraction which results from the reenforcing act must necessarily be due to changes occurring within the peripheral mechanisms. How might the ability of a muscle to respond to a blow on its tendon be increased by a reenforcing action? Two ways suggest themselves, viz.:—

1. The tonus of the muscle might be increased as a result of an increased activity of the spinal centres, which might be caused by the development of a voluntary action, a painful sensation or an active emotion or thought.

2. The irritability of the muscle might be increased in some inscrutable way by the reenforcing process.

I made a careful study of the quadriceps muscle and tried to discover whether it gained in tension or in irritability when the hands were clinched. I found it difficult to construct an apparatus capable of measuring delicate changes in muscle tension, but finally fixed upon one which answered the requirements fairly well. It recorded the smallest contraction of the quadriceps which I could learn to make voluntarily, and this contraction was so slight that it could not be detected by the eye or by a trained hand placed over the muscle. It seemed as if a smaller increase in tension than this could scarcely be regarded as sufficient to influence the ability of the muscle to respond to the blow, either because the tenser muscle fibres would favor the transmission of vibrations, or because, the slack having been taken up, the muscular contraction would reveal itself more readily.

The apparatus used to record the contraction of the quadriceps consisted of a long, light, stiff lever, the axis of which was fastened by an elastic band upon the ligamentum patellae. The lever rested, near its axis, on the lower edge of the patella. When the quadriceps contracted it made the ligament more tense, and at the same time tilted the patella; both of these movements caused the recording end of the lever to descend. The lever magnified the movement of the ligament and patella about twenty times.

The man lay on his back, on a bench made with adjustable segments, which supported the head, back, thighs, legs and feet in any desired degree of flexion. A control lever, which recorded every movement of the head of the tibia, wrote the movements of the knee caused by the respiration, the pulse and jars.

A Marey's tambour, connected with a dynamometer, wrote with its lever the moment that the reenforcing movement of clinching the hands was performed.

Not to go further into details, suffice it to say that no contraction of the quadriceps was seen to follow the most active hand clinch in the case of any of the normal men experimented on, though such an action was very potent in reenforcing the knee-jerk.

There is one experiment which deserves separate mention. The young man in question had no knee-jerk, but showed an active reenforced knee-jerk. It seemed as if in his case, at least, one might find a change in the tension of the quadriceps, i.e. if the knee-jerk which appeared when he reenforced depended on an increase of tonus, but none was found.

From these experiments it would seem that such an act as clinching the hands, though capable of reenforcing the knee-jerk, affects the tension of the quadriceps muscle little, if at all, under normal conditions.

Finding no increase in the tonus of the muscle when the hands were clinched, I proceeded to test the irritability of the muscle at the time that the reenforcing act was being performed. I used as a test, the strength of the induction current required to call out the least contraction which the lever already described was capable of recording. No increased irritability to electrical stimulation was discovered. It may be said that the irritability of the muscle to mechanical stimuli may, nevertheless, have been enhanced. This seems doubtful, however, for as a rule when the irritability of a muscle is increased, it responds more readily to all forms of stimuli.

In short, I was unable to find any evidence that, in the case of normal men, lying at rest, such an act as voluntarily clinching the hands has any effect on either the tension or the irritability of the muscle. This result corresponds with that of Mitchell and Lewis[1], who found that muscular contractions called out by electricity cannot be reenforced, a result which would be inexplicable in case the reenforcing influence affected the peripheral mechanisms.

If these results are correct, the knee-jerk cannot be a purely peripheral phenomenon and is, probably, in spite of the short time, a reflex process. This conclusion is borne out by the results of experiments which I made at the College of Physicians and Surgeons of New York, during the past winter.

These experiments were made on twenty-five medical students, all of whom were, as far as could be judged, in good health. It is worth mention that they were wholly unfamiliar with the work and that they had no idea of what was expected of them.

The apparatus was the same as that employed by me in the experiments reported in the *American Journal of Psychology*, Oct., 1887. It consisted of a couch, on which the subject lay on his left side; a support for the right thigh; a swing for the right foot, suspended by a long cord from the ceiling; a recording needle, which was attached to the right heel, and which by writing the movements of the foot gave a magnified record of the flexion and extension of the knee; and finally a hammer which delivered a blow of constant and known force.

A clear understanding of the results obtained is only to be reached by a careful analysis of the conditions of the experiment. When the subject is placed on the knee-jerk couch with his thigh on the

[1] "Physiological Studies of the Knee-jerk, and of the Reactions of Muscle under Mechanical and other Excitants," by S. Weir Mitchell, M.D., and Morris J. Lewis, M.D., *The Medical News of Philadelphia*, Feb. 13 and 20, 1886.

support and his foot in the swing, the knee assumes a position of partial flexion. If the experimentor draws the lower leg forward, so as to increase the extension of the knee, or backward, so as to increase the flexion of the knee, and then release it, the leg swings like a pendulum backwards and forwards for eight or ten times, each oscillation being smaller than the preceding, until the leg becomes quiet in the original position of rest. What are the forces which determine how much the knee shall be flexed when in the position of rest?

1. The force of gravity, which tends to bring the swing and foot directly under the point of suspension of the swing.
2. The amount of flexion of the hip joint and the consequent degree of tension of the two joint muscles on the front and back of the thigh.
3. The tension of the muscles on the front and back of the thigh dependent on their natural length and elasticity.
4. The contraction of the muscles caused by nervous or other stimuli.

It may seem a contradiction to speak of muscular contraction as one of the conditions which determine the position of the leg when at rest, but, inasmuch as the theory of muscle tonus still holds, it may not be inadmissible.

