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THE ANALYSIS OF THE INITIAL HEAT PRODUCTION OF MUSCLE.

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IN the earliest experiments on this subject [Hartree and Hill, 1920*a*], using thermopiles not specially made for the purpose and a comparatively slowly acting galvanometer, it was found to be possible, but only just possible, to secure an analysis of the initial heat: the examples given then, and in another paper on the subject [Hartree, 1924], were necessarily rough, and the results rather indefinite, even when using an interval for the steps in the analysis as long as 0·2 or 0·25 sec. Later, however, quicker thermopiles consisting of a single layer of thin wire were made, and the galvanometer was improved, the resulting analyses being much more definite. An example was published [Hartree, 1925], unfortunately without numerical details; these, however, have been supplied since [Hill, 1930*a*: Appendix by Hartree]. In various other investigations [*e.g.* Hartree and Hill, 1928] the improved methods have been employed. The indefiniteness of the earliest results has recently been criticized by Amberson [1930], and the suggestion made that the relaxation heat might indeed not exist at all. It was necessary, therefore, to examine the matter in detail again, particularly as regards the relaxation heat.

As a preliminary the thermopiles were further improved. Only those of the 1925 type were used. The "hot" junctions of the old thermopiles were thinned, and the shellac insulation reduced in thickness as far as possible: also a further thermopile was made having 64 pairs of constantan-iron junctions and thinner wire (No. 38 S.W.G., 0·152 mm. diameter), which has given the best results: its resistance was 13·8 ohms and that of the galvanometer 12·5 ohms: it developed half its maximum current, in response to instantaneous warming of the muscle on it, in 0·05 sec. (see below).

In recent years the astatic moving magnet galvanometer has been greatly improved by Mr A. C. Downing. One of his instruments was installed, with special arrangements for critical damping at comparatively low sensitivity. This was of such excellence that the drum on which photographic records were taken could be placed more than 2 metres from the galvanometer (which was entirely unshielded magnetically) without any tremor of the spot of light being visible, even on records read to 0·1 mm. This alone nearly doubled the effective sensitivity, which was already considerably higher than that of the preceding instrument; consequently, with the sensitivity required, the galvanometer could be adjusted to a much shorter period, thereby improving the accuracy of the analysis.

A third improvement, employed on some occasions, consisted in using practically instantaneous heating for the "control" curves. This requires a strong induction shock to be passed through the dead muscle and, with the thin insulation on the face of the thermopile, this could not always be done without sometimes producing unsteady starts on the control curves (due to leak of the heating current into the galvanometer), which make these curves useless. In every case where an "instantaneous control" was employed, curves were taken by passing the shock through the muscle first in one direction, then in the other—the exact agreement of these at the start affords a perfect test for sufficient insulation. Such instantaneous controls rise at the start considerably more quickly than those even for quite a short time of heating (*e.g.* 0·05 sec., which was usually employed), with the result that, using the former, the choice of heats to suit each step in the analysis is more limited, and the whole process consequently more definite.

Examples are given below in Tables I and II (pp. 4, 22) in which both kinds of control were taken in the same experiment.

The results obtained by using such a control curve must evidently be plotted as *points*, corresponding to the estimated heat liberated at the various *instants* used in the analysis, and *not* as short horizontal lines showing "*blocks*" of heat liberated *during the intervals*; the latter method perhaps best shows the results when the time of heating for the control curve is the same as the interval adopted for the analysis, though in this case it might be equally good to show the heats by points plotted at the centre of each interval.

In the intermediate case, frequently employed, the time of heating for the control curve is 0·05 sec., and the interval for the analysis is 0·1 sec.; then the results will be the estimates of the heats produced from 0 to 0·05 sec., from 0·1 to 0·15, from 0·2 to 0·25 sec., etc., and are best plotted as *points* at the centres of these intervals. Theoretically, with perfect records and controls, the smaller the intervals used in the analysis the better will be the estimate of an observed heat production: practically, however, there is a limit to the smallness of the interval, imposed by the definiteness of the result, and this depends on the rapidity of action of the recording instruments (see Appendix IV, p. 25).

If the interval be halved it will take about four times as long to carry out an analysis (which is already sufficiently laborious), and if the effect of halving the interval is to make the results of the analysis indefinite (or "oscillatory" as often happens[1]) the time taken will be wholly wasted, as the result obtained by using the longer interval will give actually a better idea of the course of the heat production being investigated.

With the apparatus as recently improved, very fairly definite results are found by using an interval of 0·1 sec. Further, it is well to use intervals of 0·05 sec. for the first two steps, during which the heat production is large and the rate varying quickly. This will always give a better idea of the early heat production than can be obtained by using 0·1 sec. intervals from the start; the latter method, moreover, is usually accompanied by an unavoidable negative remainder at 0·1 sec., showing that intervals of 0·1 sec. from the start cannot give a good representation of the actual heat production. This constitutes one of the underlying difficulties, since the initial outburst of heat (after a twitch) is so rapid that in exceptional cases it seems to be completely over in less than 0·1 sec., and in all cases the heat rate varies very rapidly during the first 0·2 sec. If the first step in the analysis is doubtful, or to some extent wrong, it may well affect the next one or two steps in a lesser degree. Preference, therefore, is given to the starts with 0·05 sec. interval for the analysis, but it is found that it is of no use to continue with such a short interval, as in this case the solution becomes indefinite. Further, it is obvious that even the use of an interval of 0·05 sec. cannot possibly determine the true shape of a curve which starts at 0, rises to a high maximum between 0·05 and 0·10 sec. and falls to a small value soon after 0·10 sec., as is usually the case. Any curve, in the subsequent diagrams, which is drawn above the first 0·2 sec. must be taken as giving only a rough idea of the rate of heat production during that time, and it must not be taken to represent the true heat rate at every instant during that time; to do this would require much more rapid recording than could be obtained by present methods.

Although the actual shape of the first part of the heat curve is indeterminate, the analysed results do give some information about the nature of the initial breakdown. Taking four cases of a single twitch, in which there was not a sudden dip in the heat curve just after the initial breakdown (which may be due to an error as explained later), the average results, using controls with instantaneous heating, were, heat at 0 sec., 0·05; heat at 0·05 sec., 0·19; heat at 0·10 sec., 0·13; from which it is clear that the initial breakdown produces heat which starts at a low rate and reaches its maximum rate at about 0·06 sec. Four similar cases of

[1] *I.e.* too large an estimate at one step being necessarily followed by too small an amount at the next, in order to keep small the remainders arising in the course of the analysis.

