

LOMBARD (W.P.) *With the compliments
of the writer
where*

THE EFFECT OF FATIGUE
ON
VOLUNTARY MUSCULAR
CONTRACTIONS.

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BY

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THE EFFECT OF FATIGUE ON VOLUNTARY MUSCULAR CONTRACTIONS.¹

WARREN P. LOMBARD, M. D.

In March, 1889, I had the good fortune to spend three weeks in the physiological laboratory of the University of Turin. It is with much pleasure that I take this opportunity to express my appreciation of the great courtesy of Professor Angelo Mosso and his assistants. It was only by their advice and aid that I was able to make the research recorded in this paper.

Apparatus and Method.

The research was begun at the suggestion of Professor Mosso, who proposed that I should continue Dr. Maggiora's² work on the fatigue of voluntary muscles, and who placed the apparatus which Dr. Maggiora had used entirely at my disposal. This apparatus, which is very simple and satisfactory, has been described at length by Professor Mosso—*Li Ligi Fatica Studiate nei Muscullo dell Uomo*, R. Academia dei Lincei, 1889.

All the experiments were made upon men, and most of them on the flexor muscles of the second finger. The muscles were stimulated voluntarily or electrically, and the corresponding movements of the finger were registered.

The record was made by a pen which was carried by a little car. The car was supported by two parallel horizontal steel rods, upon which it slid with very little friction. A string, fastened by a leather loop to the finger, pulled the car in one direction, and a cord, which passed over a pulley to a weight, drew the car in the opposite direction. Thus, when the muscles contracted, the finger was flexed and the car was drawn forward, and when the muscles relaxed, the weight caused the finger and the car to return to their original posi-

¹ This paper was read before the Physiological Congress at Basel, Sept. 29th, 1889.



tions. The movements of the car were recorded by a pen on the horizontal drum of a Baltzar kymographion.

The subject was seated during the experiments. The hand and arm were securely fixed on a convenient rest, and, in spite of the violent muscular contractions which were often required by the experiments, made no movement of a kind to influence the record. This question was carefully studied. Also the action of the finger was watched, to see that all the joints moved with each contraction, in other words, that all the muscles which assist to flex the finger were contracted.

Discovery of the Periodicity.

As the first step of the proposed research, it was necessary for me to ascertain the normal curve of fatigue of my muscles, because Dr. Maggiora had found that this varies in different individuals. In these experiments, I voluntarily contracted the flexor muscles of the second finger of the left hand every two seconds. The signal was the sound made by the interrupter of an electric clock. Each contraction was the strongest possible, and, as the weight was three kilograms, the muscles soon began to weary. The drum revolved slowly and the following curve of fatigue was recorded:—

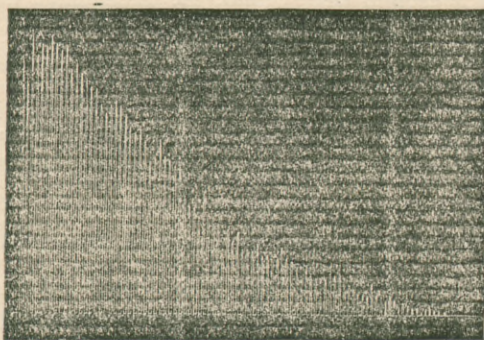


FIG. I.

Several records closely resembling this were obtained. On the second day, however, the work was continued in one experiment longer than usual, because I was determined to fatigue the muscle so completely that no contraction should

be possible. After 110 seconds of continuous work, I could hardly stir the weight, and thought the experiment nearly at an end. To my surprise, however, I began to recover the lost power, and during the next half minute each of the succeeding contractions was higher than the one which had preceded it. The effect of fatigue then began to manifest itself again, and the contractions became smaller. I concluded that I had made a mistake, that I had not exerted all my will power before, and I determined for the rest of the experiment to do my best. As the contractions grew smaller I threw all my energy into each attempt to raise the weight. I was conscious that, as is always the case during violent muscular exercise, I was contracting many muscles of the body, and that my face was flushing under the strain; nevertheless, the contractions became gradually less, and I supposed that I had finally succeeded in tiring out the muscle, when, to my astonishment, I began to recover my power a second time. The contractions became stronger, reached a maximum and fell, only again to recover. In short, for some inexplicable reason, during the twelve minutes that the work was performed, the ability to voluntarily contract the muscles with sufficient strength to raise the weight, decreased and recovered five times. During the intervals of decreased strength the power was almost entirely lost, while during the periods of recovery, the force was equal to that shown half a minute after the beginning of the work. Fig. II, Plate I, is a better witness than any words.