Most of the forces enumerated act constantly and continuously. If the body and thigh are immovable, the tension of the muscles of the thigh, as far as it is governed by the position of the hip joint, will be uniform; the elasticity of the muscles will undergo but little change during short intervals of time; the influence of the force of gravity will remain the same; therefore, any change of the knee from the position of rest, must be caused by a difference in the amount of contraction of the antagonistic flexors and extensors.

If these muscles were in receipt of tonus impulses which were continuous and constant, their length would undergo no change on this account; if, however, they received irregularly tonus impulses of varying amounts, their length would change frequently. I was curious to find whether such variations actually occurred, but in the few experiments which I made, I could not discover that the knee moved at all from the position of rest when the subject was calm and was lying quietly.

Now what happens when the ligamentum patellae is struck? The blow is immediately responded to by a contraction of the muscles on the front of the thigh, the knee is extended, and the foot is swung forward.

As the extensor muscles cease to contract, the elasticity of the flexor muscles together with the force of gravity cause the foot to swing back; the force of the backward swing is sufficient to carry the foot beyond the position of rest and to flex the knee, though not as greatly as the contraction of the muscles had extended it; this flexion of the knee is in turn followed by extension, and this by a second movement of flexion, and so on, each act being less than the preceding, until after eight or ten oscillations the knee becomes quiet in the position of rest.

Such is the ordinary sequence of events following a blow on the ligamentum patellae, and, when the subject is in a placid condition, the knee actually returns to the original position of rest time after time, as often as the experiments are repeated. This is illustrated by experiments on S, recorded in Table I., during which the knee invariably returned to the original position of rest.

Description of Table I.

The table is to be read from left to right. In the first column is the number of the observation; in the second, the extent of the knee-jerk or first movement of extension; in the third, the first backward oscillation of flexion; in the fourth, the second oscillation of extension; in the fifth, the second oscillation of flexion; while in the sixth column is recorded the change in the position of the line of rest from that which it occupied before the blow was struck. In this, as in all succeeding tables, the sign + signifies a movement in the direction of extension, recorded in the charts as an upward movement, while the sign – indicates a movement of flexion, recorded in the charts as a downward movement. The figures give the extent of the movement in millimetres. The measurements were all made from the line of rest which was drawn just before the blow was struck.

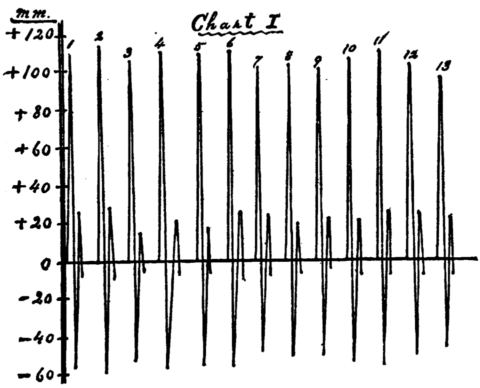
TABLE I.

S, Curve 31.

No. of Obser-vation	1st Extension or Knee-jerk	1st Flexion –	2nd Extension +	2nd Flexion –	Change of position of line of Rest
1	110	55	26	7	0
2	113	58	28	9	0
3	105	52	15	5	0
4	111	56	21	7	0
5	109	55	18	6	0
6	111	55	27	9	0
7	102	49	24	7	0
8	103	50	20	6	0
9	101	50	23	6	0
10	106	53	21	7	0
11	110	55	25	8	0
12	103	51	24	8	0
13	96	46	21	7	0
14	103	51	21	?	0
15	105	52	20	?	0
16	84	43	18	7	0
17	83	42	20	7	0
18	92	45	22	8	0
19	103	52	25	9	0
20	96	48	25	8	0
21	95	47	24	8	0
22	84	39	19	7	0
23	88	43	21	7	0
24	99	50	26	9	0
25	92	45	23	7	0
26	95	48	25	?	0
27	92	46	22	8	0
28	99	51	27	9	0
29	106	53	30	10	0
30	108	55	30	10	0
31	111	56	31	10	0
32	98	46	22	6	0
Average	100	50	23	8	

The regularity of the oscillations is well shown in Chart I., which was constructed from the same curves as this table. The extent of the movements has been reduced three-fourths, which necessitated the omission of the final small oscillations.

S, Curve 31.



As has been said, it is usual for the knee to return to the original position of rest when the subject is in a tranquil frame of mind. When, however, the subject is excited, it is much more common to see the knee become quiet in a different position, and be either more extended or more flexed than before the blow was struck. This is illustrated by the measurements given in the following Table.

Description of Table II.

In this table are collected the changes in the position of the line of rest which occurred in experiments on seven different men. The observations are arranged in columns. At the head of each column is the letter which stands for the subject, and beneath this is the number of another table in this paper, in which the same results are given. Below this heading are recorded the successive changes in the position of the line of rest. The measurements are given in millimetres, and each was made with reference to the position of the line of rest at the end of the preceding observation. The sign + shows that the variation was in the direction of extension, and the sign – that it was in the direction of flexion.

TABLE II.