TABLE I. Numerical details for

Sec.	0		0·1		0·2		0·3		0·4		0·5		0·6	
Twitch: Fig. 1	0		10½		96		249		398		516		611	
0·05 sec. control	0	5	48	143	273	408	536	646	736	806	858	897	926	948
Heat	·19	·26	·145		·04		·045		·06		·135		·09	
Instantaneous control	0	19	92	217	353	485	603	702	781	842	888	921	944	961
Heat	·06	·23	·27		·065		·045		·04		·125		·105	
Twitch: Fig. 7	0	.	10½		88½		238		401		534		640	
Heat (by instantaneous control)	·08	·16	·28		·15		·05		·01		·195		·04	
Twitch: Fig. 2	0	.	8		88		262		436		563		646	
Instantaneous control	0	17	86	199	333	466	588	693	777	843	892	928	953	971
Heat	·075	·095	·515		·025		0		·015		·025		0	
Twitch: Fig. 5	0	.	9		85		210		336		451		559	
Heat	·06	·26	·15		·04		·09		·10		·11		·105	
Twitch: Fig. 6	0	.	8		77		194		315		427		525	
Heat	·045	·25	·14		·045		·11		·055		·09		·13	
Twitch: Fig. 3	0	.	9½		122		322		503		631		711	
Instantaneous control	0	17	86	195	324	453	569	670	751	815	865	903	930	951
Heat	·02	·45	·33		0		0		0		·015		·125	
Twitch: Fig. 4	0	.	4		46½		142½		266		395		521	
Instantaneous control	0	5	37	104	196	301	408	512	606	688	758	815	861	897
Heat	·09	·20	·21		·11		·065		·125		·11		·085	
Stimulus 0·2 sec.: Fig. 8	0	.	8		73		212		373		501		586	
0·05 sec. control	0	6	59	176	329	484	619	732	817	879	921	949	967	979
Heat	·11	·14	·20		·17		·02		·03		·025		·005	
or	·165	.	·305		·15		·015		·04		·02		·005	
or, using 0·1 sec. control	.	·255		·27		·10	.	·025	.	·025	.	·025	.	0

0·1 sec. tetanus, using controls of 0·05 sec. heating, gave average results: heat 0 to 0·05 sec., 0·15; heat 0·05 to 0·10 sec., 0·19; heat 0·10 to 0·15 sec., 0·06; thus, as before, the maximum rate is about 4 $\times$ (initial heat) per sec.

It may be mentioned that, when starting with two steps of 0·05 sec. and continuing with steps of 0·1 sec., it is not necessary to measure up the "live" curves by 0·05 sec. at all, but the control curves must be determined at each 0·05 sec. for the length of time covering the whole analysis, as given in Tables I and II.

Further points about the analysis will be considered in the Appendices.

It is of interest to compare the control curves obtained under different conditions. The maximum deflection is taken to be 1000, one unit representing about 0·1 mm. on the record. In the second case referred to [Hartree, 1924] the deflection at 0·5 sec. was 44, and in the first case [Hartree and Hill, 1920*a*] it was considerably less. For the 1925 thermopiles and galvanometer the deflection at 0·5 sec. was 486, and for those

Figs. 1 to 8 in the text.

0·7		0·8		0·9		1·0		1·1		1·2		1·3		1·4		1·5
705		797		874		926		959		979		989		996		999
964	975	983	989	993	996	998	999	1000	1000	1000	1000	999	998	997	996	994
·025		·005		0		·01		·005				.		.		.
974	983	988	993	996	998	999	1000	1000	1000	999	998	997	996	994	993	991
·045		·005		·005		0		·01		.		.		.		.
746		836		901		945		971		987		995		999		1000
·015		·015		·005		·005		.		.		.		.		.
697		736		791		856		913		956		982		995		1000
983	991	996	999	1000	1000	999	997	995	992	989	986	983	980	977	974	970
·13		·09		·035		·01		·005		·005		.		.		.
665		764		847		909		951		978		992		998		1000
·04		·03		·02		·005		·005		.		.		.		.
619		717		807		881		935		968		988		997		1000
·065		·065		·005		·005		·01		.		.		.		.
770		829		889		934		967		985		995		999		1000
965	975	983	989	993	996	998	999	1000	1000	1000	999	998	997	995	994	992
·045		·015		·007		.		.		.		.		.		.
642		752		840		906		948		976		989		997		1000
926	948	965	977	985	990	994	997	999	1000	1000	999	998	997	995	993	991
·005		·005														
640		671		698		756		843		917		969		994		1000
988	994	997	999	1000	1000	1000	999	999	998	996	994	991	989	986	984	981
·005		·15		·14		·015		·01		·005		.		.		.
0		·16		·135		·015		·01		·005		.		.		.
.	·015		·195		·095		·01		·01		.		.		.	

used in recent experiments it was from 800 to 900. Of course the time of heating used in each case will affect the result, but the above is a fair comparison for a short time of heating, about 0·1 sec.

Since the accuracy of the analysis depends to a large extent on the quickness of rise of the control curves quite soon after the start, it might be further mentioned that with recent recording and instantaneous heating the deflection at 0·05 sec. is more than twice as great as that at 0·25 sec. in the 1924 case referred to above; consequently, an analysis in the latter case, carried out with an interval of 0·25 sec., is not so definite as a recent one carried out with an interval of 0·05 sec., and cannot be compared, as regards definiteness of result, with a recent analysis carried out with an interval of 0·1 sec., as is usual.

Let us consider some actual results, all at 0° C. on *Rana temporaria*. In most of the experiments only single twitches were taken, as this is the more fundamental case. Here the total heat is comparatively small, so

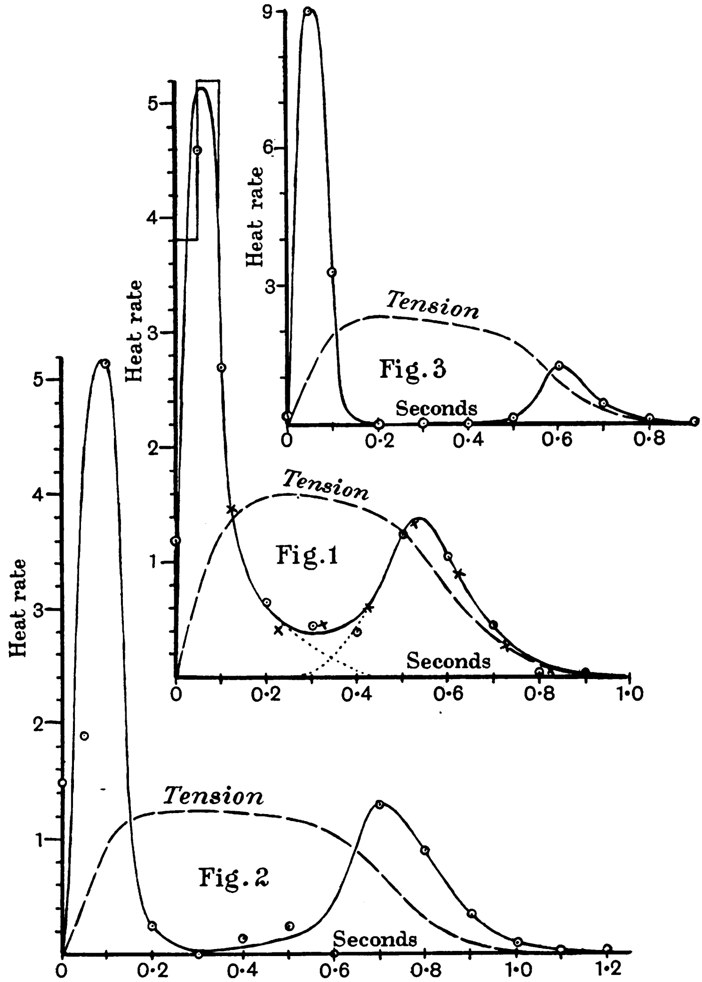

Fig. 1. Single twitch at 0° C. (5. iv. 30, sheet 3). "Normal" case. Relaxation heat fairly distinct. The dotted line starting at 0·25 sec., when the tension starts to fall, suggests the correct start for the heat due to mechanical relaxation.