The recovery of power which I observed in this and in similar experiments interested me so much that I gave up the intended research and devoted my time to studying its nature and cause.

Constancy of the Phenomenon.

A few days of work showed that the observations which have been described were not exceptional, but that in my case, at least, the periodic loss and recovery of force could be found every day and at all times in the day; on the muscles of both arms, and on the extensors as well as flexors; with weights of $\frac{1}{2}$, 1, 2, 3 and 4 kilos.; and when the muscles were contracted at intervals of 1, 2 and 4 seconds.

Experiments upon Others.

Unfortunately, lack of time prevented extended experiments upon others; nevertheless, the power to voluntarily contract the muscles was seen to vary in a like manner in the case of two other strong, healthy men. Fig. III, Plate II, is a reproduction of the record obtained from one of these experiments.

The phenomenon is, therefore, normal. It is, however, far from sure that it can be found well marked with all men. I failed to obtain it in a few experiments which I made on six other men, although in some of them suggestive irregularities were seen. As has been said, the phenomenon is distinctly a result of fatigue, and, therefore, the experiments are not agreeable. Men are very differently constituted, both as regards their ability to concentrate their efforts, and to continue muscular work after fatigue has made it painful. One sees this exemplified in races, on the march, and whenever long continued and violent muscular exertion is required. I do not know that these constitutional differences have ever been satisfactorily explained, or, indeed, that anyone has a well defined idea of the physiological conditions which are essential to endurance and tenacity.

Study of a Characteristic Experiment.

In long continued experiments with weights lighter than that which was employed in the experiments recorded in Fig. II, Plate I, the alternating loss and recovery of power, though appearing later, is even more striking. Fig. IV, Plate I, records an experiment on the flexor muscles of the second finger of the left hand, with a weight of half a kilogramme. The muscles were voluntarily contracted every two seconds, and each time with the utmost force. In this case the difference between the height of the contractions during the interval in which the voluntary power was lost, and the periods when the muscle responded well to the will impulse, was very great. For the first half minute of this experiment, the height of the contractions varied from 53 to 57 mm., and averaged 55 mm. They then began to decrease in size, and at the end of $9\frac{1}{2}$ minutes had fallen to 5 mm. The

The difference between the size of the contractions during the periods of power and intervals of weakness was remarkably constant. This is well seen in the following table, in which the highest contraction of each period is placed by the side of the lowest contraction of the following interval. The height of the contractions is stated in millimeters.

TABLE II.

Highest contraction of the period.	Lowest contraction of the following interval.
48	8
45	4
48	5
47	5
47	6
49	7
47	9
50	6
40	7
48	7
47	8
47	8
48	13
48	10
47	8
47	6
48	4
49	4

The regularity seen in this table is the more surprising when one reflects that it depended not only on the action of mechanisms within the spinal cord, of the nerves, the nerve ends and muscle fibers, but also on the ability of the subject of the experiment to give each time the strongest will impulse possible. The fact remains the same, however, that in each of the periods of recovered power the highest contraction was of about the same size, and that it was nearly as vigorous as the contractions which were made at the beginning of the experiment.

It is also noteworthy that during the intervals of decreased force the strength was lost each time to almost exactly the same degree.

On the other hand there was but little regularity in the length of the succeeding periods. Stated in seconds their lengths were, viz.—66, 48, 38, 30, 34, 32, 24, 28, 62, 32, 34, 28, 44, 26, 28, 38, 34, 26.

There was also great difference in the time elapsing before the highest contraction of each of the successive periods was

reached. Stated in seconds these times were, viz.—22, 24, 16, 8, 18, 22, 14, 4, 36, 16, 16, 4, 38, 14, 10, 14, 12, 12.

Likewise the time between the highest contraction of a period and the next lowest contraction varied greatly, viz., 44, 24, 22, 18, 16, 10, 10, 14, 26, 16, 18, 24, 6, 12, 18, 24, 22, 6.

It is unnecessary to calculate the work accomplished in each period. A glance at the curve discloses that it was not the same in any two periods.

To summarize these results one may say that nine and one half minutes elapsed before the first interval of decreased power was reached. During the succeeding ten minutes the power to raise the weight was regained and lost fifteen times. The periods of recovered power varied greatly in length. The lowest contractions of the intervals and the highest contractions of the periods were irregularly distributed. In no two periods was the same amount of work accomplished. Finally the highest contractions were of about the same size in all the periods and were nearly equal to the contractions occurring at the beginning of the experiment, though in the intervals of decreased force the contractions had almost no power.

Search for the Seat of the Changes which Produce the Periods.