SUBJECT		A	G	X	D	C	L	U	C	A
No. of Table		I	V	V	V	V	VI	VI	VII	IX
	1	0	0	0	+2	+2	+ 2	− 2	+ 5	− 4
Changes in the posi-	2	0	0	0	+2	0	+ 1	− 3	− 1	− 5
tion of the line of	3	0	0	0	+1	+1	− 6	+ 1	+11	+ 5
Rest seen to fol-	4	0	0	0	0	+2	− 5	+ 7	+ 2	− 5
low the successive	5	0	0	0	+1	0	+ 1	+ 2	+ 7	+ 5
Knee-jerks	6	0	0	0	0	0	+ 6	− 7	− 5	− 7
	7	0	0	0	0	0	+ 4	− 4	+ 2	+ 1
	8	0	0	0	0	0	− ·1	− 7	− 1	+ 8
	9	0	0	0	0	−1	+ 1	+ 6	0	+11
	10	0	0	0	0	+1	+ 6	+ 4	0	+ 7
	11	0	0	0	0	0	− 1	+ ·2	0	−18
	12	0	0	0	0	+1	+ ·1	− 1	+25	+ 7
	13	0	0	0	0	0	− 1	+ 8	+ 5	− 1
	14	0	0	0	0	−1	?	+15	+ 2	0
	15	0	0	0	0	0	*	+ 6		+ 1
	16	0	0	0	0	+1	+ 2	+ 4		?
	17	0	0	0	0	0	+ 1	*		*
	18	0	0	0	0	0	+ 2	− 3		− 5
	19	0	0	0	0	0	+13	+ 3		− 8
	20	0	0	0	0	0	+ 1			0
	21	0	0	0	0	+1	− 9			− 3
	22	0		0	0	0	+18			+ 5
	23	0		0	0	0	− 1			+12
	24	0		0	0					+ 2
	25	0			0					− 5
	26	0								

* Break in curve.

During the examinations which are recorded in the first five columns there was little or no change of the position of the line of rest, while during the examinations reported in the last four columns considerable variations occurred. It was noticed that in all the cases in which marked changes in the position of the line of rest appeared, the men were in an excitable condition. Almost all the men were slightly disturbed by the first examination. In the case of A and C the records which show the greatest variations were those obtained the first time they were examined, while the records which show no variations were gained at a subsequent examination.

It is evident then that the knee may return after each knee-jerk to the position held before the blow was struck, or that it may come to rest in a new position, which may be more flexed or more extended than before the knee-jerk was called out. As has been shown such changes in position can only result from an alteration of the tension of the flexor and extensor muscles of the knee, and that this was really the cause of the change of position will become still more evident when we study the relative size of the oscillations which followed the knee-jerk.

Omitting for the present the causes for the varying degrees of tension found, let us see what effect they exerted upon the extent of the knee-jerk. It is to be remembered that the fact that the spinal cord is essential to the development of the knee-jerk is explained by those who disbelieve that it is a reflex act, on the ground that the spinal cord is indispensable to the tonus of the muscle, and that the muscle must have a certain amount of tension in order to be able to respond to blows on its tendon. If it be true that the irritability of a muscle to mechanical stimuli is dependent on its tension, it would seem that the extent of the knee-jerk would vary with the degree of tension of the muscle. In the experiments recorded there is no lack of changes of tension of the muscle or of variations in the size of the knee-jerk, but the degree of tension and the size of the knee-jerk are entirely independent of one another. The truth of this statement is proved by the following table, in which the changes in the tension of the muscles as determined by the variations of the position of the line of rest are recorded side by side with the height of the knee-jerk which was called out immediately after this change of tension.

Description of Table III.

The table is headed by the letters which represent the names of the subjects examined, and beneath each of them is the number of another table of this paper in which these same results appear. Below each letter the results of the examination are arranged in two parallel columns. In the first is recorded in millimetres the variations in the position of the line of rest which occurred in the succeeding observations, the sign + indicating a movement towards extension and the sign – towards flexion. In the second column is stated the extent of the knee-jerks which were called out when the muscles had the tension recorded on the same line in the first column.

TABLE III.

A		C		L		U		U	
IX		VII		VI		VI		(curve 61)	
Line of rest	Knee-jerk	Line of rest	Knee-jerk	Line of rest	Knee-jerk	Line of rest	Knee-jerk	Line of rest	Knee-jerk
0	81	0	63	0	−102	0	81	0	55
− 4	70	+ 5	56	+ 2	59	− 2	60	− 4	48
− 5	50	− 1	60	+ 1	51	− 3	71	+ 10	51
+ 5	56	+ 11	61	− 6	68	+ 1	77	+ 7	66
− 5	53	+ 2	44	− 5	58	+ 7	85	+ 6	47
+ 5	48	+ 7	41	+ 1	73	+ 2	?	− 2	51
− 7	61	− 5	52	+ 6	81	− 7	55	+ 3	50
+ 1	63	+ 2	49	+ 4	72	− 4	65	− 4	51
+ 8	51	− 1	55	− 1	72	− 7	95	0	67
+ 11	88	0	70	+ 1	72	+ 6	94	+ 3	60
+ 7	30	0	45	+ 6	64	+ 4	75	− 1	61
− 18	60	0	82	− 1	75	+ 2	96	− 5	67
+ 7	50	+ 25	36	+ 1	72	− 1	79	− 2	65
− 1	39	+ 5	24	− 1	66	+ 8	88	− 7	67
0	37			?	*	+ 15	81	− 7	65
+ 1	40			*	70	+ 6	75	− 3	56
?	*			+ 2	76	+ 4	*	− 0	73
*	34			+ 1	70	− 48	80	1	75
− 5	30			+ 2	83	− 3	92	+ 5	69
− 8	24			+ 13	63	+ 3		+ 12	74
0	39			+ 1	64			+ 4	72
− 3	50			− 9	70			− 18	64
+ 5	57			+ 18	61			+ 1	67
+ 12	40			− 1				+ 3	71
+ 2	49							− 4	85
− 5								+ 1	

* Break in curve.

From this table we see that the knee-jerk may be large when the tension of the muscles is high, medium, or low, and that the knee-jerk may be small when the tension of the muscle is high, medium, or low. In fact one can trace no constant relation between the amount of tension of the muscles and the size of the knee-jerk. It is interesting to see how markedly the tension of the muscles may vary without any corresponding alteration in the size of the knee-jerk. This is well seen in Charts II., III. and IV.

