

ON THE RHYTHM OF MUSCULAR RESPONSE TO VOLITIONAL IMPULSES IN MAN. BY E. A. SCHÄFER, F.R.S., *Jodrell Professor of Physiology, assisted by* MESSRS H. E. L. CANNEY AND J. O. TUNSTALL, *Students of University College.* Pl. VI.

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DIRECT evidence of the tetanic nature of a voluntary muscular contraction has hitherto been lacking, although its discontinuity is almost universally accepted by physiologists.

Enquiry into the evidence in favour of this opinion shows it to be very insufficient. Numerous observers have attempted to demonstrate the occurrence of discontinuity by means of the rheoscopic frog preparation but without success¹. The opinion is indeed based almost exclusively upon the sound of a semi-musical quality which is emitted by a voluntarily contracted muscle, this sound being supposed to give an indication of the number of successive twitches which are fused into the tetanic contraction.

This conclusion appeared to be supported by the fact that the sound of a muscle corresponds with that of a vibrating metallic reed or tuning-fork which is employed to interrupt a galvanic circuit stimulating the motor nerve. But Lovén has shown that the true explanation of this fact is entirely different from the one which has usually been accepted².

There are indeed many reasons against accepting the muscle-sound as evidence upon this subject. For in the first place the first sound of the heart which is certainly in the main a muscular sound is very similar to

¹ For the literature of this subject see L. Hermann, *Allgemeine Muskelphysik, Handb. d. Physiologie*, Bd. I., p. 47.

² Chr. Lovén, "Ueber den Muskelton bei elektrischer Reizung u. s. w." *Arch. f. (Anat. u.) Physiol.* 1881.

that of a muscle contracting under the influence of the will, and yet it seems clear from the results yielded by the capillary electrometer¹ (as well as by the graphic record of the contraction) that the contraction of the ventricle is a single continuous act. Moreover it has been shown that the note of a voluntarily contracting muscle is not constant but varies with the tension of the muscle².

In fact it is very doubtful whether the note which is heard (one of from 36 to 40 vibrations per second) is any measure at all of the rate of muscular response. The experiments of Helmholtz showed that the vibrations of the muscle correspond certainly to not more than half the number of vibrations of the note which is actually heard, and further that this note is really the resonance-note of the ear, and is capable of being modified by merely varying the resonance of the ear, as by performing Valsalva's experiment³.

The direct evidence which is afforded of the discontinuity of voluntary contractions by myographic tracings has hitherto been almost entirely neglected, or if referred to at all rejected as abnormal⁴ or as affording indications of too uncertain a character.

Tracings were however obtained by Lovén⁵ of strychnine-tetanus in the frog and toad (both primary and secondary) which showed undulations of 7 to 9 per second, a rate corresponding with the electrical variations which he had previously observed both in strychnine-tetanus and in voluntary movements of those animals. And he draws therefrom the conclusion that this must represent the rate of nervous impulses passing to the muscles.

But from what has been stated in the previous paper⁶ it is clear that the evidence afforded by such tracings can not only not be neglected but must from its constancy be accepted as giving a conclusive indication of the character of the muscular contraction. Nothing could show

¹ See the photographic records which were obtained by Prof. Sanderson and Mr Page, and published by them in this Journal. Vol. iv.

² Marey, *Compt. Rend.* LXII., p. 1171, 1866, and subsequently by others.

³ For a discussion of the value of the evidence yielded by the sound of a contracting muscle see L. Hermann, *loc. cit.*; Kronecker and Stirling, "Die Genesis des Tetanus," *Arch. f. (Anat. u.) Physiol.* 1878; Kronecker and Hall, *Arch. f. Anat. and Physiol.* 1879; and Lovén, *loc. cit.*

⁴ Cadiat (*Anatomie Générale*, T. 1. pp. 225—234) has obtained such tracings but seems to have failed to have got evidence of discontinuity, except in fatigue.