⊙ Analysis by instantaneous control starting with two intervals of 0·05 sec.

× Analysis by 0·05 sec. control, starting with two intervals of 0·05 sec. shown as "blocks."

Fig. 2. Single twitch at 0° C. (19. iii. 30, sheet 8). "Exceptional" case. Relaxation heat quite distinct. See the text.

Fig. 3. Single twitch at 0° C. (26. iii. 30, sheet 5). "Exceptional" case. See the text.

the galvanometer had to be made more sensitive, to obtain a full-sized deflection, than when a tetanus was used. This slows down the action of the galvanometer somewhat, but not enough to spoil the recording.

Fig. 1 shows the result of the analysis for one sheet of photographs (5) taken for single twitches on 5. iv. 30. As, however, there were several other experiments giving very closely similar results, it may perhaps be taken as the normal case. If it be supposed that relaxation heat starts when the tension begins to fall, it seems reasonable to suppose that the heat curve near its minimum is made up of two parts as shown by the dotted lines; the part showing the relaxation heat starts from a horizontal tangent at the point at which the tension begins to fall; the second dotted line shows the end of the first part of the diagram. On this supposition the relaxation heat (always reckoning it as a fraction of the total initial heat) is 33 p.c. In several other cases in which the heat diagram is very similar, and making the same supposition, the relaxation heats are from 31 to 33 p.c. The numerical data for this and subsequent cases will be found in Table I.

Fig. 2 shows an exceptional case after the muscle had been stimulated many times and the tension had fallen considerably. The relaxation heat appears to be distinct, rising slowly when the tension is falling slowly, having its maximum rate when the tension is falling fastest and reaching zero at the same time as the tension. It will be seen from the shape of the tension diagram that the muscle was not in a normal condition; the case will be further considered later. Here the relaxation heat was about 28 p.c. In two other experiments in which the circumstances were similar there was an even more distinct break between the two parts of the heat curve. Fig. 3 shows one of these and in this case the relaxation heat was about 20 p.c.

If all the analyses gave results similar to those shown in Figs. 1, 2, 3, 7, 8 and 9, there would be little further to be said, but it is now necessary to mention other cases in which the results look very different from those referred to.

Fig. 4 shows a case in which the relaxation heat looks much more than usual and the maximum height of the latter part of the curve is earlier than usual. If the true relaxation heat is better shown by the broken line, the difference may be due to some other cause, or to a technical error; for further consideration of this, see later. In this experiment the face of the thermopile had been covered with a thin layer of paraffin wax, subsequently planed down so that there was no trace of the "ribbing" referred to below. The rate of rise of the control curve was very much

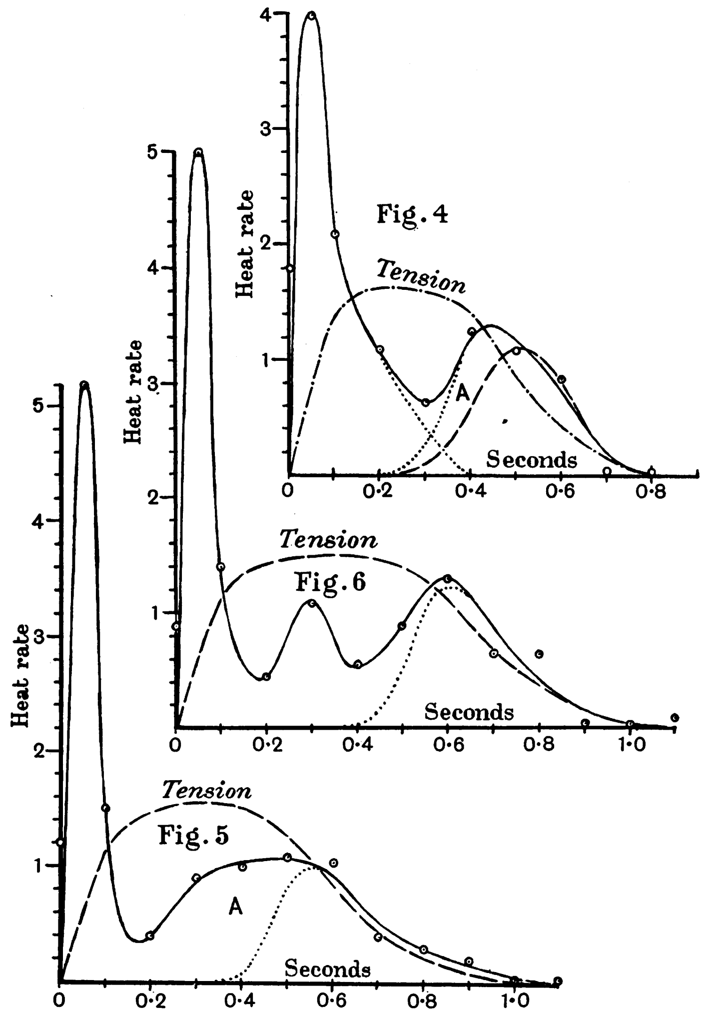

Fig. 4. Single twitch at 0° C. (29. i. 31, sheet 3). Somewhat similar to Fig. 1, but if dotted lines are drawn as in Fig. 1, the relaxation heat appears much larger than usual, and its maximum rate is earlier than usual when compared with the tension curve. It is suggested that the true relaxation is much better represented by the broken line, and the intermediate heat A is due to some other cause. See the text.

Fig. 5. Single twitch at 0° C. (19. iii. 30, sheet 1). A fairly "smooth" result but apparently showing a large amount of heat A which cannot be relaxation heat, as this must start somewhat like the dotted line, when the tension starts to fall. See the text.

Fig. 6. Single twitch at 0° C. (19. iii. 30, sheet 3). Another case apparently showing distinct heat between the initial outburst and the relaxation heat which must start somewhat like the dotted line. There were five "live" records in good agreement and the "hump" cannot possibly be avoided by the analysis.

reduced, as shown by the numbers in Table I, so the analysis was not so definite as usual.

Fig. 5 shows a case in which there is apparently an even greater amount of heat which cannot be considered as relaxation heat, as a large part of it occurs before the tension falls appreciably, and in Fig. 6 there is apparently again some heat between the initial outburst and relaxation, but so much earlier than in the above cases that it forms a distinct "hump" on the curve of heat rate.

None of the above cases is unique, and it may be said at once that when a hump, as in Fig. 6, occurs, it cannot be smoothed out in the course of the analysis without leaving quite large remainders, as may be verified from the numbers given for this case in Table I.