When a muscle is voluntarily contracted many chains of mechanisms are thrown into action. All these chains are connected with the areas of the brain originating the will impulse. The successive links are formed by the mechanisms within the central nervous system, the centrifugal nerves, the nerve ends, and the muscle fibres. Which of these organs is the seat of the changes which cause the loss and recovery of voluntary power?

The periods do not appear until after considerable work has been performed. The greater the weight and the more frequent the contractions the sooner they occur. Indeed, they seem to be essentially connected with the fatigue of the mechanisms involved in the voluntary movement. It is well known that muscles weary rapidly if deprived of blood, and

as Dr. Maggiora has shown they recover their strength with equal rapidity if treated with massage during the intervals of repose. These facts suggest that the periods are the result of circulatory changes in the muscle.

With the hope of ascertaining the truth of this supposition I made the following experiment. I contracted the flexor muscles of the second finger, weighted with 2800 grammes, every two seconds, and each time as vigorously as possible. When fatigue had become great, and the intervals of loss and periods of recovery of force were very marked, the muscle was subjected to massage. The work was continued during the massage with the same regularity. At the end of a few minutes, the effect of the massage was seen in the flushed skin and in the fact that the muscular contractions during the intervals of decreased power were somewhat higher than before. Nevertheless, the periods continued to occur. In other words, the increased circulation caused by the massage, though slightly strengthening the muscle, did not remove the periodicity. Fig. V, Plate II, is a reproduction of the record of this experiment. The arrow marks the moment at which the massage was applied.

Another form of experiment was then resorted to, in order to see if the irritability or strength of the muscle was less at the moment that the voluntary contraction was weakest. The condition of the muscle was tested at the beginning of the experiment by a tetanizing induction current, applied at intervals of two seconds, during about half a second, the muscle raising a kilogramme at each contraction. After ten contractions the electricity was stopped, and the subject began to voluntarily contract the muscle every two seconds, and always with his whole force. When the periodicity had become well defined, the muscle was again tested with electricity. The test was made during an interval when the most vigorous voluntary effort was incapable of raising the weight. It was found that the response to electricity was about the same, and that the muscle was still capable of doing work. Moreover, although the electric stimulations were applied regularly, every two seconds, for some minutes, no recurrence of the periodicity was seen. When the electricity was dis-

continued and voluntary contractions again commenced, the periods soon returned. It is worthy of note that the periodicity did not appear immediately, however. It seemed as if the mechanism which was the seat of the changes producing the phenomena, had had an opportunity to partially recover during the time that the muscle was contracting in response to the electric irritations. The difference in the form of the record obtained, when the muscle is irritated directly by electricity, and when it is stimulated voluntarily, is well illustrated in Fig. VI, Plate II. The whole curve is the record of one continuous experiment, and contains two groups of periods, obtained when the muscle was voluntarily contracted, and, between them, the series of contractions which were called out by direct electrical stimulation of the muscle. These experiments, and others in which the muscle was stimulated by electricity every two seconds for a long time, and was seen to weary without any sign of periodic loss and recovery of power showing itself, forced me to conclude that the phenomenon did not originate in the muscle.

The nerves and nerve ends were next studied. The record of one of the experiments is given in Fig. VII, Plate I. The median and ulnar nerves were irritated by a tetanizing induction current, applied every two seconds, for about half a second, one of the moist electrodes being placed on the skin over the sternum, the other over the region of the nerves on the inside of the upper arm. The record was taken from the second finger, and the weight was one kilogramme. It was with difficulty that the most favorable point for simultaneously stimulating both nerves was found; at last, however, all the phalanges were seen to move in response to the irritation, and it was evident that all the muscles which help to flex the finger were receiving the nerve impulse.

After the muscles had contracted ten times, (see *a* on curve,) the irritation was stopped and the muscles were voluntarily contracted every two seconds, and always with all the force possible. The periodicity appeared in this case sooner than was usual, perhaps because the subject was tired, on account of the many experiments of the preceding days. After 209 contractions, about seven minutes' work, when the

periods had become very decided, the effect of electrical stimulation of the nerves was again tried (see *b* on curve); the muscle contracted less than at the beginning of the experiment, but, though the irritations were given every two seconds for nearly two minutes, no periodicity manifested itself. When the voluntary contractions were begun again the periods occurred as before.

It is worthy of observation, that, in this case, as in that already referred to, of direct electrical stimulation of the muscle the first period after the electrical stimulation was stopped was longer than those which occurred just before the stimulation with electricity, which suggests that the mechanisms which are the seat of the changes which cause the periodicity, had time, while the nerves and muscles were working under the influence of the electrical irritations, to partly recover from their fatigue. That the recovery was incomplete, was shown in the rapidity with which short periods made their appearance.