⁵ Lovén, "Ueber Strychnine-tetanus u. willkürliche Muskelaction." *Centralb. f. d. med. Wissen.* 1881. Compare also Kronecker and Hall, *loc. cit.*

⁶ Horsley and Schäfer, "Experiments on the character of the muscular contractions which are evoked by excitation of the motor tract." *This Journal*, p. 96.

the character of a voluntary or spontaneous contraction more distinctly than the tracing which we have reproduced in Pl. V. Fig. 2 *B*. In this it is possible to analyze the curve of a voluntary tetanus just as easily as the curve of a tetanus produced by directly exciting the motor nerve or the muscle itself by an interrupted current.

The method adopted for registering the contraction of the voluntary muscles in man in obedience to the will is similar to that employed by Mr Horsley and myself for recording the contraction of those muscles in animals in obedience both to excitation of the motor tract and to volitional impulses but of course with the omission of the excitation-apparatus. The muscle, the contraction of which it was desired to record, was allowed to come in contact with the button of a receiving tambour, and the swelling of the contracting muscle was thus allowed to compress the air within this, and to cause a corresponding ascent of the lever of the recording tambour. This method of conducting the experiments is shown in Plate VI. Fig. 1 as applied to the *opponens pollicis*, which is the muscle we have mostly employed in the investigation.

Occasionally however we have caused the part moved, instead of the muscle, to act upon the myograph, without obtaining any difference of result.

The curve of a voluntary muscular contraction obtained by this method invariably shows, both at the commencement of the contraction and during its continuance, a series of undulations which succeed one another with almost exact regularity, and can, as it would seem, only be interpreted to indicate the rhythm of the muscular response to the voluntary stimuli which provoke the contraction. A characteristic tracing of the commencement of a voluntary contraction in man, as recorded upon a rapidly moving surface, is shown in Plate VI. Fig. 2. The undulations above referred to are plainly visible and are sufficiently regular in size and succession to leave no doubt in the mind of any person who has seen a graphic record of muscular tetanic contraction produced by exciting the muscle through its nerve about 10 times in the second, that the curve here represented is that of a similar contraction. Another tracing taken on a more slowly moving surface is represented in Fig. 4 and one on a surface moving at an intermediate rate in Fig. 3.

Undulations similar in character and rate are observed during the whole extent of time that the contraction is maintained. Throughout each tracing they are tolerably regular as regards rate, although they

often exhibit irregularities of height, which are much more marked in some individuals than in others.

Occasionally the regularity is interrupted by a longer and larger wave usually covering the extent of two of the smaller undulations—an occurrence which is probably due to a more complete summation than usual of the effects of two successive nervous impulses.

Although there is a good deal of variation in the character of the tracings obtained from different individuals, and even tracings obtained from the same individual at different times and under different conditions yet the rate of succession of the waves only varies within comparatively narrow limits¹.

Almost all the persons whose voluntary muscular contractions have been investigated show a rhythm of muscular response to voluntary impulses, of about 10 per second. A few show an almost constant rhythm of about 8 or 9 per second, and in one or two cases the rate was as high as 11 or 12. The extreme variations obtained in single seconds have been from 8 to 13. A computation of the results yielded by a large number of tracings obtained from more than twenty individuals, mostly men under thirty years of age, gave the number 9.795 as the average rate per second.

The experiments upon which these numbers are based have been principally conducted by Messrs H. E. L. Canney and J. O. Tunstall. From the tracings which they obtained, twenty-eight were selected for computation, as exhibiting the muscular undulations most distinctly. In these tracings vertical lines were drawn from the time markings to the myographic record, and the number of waves in each second were counted wherever they could be clearly made out. Portions of tracings which have thus been treated are given in the accompanying figures (Figs. 5, 6 and 7 of Plate VI.). Of these the first (Fig. 5) is one in which the muscular waves are extremely accentuated² and very regular as to number, being as nearly as possible 10 per second. The second exhibits a somewhat more rapid succession of waves (about 11 or 12

¹ The undulations are in some instances far less marked than in others. This may be partly due to the mode of application of the tambour-button to the contracting muscle, but there are certainly differences due to the varying condition of the muscular and nervous systems of the subjects of experiment. Sometimes the occasional irregularities are very strongly marked, and give a zigzag appearance to the curve when traced upon a slowly moving surface, but in spite of these differences of height the regularity of succession of the undulations is generally remarkably uniform.