It should be remarked that the analyses have *always* been carried out so as to give the smallest possible remainders, leaving any smoothing for the plotted results. Further, when using instantaneous controls (except in the case of Fig. 4), it is usually impossible to alter any of the points, except those near the start, by as much as 0·1 on the scale of heat rate from the position given without making appreciably larger remainders. The vertical scale, labelled heat rate, is, in each case, very nearly the initial heat per second. The analyses are always carried out with both "live" and "control" curves reduced to the same maximum 1000. Thus the unit of heat is that heat which gives a control maximum of 1000 and the total initial heat can only be expressed in that unit after completing the analysis and adding up the heats found at the various times. For a single twitch with a fast thermopile the initial heat is usually not more than about 1·01 units, but for a longer stimulus the initial heat will be considerably greater, when expressed in such units.

It is now necessary to offer some explanation for the very different shapes of the curves of heat rate. The same type did not persist throughout any one experiment when several sheets of photographs were taken (Figs. 5, 6 and 2 in this order, but with several intermediate stimuli, refer to the same experiment), and it can merely be noticed that a type like Fig. 5 only occurred in early records, and a type like Figs. 2 and 3 only in very late records, in which the muscle was in a peculiar state (see later).

There are two alternatives for the occurrence of heat between the initial outburst and the relaxation heat. It may be due to a real heat production which, in these cases, is later than usual, or it may be due to some technical error in the recording. A real heat production between the initial outburst and relaxation may be due to three causes: (*a*) a secondary chemical reaction following the primary breakdown caused by the stimulus; (*b*) a thermo-elastic effect [Hartree and Hill, 1920*b*] which would produce equal amounts of heat but of opposite sign when the tension is rising and falling; the latter part would probably be inseparable from the relaxation heat, but the former should not be overlooked as it may affect the form of the heat curve when the tension is rising; (*c*) friction, the effect of which is probably negligible, as the contractions were nearly isometric. The thermo-elastic effect cannot account for heat when the tension is nearly constant, so (*a*) appears to give the only possible explanation if the heat production be real.

The principal technical difficulties seem to be: (1) non-uniformity of heat production through the muscle substance during contraction. Suppose for example that the inside of the muscle (next to the face of the thermopile) is more active, and so rises to a higher temperature than the outside; the effect on the thermopile (compared with the case in which the same heat is produced uniformly, as may be assumed for the controls) is that the junctions first rise in temperature too fast and soon afterwards, depending on the thickness of the muscle, too slowly, with corresponding effects on the apparent heat production. Such effects would be greater in general with thicker muscles, but no correspondence of the kind has been observed between the thickness of the muscle and the apparent heat now being considered. Very probable causes of such non-uniformity would be (*a*) any damage done to parts of the muscle during dissection, (*b*) insufficient stimulation of some parts of the muscle.

(2) Change of position of the muscle on the thermopile, or change in the degree of contact, as the tension alters. Even when the contraction is, on the whole, strictly isometric, it can be observed that there is some motion of the muscle on stimulation. Probably the pelvic end, having a greater cross-section than the other, extends the latter somewhat as the tension rises, and there may also be a small change in the shape of the cross-section. The more likely source of trouble, however, is the effect of the degree of contact. By this is meant that when the muscle tightens the thermal conductivity between it and the thermopile may be different from that when taking the controls. Any depressions on the face of the thermopile would tend to be bridged over by the muscle as its tension rises, and even if the face were perfectly flat there would be a tendency for the muscle as it tightens to squeeze out some of the moisture between itself and the face of the thermopile. With a very thin thermopile the muscles must be carefully mounted so that both have good contact.

The thermopiles used in these experiments were all of the type with soldered hot junctions; all irregularities due to the soldering were removed, before mounting on the frame, by filing and rubbing down, but the general result of using as little shellac as possible was to leave the face of the thermopile very slightly ribbed, which may have accentuated the possible troubles here considered. It is doubtful, however, whether any serious error is due to this effect, and a few experiments (Fig. 4, and other cases), using thermopiles with faces made as plane as possible with paraffin wax, show similar irregularities.

If the thermal conductivity between the muscle and the thermopile were diminished as the muscle tightened, a delay would result in the time at which the heat was recorded by the thermopile when the tension was large, and the delay would disappear when the tension fell. This delay, coupled with some negative thermo-elastic effect, may well account for the sudden dip in the heat curve frequently observed soon after the initial breakdown (see Figs. 5 and 6), this dip being occasionally apparent even during the time of stimulating, when the muscle was given a tetanus of 0·2 or 0·3 sec.

A case similar to Fig. 6 has been considered [Hartree, 1925, p. 273], the numerical solution being given later [Hill, 1930 *a*, Appendix by Hartree]; the solution shows a distinct hump at 0·3 sec., but unfortunately in the original paper this hump was smoothed off into the later rise and called part of the relaxation heat, making this much too large and having too early a maximum. Seeing that the paper referred to was principally concerned with the *difference* between two relaxation heats, possibly not much harm was done as they were treated in the same way; but the figure given is misleading and it is now realized that the true relaxation heat should be shown by a curve starting from the base line with a horizontal tangent at about 0·3 sec. (when the tension began to fall). The hump then left is either due to some technical error (such as a delay in heat recording), or to a separate real heat production (such as a secondary chemical action). The varying occurrence of these humps seems to suggest that they are more probably due to technical error than to a real heat production, but seeing that in different states of the muscle such heat might well occur at different times the point cannot be definitely decided.

A word further might be said about the thermo-elastic heat, as the writer is of opinion that this is apparent, being negative when the tension rises and positive when it falls. In one or two cases, in which the "delay," referred to above, seems to have been rather large, the analysis requires a small negative heat soon after the initial outburst; it does not seem possible that this can be produced by a delay effect, so it may be due to the superposition of a negative thermo-elastic effect.

Further, examination of a large number of records shows that in the majority there is a small rise in the heat curve, fairly soon after the tension has begun to fall, which does not appear to be part of the much larger and faster rise towards the maximum rate of relaxation heat. If it may be supposed that the thermo-elastic heat mostly occurs fairly soon after the tension has begun to fall, this may show a positive thermo-elastic heat of 5 to 10 p.c. of the total initial heat; but if, on the other hand, the thermo-elastic heat occurs during the whole time of relaxation it will obviously be impossible to separate it from the relaxation heat, and the small rise in the heat curve may after all be due to a quick improvement in the thermal conductivity as the tension falls.

In some cases, especially when relaxation was rather fast, this possible small rise merged into the relaxation heat, as in the case given in Appendix II, making the relaxation heat 35 or 36 p.c. in this and similar cases, instead of about 29 to 30 p.c., which is the mean value for several experiments in which the small rise appeared distinct and was not included.

Comparatively few experiments were made with a tetanus longer than 0·1 sec., but Fig. 8 shows a case of some interest. The tetanus was here 0·2 sec. and it happened that the tension remained nearly constant for an unusually long time after the stimulus. While the tension was constant (the muscle not being stimulated) there was very small heat production and consequently the galvanometer had nearly reached a steady level before relaxation started. Since the relaxation heat is here of considerable size and of somewhat short duration it makes a very striking rise in the galvanometer deflection, as shown in the figure.