In the cases just studied, the tension of the muscles was determined by the position of the line of rest just after the oscillations caused by the preceding knee-jerk had ceased. Ordinarily no further change in the line of rest was seen to occur in the interval elapsing before the next blow was struck. This was found to be the case by experiments in which the records were taken on a revolving drum. Occasionally, however, such changes were seen, and in the following table two cases are reported in which considerable variation in the position of the line of rest occurred in the intervals between the succeeding knee-jerks. Since in these cases the tension of the muscles was changing almost at the moment that the blow was struck, one might expect to find here, if anywhere, that the extent of the knee-jerk was influenced by the tension of the muscles.

Description of Table IV.

The table is headed by the letters representing the names of the two men on whom the examinations were made, and by the numbers of the tables in which these results again appear in this paper. The results of the examinations are given in four columns placed beneath these letters. In the first column is recorded the position of the knee-joint just before the blow was struck; in the second, the extent of the knee-jerk; in the third, the position of the knee immediately after the oscillations had ceased; and in the last column, the change in the position of the knee, occurring in the interval before the next blow was struck.

TABLE IV.

Q [Table VIII. p. 141.]				A [Table IX. p. 142.]			
Position of line of rest just before blow was struck as compared with the original line of rest	Extent of the Knee-jerk	Change of the line of rest from position held just before blow was struck	Further change of line of rest in the interval of quiet	Position of line of rest just before blow was struck as compared with the original line of rest	Extent of the Knee-jerk	Change of the line of rest from position held just before blow was struck	Further change of line of rest in the interval of quiet
0	83	+ 10	− 9	0	53	− 6	+ 1
+ 1	65	+ 4	− 3	− 5	40	− 4	+ 1
+ 2	56	+ 2	− 1	− 8	41	+ 3	+ 1
+ 3	55	+ 1	− 2	− 4	20	− 2	+ 2
+ 2	42	+ 3	− 2	− 4	20	− 5	+ 2
+ 3	59	+ 3	− 2	− 7	50	+ 4	+ 1
+ 4	26	0	− 1	− 2	60	− 3	+ 1
+ 3	53	+ 2	− 4	− 4	30	− 2	+ 1
+ 1	36	+ 4	− 2	− 5	17	0	+ 1
+ 3	39	0	− 2	− 4	39	0	0
+ 1	52	+ 3	− 2	− 4	49	+ 4	0
+ 2	42	− 5	− 8	0	36	− 1	0
− 11	70	+ 20	− 4	− 1	44	+ 8	+ 1
+ 5	32	− 1	− 4	+ 8	20	− 1	0
0	54	+ 3	− 1	+ 7	55	+ 3	− 1
+ 2	58	− 1	− 2	+ 9	33	− 2	0
− 1	50	0	0	+ 7	26	− 3	+ 2
− 1	44	+ 3	− 1	− 6	44	+ 11	− 2
+ 1	32	+ 4	− 1	+ 15	32	+ 8	− 5
+ 4	56	+ 6	− 4	+ 18	26	− 3	− 1
+ 6	47	0		+ 14	36	− 3	− 1
				+ 10	36	+ 1	− 1
				+ 10	26	− 2	− 1
				+ 7	26	− 2	0
				+ 5	33	0	0
				+ 5	24	− 1	0
				+ 4	31	+ 5	0
				+ 9	54	− 5	
				+ 4			

Even in these cases one fails to find any correspondence between the size of the knee-jerk and the changing tension of the muscles, as recorded in the third and fourth columns, or the tension of the muscles compared with the amount which they had at the beginning of the examination, as stated in the first column.

Since the tonus of the muscles is without influence upon the size of the knee-jerk, the tonus theory can hardly be taken as a satisfactory explanation of the dependence of the phenomenon upon the spinal cord. A study of these experiments reveals, moreover, that not infrequently the *flexors* as well as the *extensors* contracted in response to the blow on the ligamentum patellae. This result is a very strong argument in favor of the view that the whole process is reflex. The contraction of the flexors was shown not only by the marked changes in the position of the line of rest which occasionally occurred, but it was plainly visible in the effect which it exerted upon the extent of the oscillations of the leg following the knee-jerk.

If one refers to Table I. and Chart I. he sees that the averages of the oscillations occurring in these extremely regular observations were :—

1st extension = 100, 1st flexion = 50, 2nd extension = 23, 2nd flexion = 8.

In other words, he notices that the first flexion equalled about half the movement of the knee-jerk, the second extension was a little less than half the first flexion, and that the second flexion was a little more than a third of the second extension. A glance at Table V., however, shows one that this proportion is far from constant, even in the case of men who are calm and quiet at the time of the experiment. Table V. has the same form as Table I.

The averages obtained from this table are as follows, viz.:—

	1st Exten.	1st Flex.	2nd Exten.	2nd Flex.
G.	+ 31	− 14	+ 7	− 3
X.	+ 34	− 14	+ 8	− 4
C.	+ 94	− 47	+ 25	− 8
D.	+ 33	− 14	+ 8	− 3

These averages show a general tendency for the second extension to be larger in proportion to the first flexion, than the first flexion to the first extension or the second flexion to the second extension, a result which one would scarcely expect in case the oscillations were caused by the force of gravity and the elastic recoil of the muscles. The size of the second extension suggests that the extensors in these cases did not immediately relax.

The above experiments were upon men who were calm at the time of the examination. This was seldom the case at the first examination. The fact that a stranger was about to experiment

TABLE V.