During this experiment the subject had the curiosity to try the effect of continuous voluntary contractions of the muscles. He avoided looking at the curve lest he should be influenced by it. He raised the weight as high as possible and did his best to keep it at that height. He was conscious of the loss and gain of power, but was not aware, until afterwards, that his finger had written a curve which corresponded to a silhouette of the records of the intervals of loss and periods of gain of power which were recorded when the muscles were contracted every two seconds.

The effect of electrical stimulation of the muscles was tried a third time, and it was found that the muscles contracted higher than at the beginning of the experiment, (see *c* on Fig. VII, Plate I.) The writer lays but little stress on the difference in the height of the contractions obtained with the electric current in the three observations of this experiment, because it is probable that they were caused by slight changes in the position of the electrode on the arm. The important fact demonstrated by this experiment is the absence of periods from the curves obtained by stimulating the nerves by electricity, and, that too, at a time when the periodic

variations during the voluntary contractions were very marked.

By chance, the third time that the voluntary contractions were begun coincided with the part of the period when a vigorous contraction was possible and one high contraction was recorded. Immediately after, however, the cause which produces the intervals asserted itself, and the contractions became smaller. The record looks as if part of a period had been cut off; (see the first contraction following series marked *c* in Fig. VII, Plate I.) This chance observation, which was repeated in another part of the experiment not given in the plate, is very important, because it shows, both by its shape and the time of its occurrence, that the changes which cause the periods continue after the voluntary action has ceased.

Although the foregoing experiments suffice to show that the periodic variations were of central rather than peripheral origin, I sought a method of experimentation which would enable me to form a clearer idea of the relative influence exerted on the height of the contractions by the fatigue of the muscles and the changes occurring in the central nervous system. At the suggestion of Professor Mosso the following form of experiment was adopted. The flexor muscles of the second finger, weighted with one kilogramme, were stimulated every two seconds. Two different forms of stimuli were employed, electrical and voluntary stimuli, and they were applied alternately. During the electrical irritation, the nerves and muscles were stimulated by a tetanizing induction current, one of the electrodes being placed over the sternum, the other over the muscle. Fig. VIII gives the results of a part of this experiment, and looks as if the records of the response of the nerves and muscles to electrical stimuli and to voluntary impulses had been superimposed.

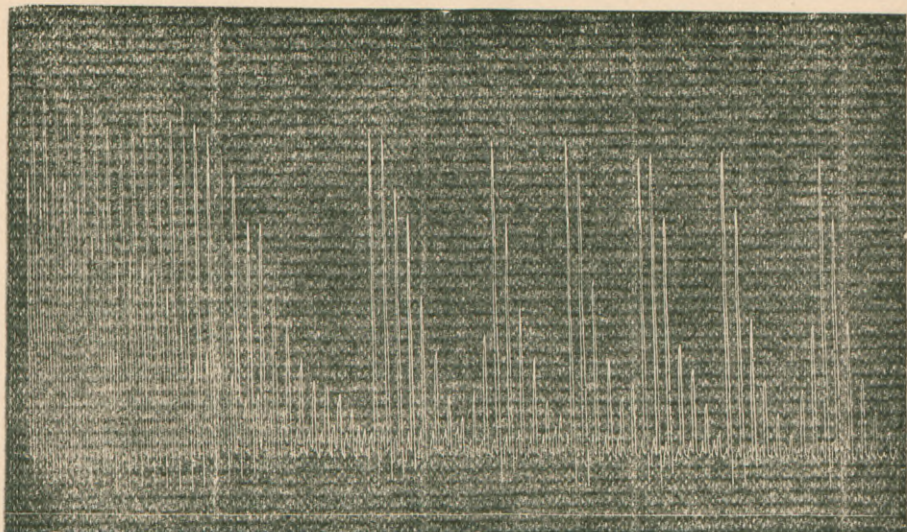


FIG. VIII.

The records of the voluntary contractions differ entirely from those written by the contractions produced by the electrical stimulation of the nerve. The voluntary contractions do not begin to decrease in size as soon, and when they commence they lessen much more rapidly. There is a moment when the response to the two forms of irritation is about the same, but the voluntary contractions soon begin to increase in height, and from this time on, the shape of the two records is as different as possible. The condition of peripheral organs, as shown by the response of the nerves and muscles to electricity, varies but slightly and irregularly, while that of the central nervous mechanisms, as shown by the extent of the voluntary contractions, undergoes marked and rhythmical alterations. The difference in the relative height of the two curves is due in part to differences in strength and effectiveness of the two forms of irritation.