² This extent of muscular vibration is such as usually only accompanies severe strain (which however was absent in this case). That the vibrations of straining muscles are indications of the discontinuity of voluntary muscular action was first pointed out by Brücke. *Sitzungsb. d. Wiener Akad.* LXXV.

per second) and they are smaller and more uniform. In the third tracing on the other hand there is much more general irregularity, nevertheless the number of waves in the several seconds varies but little. It will be observed that these three tracings as well as that shown in Fig. 4, which exhibits the commencement of a contraction curve, are taken upon a much more slowly moving surface than the tracings given in Figs. 2 and 3; hence the apparently sharp character of the waves, especially those of larger extent.

The following gives the results of the computations made by Messrs Canney and Tunstall in the form of a table:—

Subject of Experiment	No. of tracing	No. of secs. counted	Maximum rate per sec.	Minimum rate per sec.	Average rate per sec.
E. A. S.	I*	9	11	8.5	9.8
	II	38	13	9	10.9
J. A. M. W.	I	48	11	9	9.8
S. H. M.	I	70	11	8	9.0
W. H. H.	I	34	13	9.5	10.8
	I	90	12	9	9.9
H. P. D.	II	43			10.5
H. R. B.	I	38	12	8	9.8
R. L. R.	I	24	12	8	9.6
	I	30	10	9	9.8
J. O. T.	II*	15	12	9	10.0
	III	23	12	9	10.9
L. W. P.	I	25	12	8	9.4
H. E. C.	I	42	10	6	8.0
	II	21			9.0
G. E. R.	I	44	13	8	10.5
	II	23	12	9	10.1
C. D.	I	44	12	8	11.0
J. E. D.	I	28	10	9	9.7
C. C. S.	I	21	10	8	8.8
W. P. M.	I	30	10	9	9.8
	II	42	13	9	10.5
E. B. H.	I	32	10	8	9.2
	II	26			9.3
H. L.	I	20	13	9	10.4
J. W. J.	I	45			9.5
C. P. T.	I	29			9.6
J. B.	I	12			8.6

These results of Messrs Canney and Tunstall have already been partly

published in the *Journal of Physiology*, Vol. VI. (*Proceedings of the Physiological Society* for March 21, 1885).

In all except two of the cases recorded in the preceding table, the tracing was obtained from the opponens pollicis muscle; in the two exceptions which are marked with an asterisk the contraction of the biceps brachii was recorded. Moreover in all the experiments of this series the work done by the muscle was minimal, and the nervous and muscular strain also minimal. Another series of experiments is now in progress, having for its object to determine the effect upon the character of the muscular response of strain and fatigue, as well as the action of drugs and other conditions influencing the nervous and muscular systems.

General conclusions. The following conclusions may be drawn from the results of the experiments here given, taken in connexion both with those recorded in the preceding paper and with well-known pathological rhythmic phenomena.

1. A prolonged voluntary contraction in man is an incomplete tetanus produced by from 8 to 13¹ successive nervous impulses per second. About 10 per second may be taken as the average.

2. The average rate of muscular response to volitional impulses is approximately the same in man as in other mammals that have been examined.

3. The average rate of muscular response to volitional impulses in man is approximately the same as the average rate of muscular response to rapidly recurring excitation of the nerve-centres in animals.

4. The average rate of muscular response to volitional stimuli in man is approximately the same as that obtained both in man and animals as the result of pathological or other excitation of the cortex cerebri producing epilepsy, although in the latter case the impulses tend to undergo summation and thus to cause the appearance of clonic contractions of slower rhythm.

5. The rate of muscular response to volitional stimuli in man is nearly the same as the rate of muscular response which is due to activity of the spinal cord alone.

¹ Possibly more in some instances.