G, curve 10					X, curve 55					C, curve 23					D, curve 39				
1st Exten. i.e. Knee-jerk +	1st Flex. −	2nd Exten. +	2nd Flex. −	Change of line of rest	1st Exten. i.e. Knee-jerk +	1st Flex. −	2nd Exten. +	2nd Flex. −	Change of line of rest	1st Exten. i.e. Knee-jerk +	1st Flex. −	2nd Exten. +	2nd Flex. −	Change of line of rest	1st Exten. i.e. Knee-jerk +	1st Flex. −	2nd Exten. +	2nd Flex. −	Change of line of rest
68	31	14	6	0	29	11	7	3	0	108	42	31	1	+2	45	18	11	3	+2
21	11	6	3	0	29	?	?	?	0	117	59	33	9	0	82	22	15	3	+2
43	19	10	4	0	31	16	9	4	0	146	79	47	17	+1	68	20	13	4	+1
80	37	18	7	0	31	15	9	4	0	122	58	32	8	+2	51	21	11	5	0
65	29	13	5	0	43	19	11	4	0	125	47	26	5	0	27	12	6	3	+1
54	21	10	4	0	31	12	8	3	0	122	61	32	10	0	31	16	8	4	0
41	16	9	4	0	42	18	10	4	0	115	60	33	9	0	21	7	4	2	0
18	8	4	3	0	38	16	9	4	0	128	59	32	9	0	21	9	5	2	0
24	10	6	3	0	46	21	11	5	0	113	61	32	10	−1	32	17	9	4	0
23	10	6	3	0	26	11	7	3	0	110	57	31	?	+1	42	24	13	6	0
30	11	7	3	0	40	17	10	5	0	95	48	25	?	0	57	31	18	8	0
15	7	4	2	0	38	17	10	4	0	79	37	18	4	+1	39	19	10	4	0
19	9	5	3	0	31	12.	7	?	0	82	41	19	6	0	21	9	5	2	0
15	7	4	3	0	31	12	8	4	0	93	49	25	9	−1	10	4	2	1	0
16	8	4	3	0	27	11	7	3	0	92	48	26	8	0	21	13	7	3	0
29	14	7	4	0	34	15	8	4	0	76	36	18	5	+1	19	8	5	2	0
20	9	5	3	0	33	15	9	4	0	84	43	22	?	0	24	11	6	3	0
15	6	4	2	0	39	17	10	4	0	81	41	19	6	0	17	8	4	2	0
17	10	5	3	0	34	15	9	?	0	78	39	18	?	0	20	9	5	2	0
24	12	7	4	0	27	11	7	4	0	89	48	24	?	0	37	19	10	5	0
11	5	4	2	0	45	22	12	6	0	45	15	8	?	+1	43	23	13	6	0
					33	15	8	?	0	68	34	16	?	0	31	15	8	3	0
					35	15	8	?	0	50	21	9	?	0	14	6	3	2	0
					35	15	8	4	0						24	11	7	3	0
															15	7	3	2	0
31	14	7	3		34	14	8	4		94	47	25	8		33	14	8	3	

upon them in some unknown way excited nearly all of the men, more or less. When any of them was examined a number of times, or often towards the end of the first examination when the excitement had worn off, the records were similar to those recorded in Table V. This excitement, even though slight, generally sufficed to lessen the oscillations of flexion and to exaggerate those of extension more than in the cases reported in Table V. Examples of this condition are given in Table VI.

TABLE VI.

L, Curve 15.

No. of Observation	Knee-jerk or 1st Exten. +	1st Flex. −	2nd Exten. +	2nd Flex. −	Change of line of rest
1	102	29	6	5	+ 2
2	59	31	6	2	+ 1
3	51	28	2	?	− 6
4	68	37	7	12	− 5
5	58	29	12	4	+ 1
6	73	18	17	+ 2	+ 6
7	81	0	46	+ 14	+ 4
8	72	19	18	4	− 1
9	72	18	15	4	+ 1
10	72	+ 2	39	?	+ 6
11	64	14	21	4	− 1
12	75	8	12	1	+ 1
13	72	8	14	3	− 1
14	66	18	18	?	?
15	Break in curve				
16	70	12	16	+ 1	+ 2
17	76	6	14	0	+ 1
18	70	10	27	+ 1	+ 2
19	83	7	27	+ 11	+ 13
20	63	1	3	?	+ 1
21	64	26	0	?	− 9
22	70	+ 3	36	+ 14	+ 18
23	61	7	9	2	− 1

U, Curve 52.

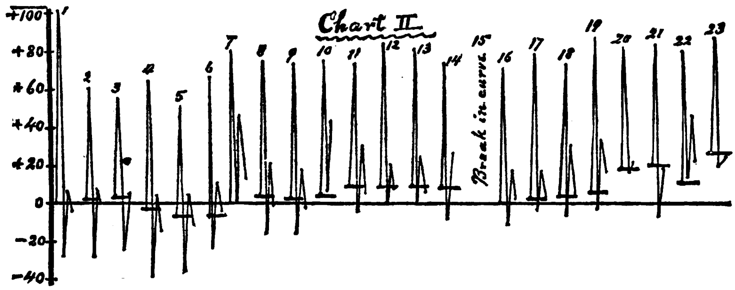
No. of Observation	Knee-jerk or 1st Exten. +	1st Flex. −	2nd Exten. +	2nd Flex. −	Change of line of rest
1	81	5	− 2	3	− 2
2	60	32	7	8	− 3
3	70	16	11	11	+ 1
4	77	11	22	1	+ 7
5	85	+ 8	9	+ 1	+ 2
6	Foot moved spontaneously				− 7
7	55	26	12	8	− 4
8	65	?	?	?	− 7
9	95	6	12	+ 5	+ 6
10	94	4	37	6	+ 4
11	75	9	30	3	+ 2
12	96	14	4	3	− 1
13	79	?	?	?	+ 8
14	88	+ 5	56	+ 7	+ 15
15	81	21	38	+ 4	+ 6
16	75	13	39	0	+ 4
17	Break in curve				− 48
18	80	0	20	6	− 3
19	92	11	35	+ 1	+ 3

Thus in the case of L, curve 15, every observation, except number 21, from number 6 through the table, shows that the first flexion was small in proportion to the first extension, the second extension was not only large in proportion but frequently larger than the first flexion, and the second flexion was very small. In observations 10 and 22 the first flexion did not even get back to the line of rest, and the same is true of the second flexion in observations 6, 7, 16, 17, 18, 19 and 22.