These and other similar experiments convinced me that the changes producing the periodicity, do not occur in the nerves, the nerve ends, or the muscles, and that they take place in the central nervous system.

Which of the central mechanisms is the seat of these changes? The will power seemed to the subject to be unabated, and experiments showed that he was capable of contracting other muscles vigorously at the moment that he was unable to lift the weight with the finger. The result of one of these experiments is to be seen in Fig. IX, Plate I. The letter *f* marks the beginning of the voluntary contractions of the flexors of the finger, and *t* the beginning of the voluntary contraction of the extensors of the thumb. In this experiment two cords were attached to the recording apparatus; one was fastened to the second finger, the other to the thumb. The second finger was then contracted voluntarily at intervals of two seconds, each time raising a weight of 2800 grammes as high as possible. After a few minutes the periods became well developed. In one of the intervals, when the power to move the second finger was lost, the subject ceased to try to move the finger and raised the weight by voluntarily contracting the extensors of the thumb. These muscles responded well, and they were used until fatigue set in, and they in their turn demonstrated the periods. Then, at a moment when the ability to extend the thumb was lost, the work was taken up by the flexors of the finger and they were found to be capable of raising the weight nearly as high as at the beginning of the experiment.

The facts just stated prove that the loss and recovery of the ability to voluntarily contract the muscles is not dependent on changes in the strength of the will, but on alterations which take place in some of the mechanisms between the areas of the brain originating the will impulse and the centrifugal nerves. It also shows that the seat of the changes which produce the periods is different for each of the muscles, and that the change occurs in the central mechanisms which control the different muscles, independently.¹

The successive periods, though sometimes occurring with great regularity, more frequently show many variations,

¹ Last August I made a few experiments on this subject in the Physiological Laboratory of Leipzig with Dr. Max von Frey. These experiments showed still more clearly that the will power is unabated at times when voluntary contractions are markedly decreased. The results of these experiments will be reported in full hereafter.

which prevent us from attributing them solely to a rhythmical action peculiar to the central mechanisms. See statement at bottom of page 29. In another experiment the lengths of thirteen successive periods were, in seconds, viz., 24, 28, 24, 38, 26, 28, 40, 32, 24, 20, 18, 24, 32.

In still another experiment in which the muscles were voluntarily contracted every four seconds, against a weight of 2800 grammes, the following results were obtained. The first period appeared in about fourteen minutes, and during the next forty-five minutes, forty-seven periods were recorded. The number of contractions forming a period and the number of contractions which failed to raise the weight, during the intervals of decreased power, gradually increased. These changes caused by the fatigue of the central mechanisms displayed, however, many irregularities. There were many moments when it seemed as if the periodic changes had ceased. Thus the 29th and 46th periods contained respectively 48 and 33 contractions, instead of six or seven, the number found in many of the other periods. The following table will give a good idea of the eccentricities of the phenomenon. It states the number of contractions which occurred in each period, and the number of unsuccessful contractions during each interval. A contraction which failed to raise the weight half a millimetre was considered an unsuccessful contraction. As a matter of fact the muscle always contracted somewhat.

TABLE III.

Number of contractions in a period.	Number of unsuccessful contractions in the following interval.	Number of contractions in a period.	Number of unsuccessful contractions in the following interval.
206	0	1	1
12	0	7	1
12	0	1	2
13	0	6	0
20	0	17	0
18	0	48	4
15	1	7	1
11	2	2	1
16	1	6	2
19	0	12	3
7	3	5	1
11	4	6	1
12	3	1	1
15	0	6	5
4	4	7	1
13	2	8	7
11	1	7	3
11	7	6	3
12	7	6	6
9	2	7	4
6	4	6	5
12	?	7	0
?	?	33	3
7	2	7	1

Summary of Results and Conclusions.

I found that if I voluntarily contracted a muscle frequently, and each time raised a weight with my utmost force, the mechanisms involved in the action gradually wearied, the contractions weakened and after a time scarcely stirred the weight. If, however, I continued, regardless of the result, to strive with the whole power of my will to frequently contract the muscle, sooner or later my force began to return. The recovery, for a short time, might be almost complete. Soon, however, the power began to be lost for a second time and throughout the rest of the experiment intervals of almost entire loss of power to voluntarily contract the muscle were seen to alternate with periods of nearly complete recovery.

Not only are the variations in the strength of the contrac-

tion of the muscle wholly out of the control of the subject, but he does not even know, when he wills a contraction, whether the muscle will respond vigorously or not.

The phenomenon was observed in the case of the extensors as well as the flexors; on the muscles of both arms; with weights of 1, 2, 3 and 4 kilogrammes; and when the muscles were contracted at intervals of 1, 2 and 4 seconds.