This is also a clear case in which the heat occurring during relaxation is closely connected with the fall of tension, *i.e.* with the degradation of mechanical potential energy. As this heat started soon after the tension began to fall, ended when the tension had fallen to its original value, and had its maximum rate at about the time the tension was falling fastest, it seems impossible to suppose that this heat (or most of it) can be due to any other cause apart from some possible thermo-elastic heat. The small intermediate hump at 0·4 sec., about 7 p.c. of the whole, may be a real heat production or the result of a technical error, as discussed elsewhere: fortunately in this case it seems to have died out before the relaxation heat had started so that the latter is probably fairly accurately represented. It amounts to 0·32 out of a total 1·03, *i.e.* 31 p.c. of the total initial heat.

Several experiments, possibly abnormal as they were done in the breeding season (March and April), showed a curious result. When single twitches were given (one every 3 or 4 minutes, and sometimes an interval of an hour or so in the middle of the series), for a time extending over several hours, *the heat remained very nearly constant but the maximum tension fell very much.* The tension diagram was usually rather flat when this happened, and since there is little heat production while the tension is nearly constant the relaxation heat had a very marked effect on the

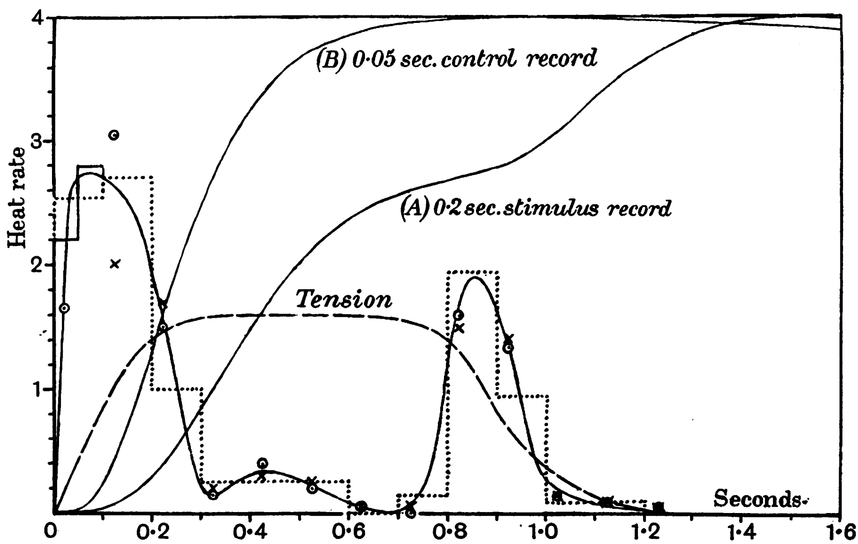

Fig. 8. Tetanus 0·2 sec. at 0° C. (25. ii. 30, sheet 5) *A* and *B* stimulus and control records.
× Analysis by 0·05 sec. control starting with two intervals of 0·05 sec.
⊙ Analysis by 0·05 sec. control using only 0·1 sec. intervals.
Dotted line, analysis by 0·1 sec. control, result shown by "blocks" only.
Full line, probable course of heat production.

shape of the galvanometer deflection curve, which was similar to that of Fig. 8. Fig. 2 shows one of these cases 7 hours after the start; here heat $H = 100$ and maximum tension $T = 25$, and originally $H = 102$, $T = 78$; the relaxation heat for the case shown was about 28 p.c., while in the early records it had been about 30 p.c. (not very distinct), so it is obvious that the actual magnitude of the relaxation heat (and of the total initial heat) had, in these cases, very little connection with the maximum tension.

Another case is shown in Fig. 3, when, after considerable exercise, the heat was the same as at first, but the maximum tension was only 28 p.c.

of the original maximum tension. The relaxation heat is here only about 20 p.c.

In the most extreme case, where the curious change of state came on much more quickly than in the above cases, the final maximum tension was about one-fifth of the original, while the total initial heat was still 89 p.c. of the original initial heat. The only possible explanation seems to be that a large part of the potential energy of the stimulated muscle (which energy is degraded into heat in relaxation) exists in the form of internal stresses which did not contribute to the longitudinal tension of the muscle as a whole; this is further borne out by the fact that in these cases the heat curve (found by analysis) usually looks too late compared with the tension curve, *i.e.* the maximum relaxation heat rate, which is usually very near the time at which the tension is falling most quickly, is in these cases often considerably later than that time; the heat curve also usually goes on for a few tenths of a second longer than the tension curve. An extreme case is shown in Fig. 7. Here, after considerable exercise and an interval of 2 hours, H was *up* 20 p.c. and the maximum tension *down* 40 p.c. compared with the original values. It cannot, however, be definitely stated that the relaxation of internal stresses is slower than that of the tension as a whole, as the same effects would be produced by the part of the muscle in contact with the thermopile being less active than the centre of the muscle, which is not unlikely after the muscle had been mounted for several hours.

To conclude the investigation, several alterations in the usual arrangements were made. Some very thin muscles were used, having a weight less than 2, instead of the usual 4 to 6, mg./mm. for a pair of muscles. In such cases irregularity of heat production through the muscle substance will have less effect than for large muscles. Sometimes the face of the thermopile was painted with paraffin oil (medicinal), with a view to improving the contact between muscle and thermopile or, at least, making it more uniform. Neither of these changes had any appreciable effect on the analysed heat records.

Several cases were tried in which the muscle was given different initial extensions. The muscle may be called "loose" when the initial extension is 3 or 4 mm. over a resting length of about 25 mm., the tension then being quite small, and "tight" when the initial extension is 8 or 9 mm.; in previous experiments an intermediate initial extension of 6 or 7 mm. was used. In the "tight" cases the tension diagram is very appreciably lengthened, due to the relaxation taking place more slowly [see Hartree and Hill, 1921, p. 401], and the relaxation heat is similarly affected, taking longer with a lower maximum rate. In several cases the sudden dip in the heat curve, previously mentioned, soon after the initial out-