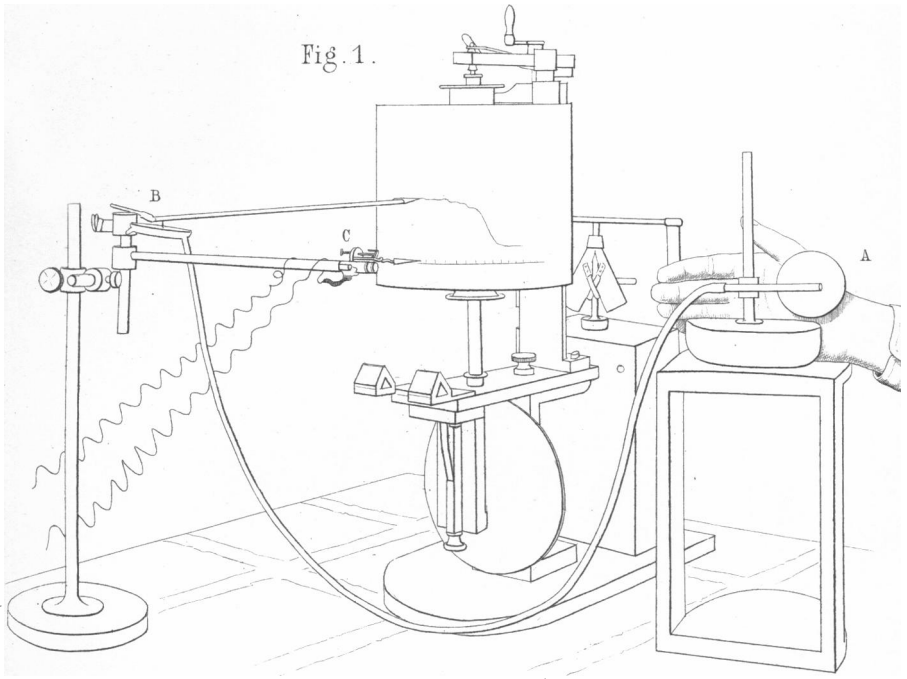


Fig. 4.

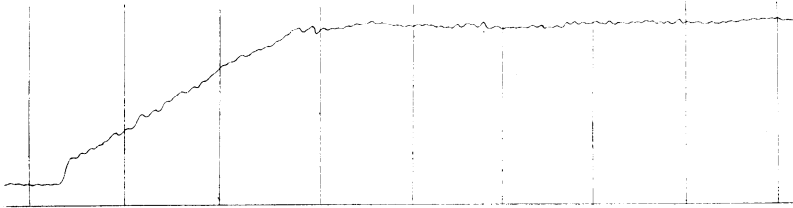


Fig. 5.

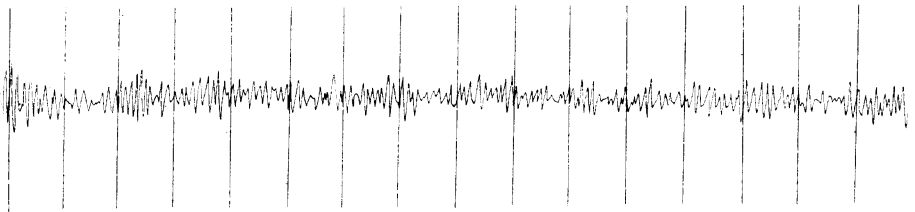
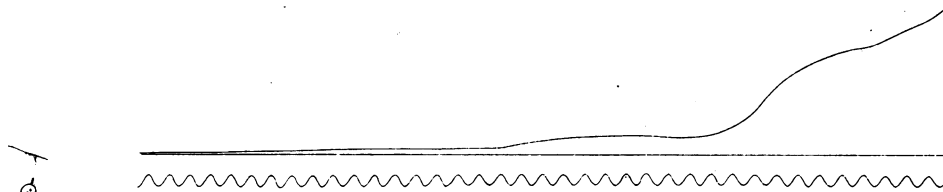


Fig. 2.