The alternate loss and recovery of power which has been described is evidently the result of fatigue, because it is well marked only after the work has been continued for a considerable time, and it appears more quickly when the contractions are frequent, and the weight is large.

That the periodic loss and recovery of voluntary control over the muscle is not due to nutritive changes in the muscle itself, is shown by the fact that massage, though strengthening the muscle, does not do away with the periodicity. Moreover, they do not seem to be dependent on variations in the irritability of the nerves, the nerve ends, or the muscle, because at a moment when a voluntary contraction is almost impossible, the muscle responds well either to direct electrical stimulation, or to electrical stimulation of its nerve. Moreover, periodic variations of the force of the contractions are never seen in experiments in which the muscle or its nerve are frequently stimulated with electricity. Further, if a muscle be voluntarily contracted vigorously and frequently, until the periodic loss and recovery of force has become well marked, and then the voluntary contractions be replaced for a minute or two by contractions called out by electrical stimulation of the nerve, the periods immediately cease, although they return again as soon as voluntary contractions are resumed. Finally, it is worthy of note, that, in such an experiment, the periods are somewhat less frequent when the voluntary contractions are first resumed than they were just before the electricity was applied. In other words, that, while the nerve and muscle were working in response to the electric stimuli, the mechanism which was the seat of the changes causing the periodic variations of force had time to partially recover from its fatigue.

It seems almost certain, therefore, that the periodic loss

and recovery of power to make vigorous voluntary muscular contractions, which was seen in the experiments that have been described, was due to changes which occurred not in the peripheral mechanisms, but in the central nervous system. The periods do not, however, seem to be due to variations in the strength of the will power, because at a moment when it is impossible to make a strong voluntary contraction of one muscle, other muscles can be contracted with the usual vigor. The alterations which cause the periodicity must therefore be considered as located in some of the central nervous mechanisms, which lie between the areas of the brain which originate the will impulse, and the centrifugal nerves.

The experiments threw but little light on the nature of these changes. As has been said they are the result of fatigue, and they do not cease to occur as soon as the voluntary contractions cease, but their influence may be recognized for some minutes, at least, after the work has been stopped. The fact that the extensor of the thumb worked well when the flexors of the finger refused to obey the will, and vice versa, shows that the changes occurred independently in the mechanisms controlling each of these muscles. Though the periods were often almost rhythmical, they displayed so many variations that one cannot attribute them solely to a functional rhythm peculiar to these mechanisms. Indeed, it is probable that they were the result of a number of conflicting influences.

In addition to the marked periodic variations which have been discussed, there were observed even at the beginning of the experiment, when none of the mechanisms were fatigued, slight variations in the strength of the contractions. These were irregularly distributed, and were probably due, in part, to the inability of the subject to give his whole attention to the work and to always make the strongest possible voluntary effort. On the other hand, it may be remarked that most processes which depend on the activity of the central nervous system are subject to similar variations, and that such irregularities may well be considered as characteristic of the action of the higher nervous mechanisms.

The results here given were obtained from experiments which were made on the writer at twenty-five different times. In the few experiments which were made upon others, the periodicity was found well developed in the case of two strong and healthy young men, but failed to appear with definiteness in the case of six others. There can be but little doubt that the phenomenon is normal. Its absence in six out of the nine men examined, may be explained, in part, by the difficulties of the experiment, but was probably chiefly the result of the functionally different nervous systems of the men examined.

Other Similar Phenomena.

That fatigue should cause the strength of voluntary muscular contractions to vary periodically is less surprising when one recalls that fatigue causes a periodicity of many processes which depend on the action of the central nervous system. If one listens to the ticking of a distant watch, the sound is heard with periodically varying distinctness. If one looks long at a white sky, darkness sweeps from time to time over the field of vision. The intensity of "after-images" is subject to rhythmical variation. If one seeks to count the waves in a curve which record the vibrations of a tuning fork, he finds that, as he wearies, his ability to continue the counting varies more or less periodically. Much the same thing is true of such mental processes as adding a long column of figures, or the following of a long continued exact line of thought. There are intervals when the mind refuses to work, and these are soon followed by periods of almost unusual clearness.

Undoubtedly these phenomena would impress us more if we did not unconsciously yield to fatigue, and did not frequently rest ourselves. Even slight intervals of rest are sufficient to prevent the amount of fatigue which is necessary to reveal the phenomenon in marked degree.

In experiments made by the writer in Leipzig,¹ 1884, he found that if a constant temperature, high enough to cause

¹ Die räumliche und zeitliche Aufeinanderfolge reflectorisch contrahirter Muskeln. Du Bois-Reymond's Archiv. 1885.