Examination of U, curve 52, shows a similar state of things. There are the same excessive oscillations of extension and small oscillations of flexion, in a large proportion of the observations, while the first oscillation of flexion does not get back to the line of rest in observations 5 and 14, and the second flexion does not get back in numbers 5, 9, 14, 15 and 19.

These peculiarities are well seen in the case of L, curve 15, recorded in Chart II.

L, Curve 15.



One cannot observe the tendency shown in these cases for the extensor muscles to check the oscillations of flexion and to increase the oscillations of extension, without noticing the remarkable exceptions to this tendency. Thus in L, curve 15, one sees the second extension to be very small in observations 1, 2, 3 and 4, and in observation 1 the second flexion is nearly as large as the preceding extension, while in observation 4 it is even larger. In U, curve 52, there is a still more interesting exception, for in observation 1 the second extension does not get back to the line of rest and the second flexion is larger than the second extension.

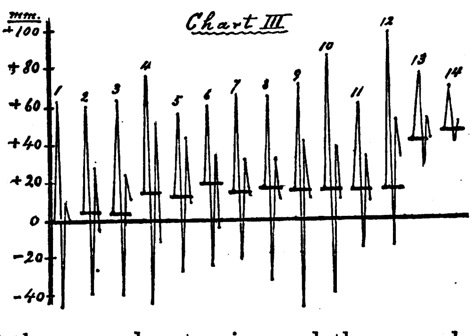
These exceptions are of the greatest interest, because they can scarcely be explained except by assuming a contraction of the flexor muscles of the knee. Such observations are of frequent occurrence and are unquestionably accurate. In certain cases, indeed, the contraction of the flexors is so strong as not only to check the second extension but to lessen the extent of the knee-jerk. C, curve 16, recorded in Table VII. and Chart III. is a case in point. The first flexion is disproportionately large in most of these experiments, and in observations 6, 8, and 9 it is as large, or even larger than the knee-jerk.

TABLE VII.

C, Curve 16.

No. of Obser-vation	Knee-jerk or 1st Exten. +	1st Flex. −	2nd Exten. +	2nd Flex. −	Change of line of rest
1	63	46	9	0	+ 5
2	56	45	23	10	− 1
3	60	44	20	+ 7	+ 11
4	61	58	36	27	+ 2
5	44	39	31	4	+ 7
6	41	44	14	24	− 5
7	52	35	16	2	+ 2
8	49	49	18	5	− 1
9	55	62	24	5	0
10	70	56	22	5	0
11	45	30	17	6	0
12	82	31	36	+ 15	+ 25
13	36	13	11	+ 2	+ 5
14	24	6	5	?	+ 2

C, Curve 16.



The size of the second extension and the second flexion together with the shape of the curve, shows that the extensors as well as the flexors were actively contracting. In cases such as the above one sees the knee-jerk, though beginning rapidly and vigorously, to be suddenly checked and changed to flexion, which movement, as has just been shown, may be even greater than the knee-jerk. This result corresponds with the observations of certain physicians, who have told me that they have come to doubt the extent of the knee-jerk as an accurate measure of the activity of the process, and that they were in the habit of basing their conclusions upon the rapidity and "jerkiness" of the phenomenon as well as upon the amount of the movement.

The fact that both flexors and extensors may be excited by the blow on the ligamentum patellae, or its results, is shown in still other cases where the oscillations of extension and flexion instead of being long and pendulum-like are short and jerky in character, so that they remind one of clonus. In these cases it is probable that both of the antagonists are actively contracting; and the leg oscillates as if swinging between two tightly stretched elastic bands. This is illustrated by the experiments recorded in Table VIII.

TABLE VIII.

Q, Curve 29[a].

No. of Obser-vation	Knee-jerk or 1st Exten. +	1st Flex. −	2nd Exten. +	2nd Flex. −	Change of line of rest	Further change of line of rest
1	83	15	14	+ 7	+ 10	− 9
2	65	12	9	+ 3	+ 4	− 3
3	56	7	7	0	+ 2	− 1
4	55	12	4	1	+ 1	− 2
5	42	3	8	+ 2	+ 3	− 2
6	59	2	11	+ 4	+ 3	− 2
7	26	9	4	3	0	− 1
8	53	3	6	+ 1	+ 2	− 4
9	36	3	10	1	+ 4	− 2
10	39	5	4	1	0	− 2
11	52	4	8	1	+ 3	− 2
12	42	9	1	7	− 5	− 8
13	70	+ 29	26	+ 20	+ 20	− 4
14	32	6	7	2	− 1	− 4
15	54	5	7	+ 2	+ 3	− 1
16	58	10	3	3	− 1	− 1
17	50	2	8	0	0	0
18	44	2	7	+ 3	+ 3	− 1
19	32	3	9	+ 3	+ 4	− 1
20	56	8	3	+ 6	+ 6	− 4
21	47	6	9	0	0	