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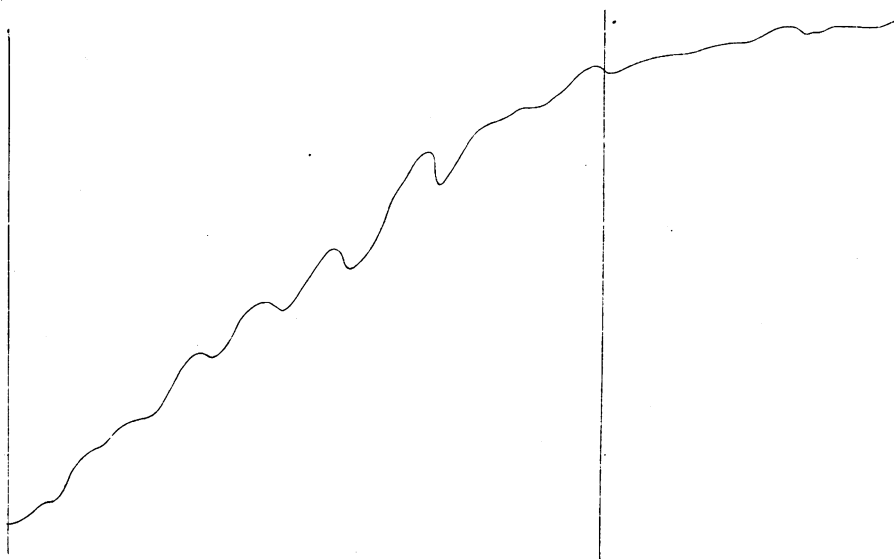
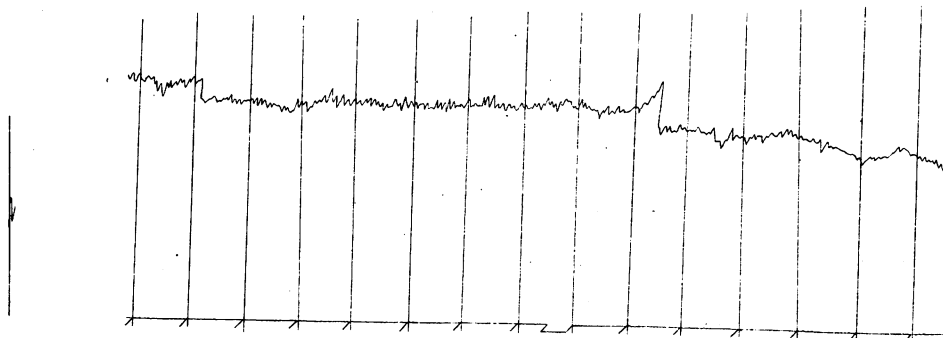


Fig. 6.



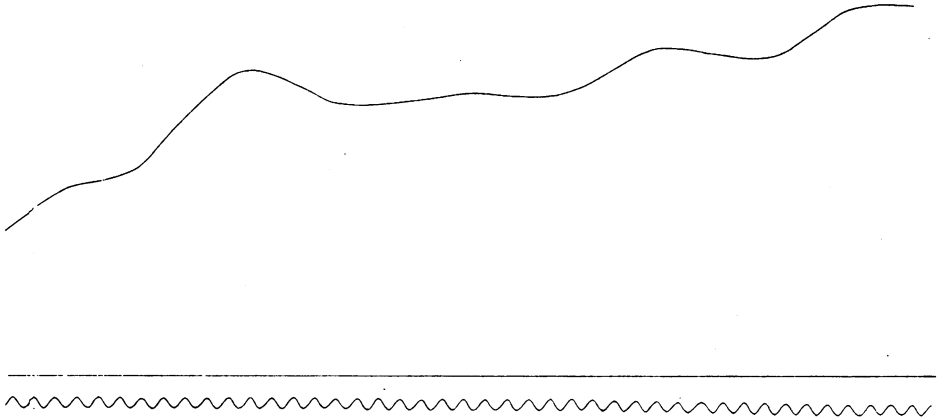


Fig. 3.