Fig. II



Fig. IV

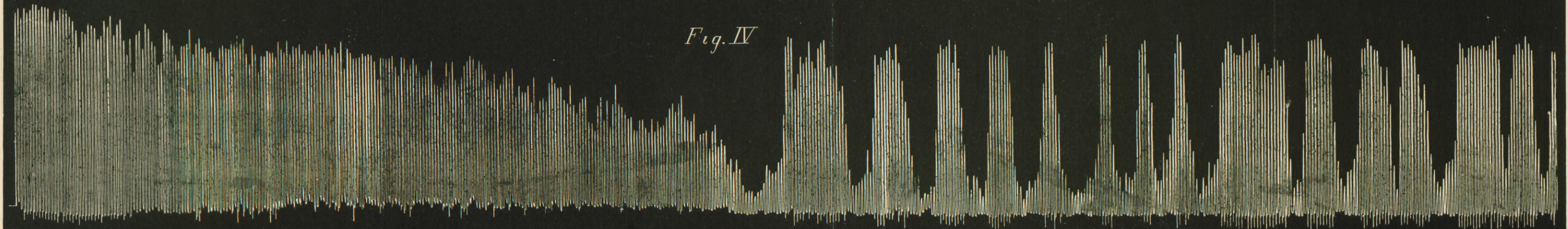
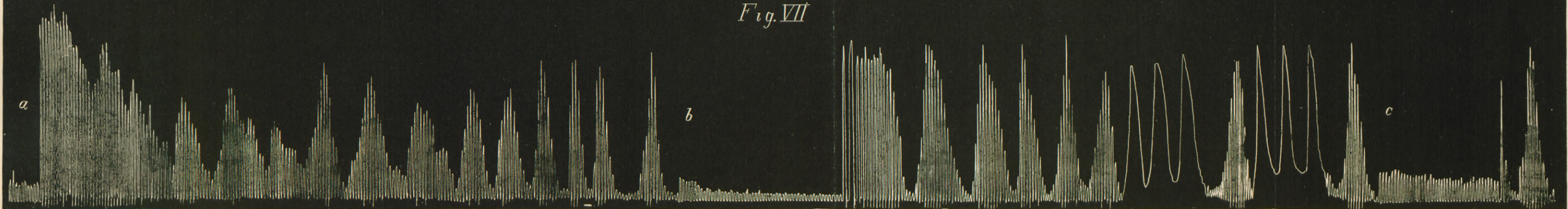