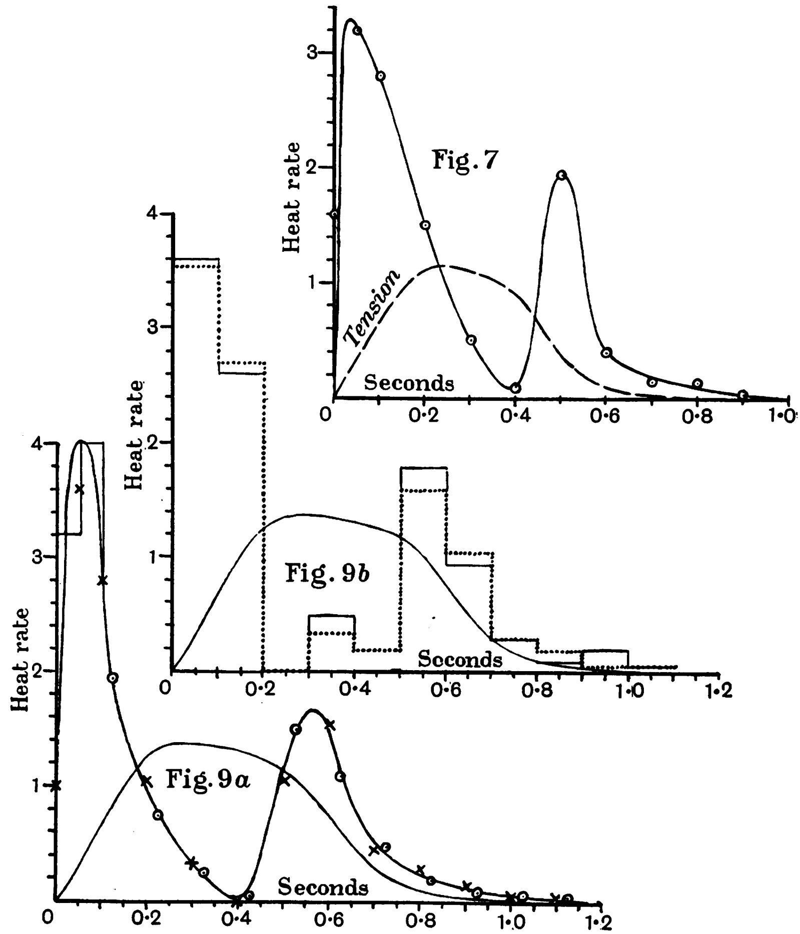

Fig. 7. Single twitch at 0° C. (5. iv. 30, sheet 4). "Exceptional" case, showing a long drawn out "initial outburst" associated with a slowly rising tension. See the text.

Fig. 9. Single twitch at 0° C. (24. iii. 30, sheet 5).

(*a*) × analysis by instantaneous control starting with two intervals of 0·05 sec. ⊙ analysis by control with 0·05 sec. heating starting with two intervals of 0·05 sec. shown as "blocks." See Table II.

(*b*) Full and dotted stepped lines show two alternative solutions using control with 0·1 sec. heating.

burst, was more distinct when the muscle was loose, which tends to confirm the supposition that this dip may be due to a delay in heat recording on account of inferior contact; but, on the other hand, when the muscle is tight the initial outburst may be more spread out than when the muscle is loose, just as the relaxation heat certainly is, and this would have the effect of diminishing the dip. Further, the comparison is not a very good one, as separate control curves have to be taken for the different extensions used. The muscle was killed when in the loose position and after the corresponding controls had been taken it was pulled out to the greater extension; after doing so the muscle is hardly likely to be precisely in the same position on the thermopile as it was after stimulation, so possibly the control curves then taken were not quite suitable. There is no appreciable change in the magnitude of the relaxation heat reckoned as a fraction of the total initial heat in the few cases where it can be distinctly found.

A few cases were considered in which, after the ordinary records in oxygen had been taken, a mixture of 10 p.c. CO_2 in oxygen was introduced into the muscle chamber. This had the effect of considerably reducing the response. The maximum tension fell to about 0·6, and the initial heat to about 0·65, of their former values (mean of four cases, not very good); the relaxation heat was reduced from about 29 p.c. to about 26 p.c. of the initial heat and was more spread out (as was the tension diagram), with a lower maximum rate than in the first case. Thus the actual amount of relaxation heat is reduced in about the same ratio as the maximum tension. The analyses in the second part of these experiments is not very reliable as the state of the muscle was continually altering and successive galvanometer records usually showed a considerable progressive change.

Experiments with iodo-acetic acid. At the suggestion of Dr E. Lundsgaard, six experiments were made on muscles poisoned with mono-iodo-acetic acid. Dr Lundsgaard himself very kindly supplied the acid in crystal form. A stock solution of 0·8 p.c. was prepared and neutralized to *p*H 7·4 with NaOH. This was added freshly on each occasion to Ringer's fluid containing 10 mg. P/100 c.c., the final concentration of iodo-acetic acid being 1/25,000. According to Lundsgaard [1930, p. 68] a concentration of 1/30,000 may be regarded as the lowest at which poisoning is complete in 1 hour, in a sartorious muscle soaked in it. Since the characteristic contracture caused by the drug seems to be very small, or long delayed, at 0° C., the muscle was in every case soaked in the drugged Ringer's fluid for 1 to 1¼ hours at room temperature (with oxygen bubbling), before being placed in the thermopile chamber at 0° C. There the muscle was further in the solution for ¾ to 1 hour before the latter was replaced by oxygen. Soaking for $1\frac{3}{4}$ to $2\frac{1}{4}$ hours in a 1/25,000 solution should have ensured complete poisoning.

There was apparently a slight harmful effect from such long soaking, since (i) the response (both T and H, but T more than H) falls for successive stimuli continually from the start (though sometimes by only a little), and (ii) most of the analyses showed a small apparent negative heat production for a few tenths of a second after the end of relaxation, as though the outside of the muscle (far from the face of the thermopile) were less active than the centre. This "negative heat" may conceivably be a genuine occurrence, but it is more likely due to an error of the kind named. Being only 1 to 3 p.c. of the initial heat (more for later records of a series), it does not affect the general result of the analysis beyond possibly making the relaxation heat appear a little too small, as there may have been an error of the same kind before the end of relaxation, masked by the relaxation heat.

Apart from this effect, *it is impossible to tell from the results of the analysis whether the muscle was under the effects of iodo-acetic acid or not.* The same conclusion has been reached by Fischer [1931] in a recent paper. According to him, comparing the heat production before and after poisoning of the same muscle, the only change resulting from the poisoning is a slight spreading out, but not an increase, of the relaxation heat. So far as the evidence of the present experiments goes the heat due to the initial breakdown, in the poisoned muscle, may be liberated rather more slowly, and the relaxation heat may be very slightly less, than in the normal muscle. The difference, however, is within the range of variation of the latter.

There is no doubt that at 0° C. the contracture characteristic of iodo-acetic acid poisoning takes a long time to appear; if this had not been the case it would have been impossible to obtain reliable analyses, since control curves taken with the muscle strongly contracted, though probably good enough for the total heat, would certainly not be good enough for an accurate analysis. In the first one or two experiments the muscle was rendered inexcitable with chloroform as soon as possible after the photographic records had been taken, as contracture was feared, but since it did not occur till much later, in the remaining experiments the muscle was stimulated to exhaustion (50 to 100 stimuli of 0·1 sec.) and even then there was little or no contracture 3 or 4 hours after the drug was first given; reliable controls could then be made without giving chloroform. Whether chloroform was given or not, contracture did finally occur if the muscle was left sufficiently long, but not for a few hours after it had been exhausted.

It has been shown by Fischer [1930, 1931] and by Meyerhof, Lundsgaard and Blaschko [1930] and confirmed in Hill's laboratory [1931] that the ratio Tl/H is unaffected, in single twitches or in short tetani, by poisoning with iodo-acetic acid, H being the total initial heat.