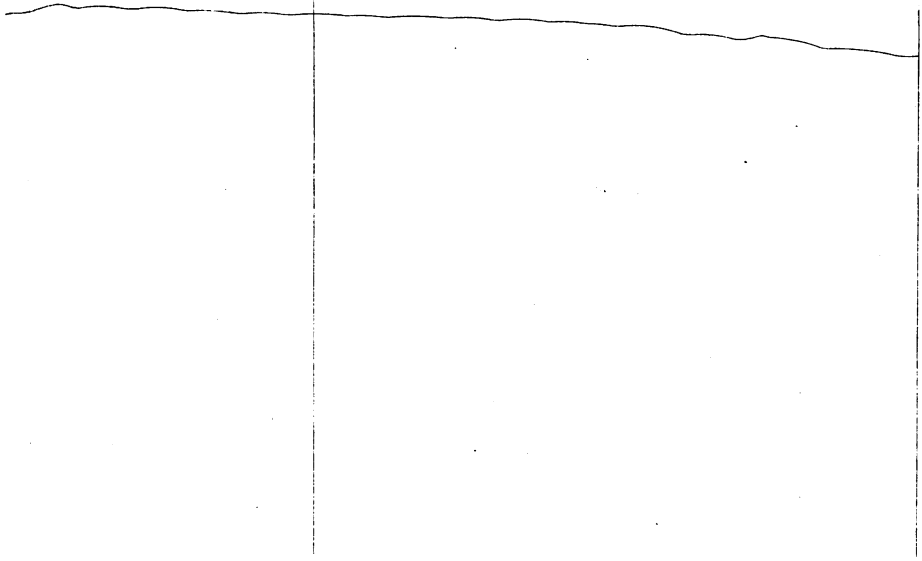
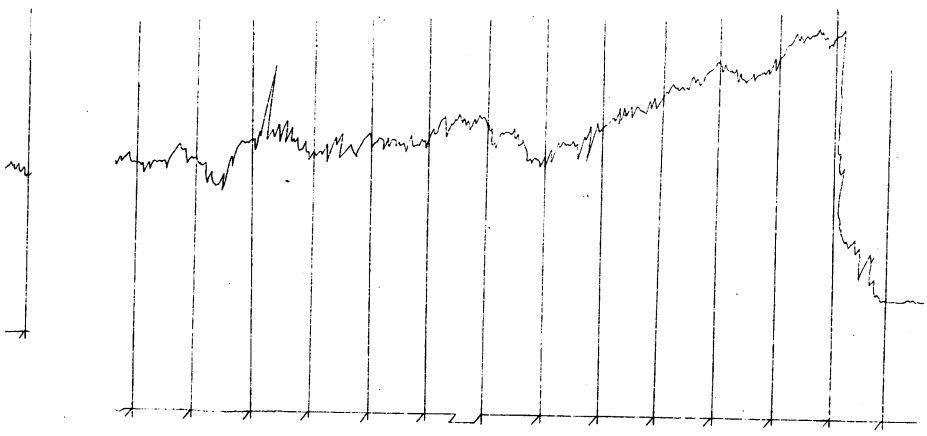


Fig. 7.



DESCRIPTION OF FIGURES. PLATE VI.

Fig. 1. Apparatus employed to record the contractions of the voluntary muscles in man (from a photograph).

A. Receiving tambour, the button of which is applied to the opponens pollicis.

B. Registering tambour, the lever of which is writing upon the cylinder.

C. Chronograph marking seconds.

Fig. 2. Tracing of the commencement of a voluntary contraction (opposition of thumb). Rapid movement of cylinder. Time in $\frac{1}{100}$ ths of a second, marked by a tuning-fork. (This tracing was obtained by connecting the thumb directly by a thread with a myographic lever, an elastic band being substituted for the usual weight.)

Fig. 3. Tracing of the commencement of a voluntary contraction (opponens pollicis) taken on a surface moving at about one-third the rate of that upon which the tracing shown in Fig. 2 was recorded. The time occupied by this tracing was marked below it in seconds and the record has been transferred to the tracing by drawing vertical lines from the time-marking; altogether three seconds are reproduced.

Fig. 4. Tracing of the commencement of a voluntary contraction (opponens pollicis) taken on a relatively slowly moving surface. Time in seconds.

Fig. 5. Tracing taken during the continuance of a prolonged voluntary contraction (opponens pollicis). The undulatory character of the contraction is accentuated in this tracing.

Fig. 6. Tracing taken during the continuance of a prolonged voluntary contraction of the opponens pollicis. The undulations are small but well marked, and are somewhat more frequent than in the other tracings here recorded.

Fig. 7. Tracing taken during the continuance of a prolonged voluntary contraction of the opponens pollicis. The curve exhibits an unusual amount of irregularity but the average frequency of the undulations is very constant.