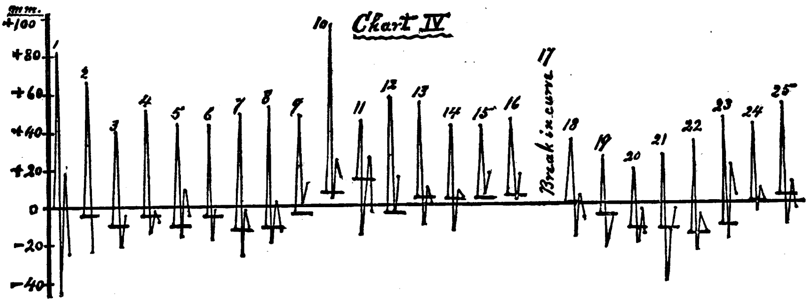
The curves recorded in this table show many irregularities, and there were other examinations made in which no prevailing tendency could be observed, but every possible variation was found. These peculiar results are explained by the fact that sometimes the flexors and sometimes the extensors of the knee exert the controlling influence. A curve 14, recorded in Table IX. and Chart IV. is a good example of the eccentricities possible to the knee-jerk.

TABLE IX.

A, Curve 14.

No. of Observation	Knee-jerk or 1st Exten. +	1st Flex. −	2nd Exten. +	2nd Flex. −	Change of line of rest
1	81	45	18	24	− 4
2	70	29	?	?	− 5
3	50	13	4	?	+ 5
4	56	17	2	4	− 5
5	53	6	18	+ 5	+ 5
6	48	14	2	?	− 7
7	61	14	10	+ 1	+ 1
8	63	8	13	3	+ 8
9	51	+ 4	15	?	+ 11
10	88	5	17	+ 7	+ 7
11	30	30	11	19	− 18
12	60	0	18	?	+ 7
13	50	14	5	3	− 1
14	39	18	4	0	0
15	37	+ 1	12	?	+ 1
16	40	2	12	?	?
17	Break in curve				
18	34	17	4	7	− 5
19	30	18	0	?	− 8
20	24	8	10	3	0
21	39	29	0	10	− 3
22	50	8	10	1	+ 5
23	57	9	31	+ 15	+ 12
24	40	7	6	0	+ 2
25	49	14	7	7	− 5

A, Curve 14.



The first oscillation of flexion was prevented from returning to the line of rest in observations 9, 12 and 15. The same is true of the oscillation of second extension in 19 and 21. The first oscillation of flexion is disproportionately large in 11 and 21. The second extension is larger than the first flexion in a large proportion of the cases, yet the second flexion is larger than the second extension in 1, 4, 11, 18 and 21. The second flexion does not attain the line of rest in 5, 7, 10 and 23.

The results of these experiments can leave no doubt that under certain circumstances, at least, the flexors as well as the extensors are thrown into contraction by the blow on the ligamentum patellae or its sequellae. This discovery is of great importance not only as enabling us to understand the character of the knee-jerk, but also as a hint as to the methods of muscular co-ordination. It has long been thought that antagonistic muscles both act at the same time and that all the movements of the limbs are the result of finely graded differences in these opposing forces. I discovered while working in Leipzig[1], that all the muscles of the frog's leg will respond nearly simultaneously to a strong reflex stimulus, and it seems to me that the experiments reported in this paper favor the view that the same thing is true of co-ordinated muscular actions in man. It is probable, however, that the contraction of the antagonist is well developed only when the action is vigorous or extended.

There can be no doubt that the blow on the ligamentum patellae resulted in a contraction of the flexor as well as of the extensor muscles in many of my experiments. How were the flexors stimulated, reflexly, or directly by the strain brought upon them by the extension of the knee?

[1] "Die räumliche und zeitliche Aufeinanderfolge reflectorisch contrahirter Muskeln." *Archiv fur Anat. u. Physiol.*, Physiol. Abthl., 1885.

I am inclined to think that the extensors and flexors are both irritated by the same process. The twitch of the tendon caused by the blow on the ligament probably irritates the ends of the centripetal nerves lying in the tendon and muscle, and these nerve ends develop a stimulus which excites the reflex centres of the spinal cord. How many reflex centres are affected and how strong a reflex action is developed depends on the strength of the irritant and on the condition of the reflex mechanisms at the time. When the person is calm and quiet, only the extensors appear to be stimulated, but when he is excited, the flexors, as well, receive reflex stimuli. The extensors are irritated first and their contraction is under way before the flexors begin to contract; nevertheless, the difference in time is not great, as is shown by the fact that the contraction of the flexors often follows that of the extensors with sufficient rapidity to prevent the completion of the movement of extension. Thus one may see at the beginning of a series of experiments, when the man is excited, very small knee-jerks though the movements are sudden and violent. Gradually, as the man becomes calmer, the knee-jerks become longer and less jerky, and, finally, as he quiets down still more, they get small again. The effect of the excitement was to cause an active contraction of the flexors almost simultaneously with that of the extensors, and this antagonistic action checked the knee-jerk before completion. As the excitement became less, the flexors were stimulated less, and the contraction of the extensors was able to show itself in a larger knee-jerk. When the subject had become calm, the extensors alone were irritated, and they received a milder stimulus, so that the knee-jerk was small again. Such was the condition in the case of C, curve 3, recorded in the following Table, X.

This explanation is in harmony with what we know of reflex actions, in general. A slight irritation will call out a reflex contraction of a few muscles, and a stronger irritant applied to the same part will excite a stronger contraction of these muscles and at the same time stimulate certain other muscles. The muscles which respond to the least stimulus also contract first when more muscles are excited by the stronger irritant.

It may be asked, however, is it not possible that the contraction of the flexors is due to a direct mechanical stimulation of the muscle fibres by the sudden strain brought upon them by the rapid extension of the knee? There are several reasons why this explanation is unsatisfactory. First of all one remembers that the flexors often contract very actively when they have been subjected to a very slight strain,

TABLE X.

C, Curve 3.