Fig. VII



f

t

Fig. IX

f

t

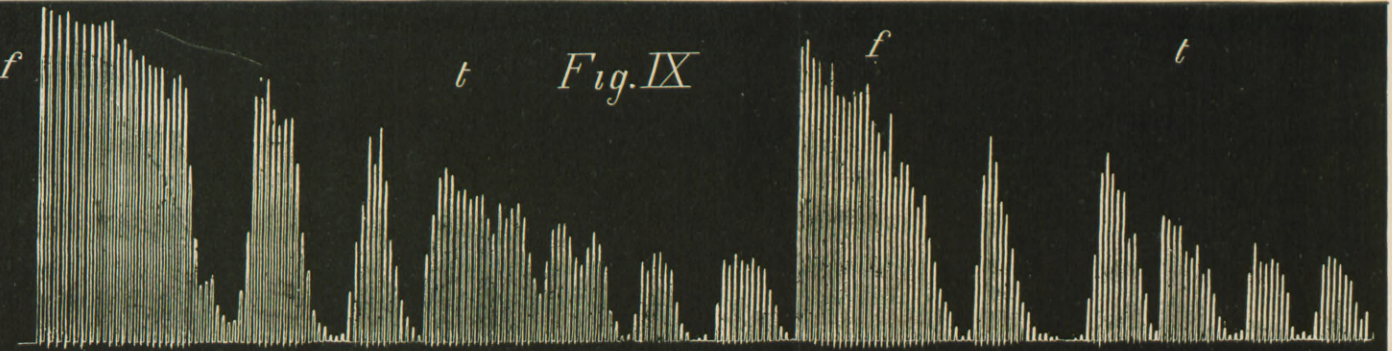
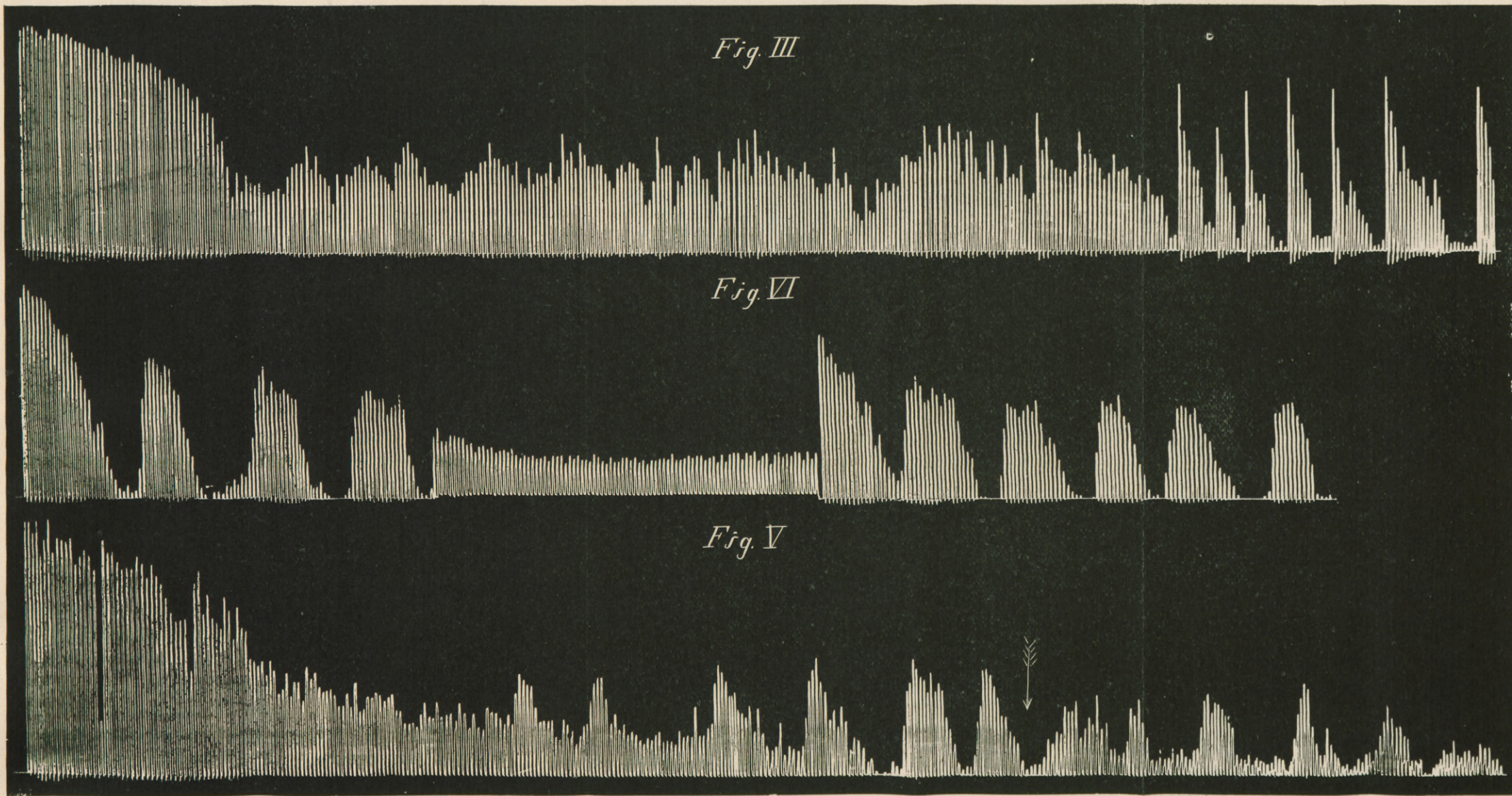


PLATE II.

Fig. III

Fig. VI

Fig. V



reflex movements, but not so high as to rapidly destroy the tissues, were continually applied to the skin of the leg of a decapitated frog, the resulting reflex action was not a continuous tetanus, but a series of tetani, which followed one another with considerable regularity. In the intervals between the tetani, the muscles entirely relaxed, and the succeeding tetani were of nearly the same height. This phenomenon seemed to be dependent upon almost rhythmical changes occurring within the spinal cord, and closely resembles the results obtained in the experiments described in this paper.

Still another process, which naturally suggests itself as perhaps of similar nature to that under discussion, is the "Chene-Stokes respiration."

It is not impossible that the gaining of the so-called "second wind," so well known to runners, may depend, in part, at least, upon conditions similar to those which caused the first recovery noticed in my experiments; further the variation in the amount of difficulty experienced in maintaining long continued violent muscular action, is probably caused by functional changes, the same as those which produced the succeeding periods which have been described.

We have as yet but few and for the most part unsatisfactory tests of the functional activity of the central nervous system. Every new method which enables us to approach this difficult question is, therefore, of great importance.