The fact that this heat, and its distribution in time, are unaffected by completely preventing lactic acid formation, is obviously one of considerable significance in the chemical dynamics of muscle, though its meaning is not yet clear. The fact that the same kind of secondary "humps" of heat production as are found in normal muscle (Fig. 6) may be seen also in poisoned ones precludes the possibility that these are specifically due to lactic acid formation following an initial phosphagen breakdown.

Discussion.

Although the accuracy of recording is such that three or four consecutive photographic records of galvanometer deflection have frequently been taken, even on the live muscle, in which the readings do not differ from their mean by more than 1, or 2 at the most, at any point in a curve with a maximum deflection of 1000, and although the accuracy of the analysis is such (see Appendix II) that practically definite results are obtained when using an interval of 0·1 sec. (improved by a start with two steps of 0·05 sec.), it must be admitted that other technical difficulties are such that the analysed results for the heat production show considerable variations which can hardly be due to variations in the real heat production, and it is probable that these variations are principally due to the varying degree of contact, and so of conductivity, between the muscle and the thermopile, as the muscle alters its tension; in other words, the control curves, on which the analysis is based, are probably not exactly suitable when the muscle is under tension.

Some conclusions, however, are quite certain. Taking the case of a single twitch at 0° C., there is invariably a large initial outburst of heat occurring at a quickly increasing rate (*i.e.* definitely not starting at its maximum rate); the maximum rate is usually at 0·05 sec. roughly, and a large part of this heat is over in 0·1 sec. in most cases. The heat production is usually small when the tension is passing its maximum value, but it is invariably considerable when the tension is falling, and in a large majority of (normal) cases the heat rate has a distinct maximum when the tension is falling fastest; further, the heat rate and the tension usually reach zero at practically the same time. Thus there is such a close connection between this later heat production and mechanical relaxation that the former is certainly a consequence of the latter (including the relaxation from internal stresses). The first very rough determinations of the relaxation heat [Hartree and Hill, 1920*a*] gave a misleading idea, as the analyses then used were incapable of determining its distribution: they did, however, demonstrate its existence.

That the relaxation heat does really represent mechanical potential energy dissipated during relaxation is confirmed by experiments [Hartree, 1925; Hartree and Hill, 1928] in which it has been shown that when work is done by a stimulated muscle the relaxation heat is correspondingly reduced. This mechanical energy is probably far less than the area of the tension-length curve [see Hartree and Hill, 1928, p. 13, etc.], and when much work is done part of the energy for this is derived afresh from an internal source as shown by Fenn [Fenn, 1923, 1924; Hill, 1930*b*]. It seems probable indeed that the best measure of the mechanical potential energy of the muscle excited isometrically is the size of the relaxation heat, which in a twitch, or a very short tetanus, is about 32 p.c. of the total initial heat.

SUMMARY.

1. Improved methods have been applied to the analysis of the initial heat production of frog's muscle, in an isometric twitch or a short tetanus. The thermopiles used have been made thinner, quicker and of lower resistance, and to give a greater E.M.F.; the galvanometer has been made more sensitive and freer from disturbances. A single induction shock has been employed for making an "instantaneous" heating control.

2. The initial heat production in a twitch occurs in two phases: (*a*) rapidly rising to a maximum and then falling off during the development of the mechanical response—the "contraction" heat; and (*b*) rising and falling more gradually during its disappearance—the "relaxation" heat. The latter is about 30 to 35 p.c. of the whole. It probably represents mechanical potential energy dissipated in relaxation.

3. Not seldom a more complex distribution of heat appears, but this may be due to technical errors and no meaning can at present be attached to it.

4. Poisoning with iodo-acetic acid, by which lactic acid formation is prevented, has no significant effect upon the distribution of heat in the initial phases of contraction.

5. Numerical data are given by which the "definiteness" of the analyses can be tested. For this kind of analysis the best heating control is the "instantaneous" one.

My thanks are due to Prof. A. V. Hill for his unfailing help and advice, and also to Mr A. C. Downing for constructing and fitting up the excellent galvanometer employed in this research.

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APPENDIX I.

Notes on sensitivity, etc.

For the case in which the sensitivity was adjusted so as to allow a full-sized deflection (100 mm.) for the heat of a single twitch at 0° C., the galvanometer being critically damped, 1 mm. deflection always corresponded to about $4{\cdot}5 \times 10^{-5}$ cal./g. With a thermopile having 64 pairs of constantan-iron junctions (resistance 13·8 ohms), the sensitivity of the galvanometer (resistance 12·5 ohms) had to be such that 1 microvolt, applied to the galvanometer only, gave a deflection of about 20 mm., which would be about 9·5 mm. in the combined circuit. These deflections refer to the photograph, distant 2·12 m. from the galvanometer. Thus the current sensitivity of the latter was, 1 mm. at 1 m. = about 8×10^{-9} amp. This of course is a very low sensitivity for such an instrument, so that its deflection was rapid even when recording the heat for a single twitch. To damp it critically with such rapid movements, without introducing mechanical disturbances, required special arrangements which will be described elsewhere by Downing.

A single induction shock passed through the galvanometer produces a maximum deflection in 0·1 sec., very closely, and the deflection is inappreciable after 0·8 sec. (so the galvanometer takes the latter time to reach a steady deflection under a constant current). If this deflection curve be used to analyse the ordinary control curve the result will evidently give the rise of current in the galvanometer, and so the rise of temperature of the junctions at different times after the heating which produced the control curve. This analysis, in fact, eliminates the "lag" in the galvanometer and it shows that, with a control curve produced by instantaneous heating, the hot junctions reach half their maximum temperature in about 0·05 sec.; they reach their maximum temperature in about 0·5 sec., but this latter time rather depends on the size of the muscle.

The thermo-E.M.F. for constantan and iron junctions is about 50 microvolts per degree, so a difference of one degree between the hot and cold junctions of the above thermopile would send through the galvanometer a current

$$\frac{64 \times 50 \times 10^{-6}}{13{\cdot}8 + 12{\cdot}5} = 1{\cdot}2 \times 10^{-4} \text{ amp.}$$

Assuming the specific heat of the muscle to be unity, one degree rise in the temperature of the muscle sends through the galvanometer a current

$$\frac{1}{4{\cdot}5 \times 10^{-5}} \times \frac{10^{-6}}{20 \times 12{\cdot}5} = 0{\cdot}9 \times 10^{-4} \text{ amp.}$$

The second number is so much less than the first principally because some of the heat must pass from the muscle to warm up the thermopile and the diminution of temperature will be more marked the greater is the thermal capacity[1] of the thermopile compared with that of the muscle. It should be noted that the difference between two numbers does not constitute an "error" of any kind, but only a diminution in the sensitivity of the arrangement; and, further, any calibration based on the theoretical E.M.F. of the junctions is of no value unless the relative thermal capacities of muscle and thermopile can be estimated, or unless that of the latter can be neglected, as in the case of a fine single junction inserted into a muscle.

The nominal "figure of merit" of the galvanometer used was about 12,000, but, since this number refers to the case when the suspension was specially fitted with a damping vane for critical damping with quick action, the actual "figure of merit" must be very much higher as the presence of the damping vane, apart from its damping effect, must increase the period very considerably.