No. of Obser-vation	Knee-jerk or 1st Exten. +	1st Flex. −	2nd Exten. +	2nd Flex. −	Change of line of rest
1	47	3	6	8	− 4
2	Trembling of muscles				+ 3
3	59	37	12	+ 1	+ 7
4	72	65	3	7	− 4
5	69	69	−10	13	− 2
6	76	27	17	1	+ 5
7	96	56	42	+17	+14
8	107	52	52	+ 2	+ 2
9	Trembling of muscles				+11
10	96	61	48	+13	+20
11	67	47	40	+ 7	+22
12	24				
13	Break in curve; start again				
14	82	44	11	5	+ 2
15	54	19	5	6	− 3
16	40	60	22	9	+ 2
17	27	54	− 1	24	−10
18	Foot moves spontaneously				+ 2
19	63	56	31	10	+ 4
20	40	54	29	5	+ 8
21	71	53	33	?	+ 2
22	45	25	13	1	+ 2
23	37	29	11	4	0
24	55	44	17	5	0
25	45	22	9	2	+ 1
26	54	46	20	8	− 1
27	53	33	16	3	+ 1
28	57	41	19	12	− 3

and that a slight strain is unable to excite a muscular contraction. In the case of the extensors, for instance, we find that depression of the ligamentum patellae even if sudden when performed by the fingers does not cause a knee-jerk; nor does sudden flexion of the knee, when produced by the hand. The still greater suddenness or jar of a blow on the ligament is necessary to the development of the phenomenon. It is probable that the same is true of the flexors, and certainly we find that sudden extension of the knee by the hand does not cause contraction of the flexors. The strain brought on the flexors by the extension of the knee must be a very gradual one, and not to be compared with the twitch which a blow on the ligament would produce. Moreover, the flexors often contract when the foot has made only a slight movement. Thus in observation 11, of A, curve 14, in Table IX., the foot had moved only 30 millimetres when the extension was checked by the contraction of the flexors. To have checked the knee-jerk at this point the contraction of the flexors must have started when the foot had moved even less than this distance. Such a slight movement of the foot would be accompanied by a stretching of the long flexor muscles of only at the most three or four millimetres. Nor is this an isolated example. In case of C, curve 3, Table X., observation 15 gives the movements—+ 27, – 54, – 1, – 24, that is to say, the extensors had only extended the foot 27 millimetres when a violent contraction of the flexors occurred which stopped the knee-jerk short and produced a backward swing of the foot of 54 millimetres. Many other, though perhaps less striking examples, are recorded in the table.

One can scarcely believe that such a slight strain would cause an active contraction of the flexors when he sees in the same examinations that a much greater strain has no such effect. It may be said that this argues as well against the theory of reflex as of peripheral irritation. This is not so, however, because we have evidence that the reflex centres are continually undergoing changes in irritability, while as far as we know the irritability of the muscles does not change much within short intervals of time.

I have already called attention to the fact that the flexors sometimes not only check the contraction of the extensors, but actually contracted further than the extensors had done. It is hard to understand how a muscle by contracting can irritate its antagonist to a stronger contraction than it itself made, unless indeed its antagonist was the more irritable of the two. This explanation will not suffice, because the excessive contractions of the flexors only appear as exceptions, and as a rule the contractions of the extensors are much the larger.

Summary of Results.

There are two theories of the nature of the knee-jerk; the one regards it a reflex action, the other a purely peripheral process. The reflex theory readily explains the intimate dependence of the phenomenon upon the spinal cord, and the time argument, owing to our meagre knowledge of reflex times, in general, is inconclusive. The peripheral theory is not tenable, because the explanation which it offers of the dependence of the knee-jerk upon the spinal cord is unsatisfactory. It assumes that muscle-tonus is continuous, and that the irritability of the muscle to mechanical stimuli is dependent on its tension; both assumptions are without proof. Moreover, the theory is opposed by many facts.

The knee-jerk may be present when muscle tonus appears to be wanting, and may be absent in the case of men who apparently have a normal amount of tonus. When the knee-jerk is lacking it cannot be restored by any amount of tension which can be artificially supplied to the muscle.

The tonus theory does not explain the difference which always exists in the size of the successive knee-jerks, for it is found experimentally that the size of the knee-jerk is not influenced by slight variations in the tension of the muscle; nor can the changes in the amount of the knee-jerk be attributed to alterations of the irritability of the muscle dependent on fine variations in tonus, because experiments show that the irritability of the muscle does not change within short intervals of time.

The peripheral theory does not explain the reenforcements of the knee-jerk, because reenforcing acts, unless very violent, do not alter the tension or irritability of the muscles.

The discovery of Mitchell and Lewis, that muscular contractions called out by electrical stimulation cannot be reenforced, is inexplicable by the peripheral theory though readily explained by the reflex theory.

Finally, occasionally the flexors, as well as the extensors, of the knee are seen to contract in response to the blow on the ligamentum patellae. This contraction of the flexor muscles is of reflex origin, and there is little reason to doubt that the extensors are irritated by the same reflex process. The idea that the flexors are mechanically stimulated by the strain brought on them by the sudden extension of the knee is untenable, because we know that muscles are not irritated by slight strains on their tendons, and the flexors are seen to contract when the knee has extended so little as to bring almost no strain upon them; moreover, in spite of the fact that muscle irritability does not change within short intervals of time, small knee-jerks may be seen to be accompanied by marked contractions of the flexors, and, immediately after, large knee-jerks by little or no flexor contraction.

Since only the reflex theory can satisfactorily explain the influence of the central nervous system over the extent of the knee-jerk, we must adopt it, and must look to future experimental work on reflex times to remove the apparent contradiction involved in the rapidity of the process.