[1] By "thermal capacity of the thermopile" is meant that of a body which shares heat with the muscle; this is greater than that of the part directly in contact with the muscle, since some heat will pass beyond that part which, in effect, increases the thermal capacity; in the case of thermopiles made by silver-plating this effect must be very considerable; in fact, a recent investigation shows that the sensitivity of such a thermopile is less than half that described above when the number of junctions is the same in each case.

APPENDIX II.

Examples of the analysis.

As an example of the analysis, the experiment of 24. iii. 30, Fig. 9, has been chosen, although it is not to be taken as typical of the behaviour of muscle. One sheet of photographs of that experiment has been used after the muscle had been in action for some 2 hours, in which case the initial outburst had become more spread out than it was originally; the muscle, however, was in such a steady state that five consecutive records were practically identical and their mean can hardly be more than a unit wrong, in a maximum deflection of 1000, at any point. The controls also were in good agreement.

In this particular case it is admitted that the tension curve does not look quite normal and, further, the heat appears to go on rather too long compared with the tension. There may possibly be a small error at the end due to the control curves being too low (at some time after the start), because the part of the muscle beyond the electrode is not heated when taking the controls, but such an error is rarely observable.

Full numerical details are given in this case (Table II), so that it may be seen, by anyone who likes to try, how very "definite" the solutions are when a control curve with short time of heating is used and the re-

TABLE II. Analysis of Experiment

Sec.	0		0·1		0·2		0·3		0·4		0·5		0·6	
0·1 sec. control	0		22		193		450		673		824		915	
0·05 ,, ,,	0	3	41	133	253	386	514	626	720	795	854	899	932	955
Instantaneous control	0	16	85	196	326	459	579	682	766	832	882	919	947	967
Heat	·05	·18	·28		·105		·035		0		·105		·155	
Twitch	0		7		75		212		360		481		570	
at 0, 0·16	0		½		34½		129½		245		344½		421	
at 0·05, 0·20	.		0		8		52½		120		185½		241	
at 0·1, 0·195	.		.		0		3½		19½		45		74½	
at 0·2, 0·075	.		.		.		½		½		6½		20½	
at 0·3, 0·025	.		.		.		.		−½		½		7½	
at 0·4, 0·005	.		.		.		.		.		½		6	
at 0·5, 0·15	.		.		.		.		.		.		0	
at 0·6, 0·11	.		.		.		.		.		.		.	
at 0·7, 0·05	.		.		.		.		.		.		.	
at 0·8, 0·02	.		.		.		.		.		.		.	
at 0·9, 0·01	.		.		.		.		.		.		.	
at 1·0, 0·005	.		.		.		.		.		.		.	
at 1·1, 0·005	.		.		.		.		.		.		.	

In the above analysis the 0·05 sec. control has been used. In this case the heat 0·16, starting at 0, has occurred between 0 and 0·05 and so is shown by the horizontal line at height 3·2 per sec.; similarly for the next step, heat 0·20 between 0·05 and 0·1. After that, when 0·1 sec. intervals have been used, the successive heats are plotted as points. For example, heat 0·195 has occurred between 0·1 and 0·15 sec., and so is plotted as a point, height 1·95 per sec. at time 0·125 sec., and so on.

mainders are kept as small as possible; by this is meant that no remainder is to be greater than 1 (in a maximum deflection of 1000), except only the first remainder when the interval for the analysis is as long as 0·1 sec. at the start; in this case it will often be found impossible to avoid making the first remainder several units negative if the subsequent remainders are to be kept small; this is because of the very variable rate of the heat production in the first 0·1 sec.

Alternative solutions are given in Fig. 9*b*, but only for the case of using a control curve of 0·1 sec. heating; these solutions have equally small remainders, but the difference in the result is quite appreciable. If the controls for shorter time of heating be used, it will be found that the possible differences in solutions leaving only small remainders are much smaller than those shown; in these cases it is rarely possible to allow a greater difference in the heats at each tenth of a second than + 0·005 at one step, − 0·01 at the next and + 0·005 at the next, without making greater remainders than those given in the example.

Fig. 9*a* shows the results of two different analyses carried out on the same galvanometer records, using different control curves. A curve has been drawn so as to be not far from any of the solutions, but taking no account of the solutions (Fig. 9*b*) obtained by using controls with 0·1 sec. heating, as these rise so slowly compared to the others. There is certainly

of 24. iii. 30. Sheet 5. Fig. 9 (*a*).

0·7		0·8		0·9		1·0		1·1		1·2		1·3		1·4		1·5
963		987		997		999		1000		998		994		990		985
971	983	991	996	998	999	1000	1000	1000	999	997	995	993	991	989	987	984
980	988	993	997	999	1000	1000	999	998	996	994	992	989	987	984	982	979
·045		·03		·015		·005		·005								
655		746		831		896		943		971		987		996		999
500		587½		671		736		783		811½		828		837½		841½
309		391		472		536		583		611½		629		639½		644
127		202		279		341½		388		416½		434½		446		451
63		132		206		267		313		341½		359½		371		376½
45		110½		183		243		288		316½		334½		346		351½
42½		107		178½		238½		283		311½		329½		341		346½
4½		30		70½		110½		143½		166		181		191		196½
0		2		14		31½		49½		63½		74½		82		86½
.		0		1½		6		13½		21		28		33½		37
.		.		½		1		3		6½		11		15		17½
.		.		.		½		½		1½		4		6½		8
.		.		.		.		½		0		1½		3		3½
.		.		.		.		.		0		0		½		−½

The results of an analysis of the same curve using the instantaneous control are given above In this case also there is no remainder greater than 1 and the solution is even more definite than that using the 0·05 sec. control.

some doubt about the early part of the curve but very little about the later part, which shows the relaxation heat clearly (with positive thermo-elastic heat probably included, see the text), the amount being 35 to 36 p.c. of the total initial heat.

The numerical data for Figs. 1 to 8 in the text are given in Table I, with the results of each analysis, firstly to show the quality of the control curves used for the case of a single twitch (especially as regards the quick rise soon after the start), and secondly to show the definiteness of the analyses; the last point can be realized only after an attempt to produce other solutions without any remainder greater than 1 (or preferably $\frac{1}{2}$, as in the example worked out).

APPENDIX III.

The interpretation of the results of analyses.

It might be supposed that the results of an analysis can give no idea of the distribution of heat during each interval, but a little consideration

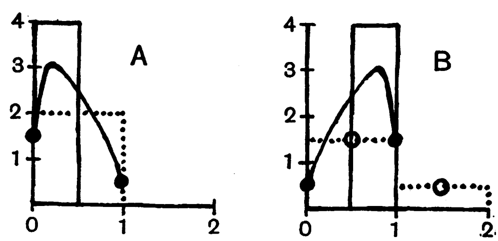

Fig. 10. Representation of a given heat by "blocks" over the intervals, and by "lumps" at the instants.

will show that this is not quite the case. Fig. 10 shows two cases in which it may be assumed that there is no heat before 0, and the intervals used in the analysis are shown by the numbers along the base.

In the case A, heat = 2 units occurs in the first-half interval, and it is required to determine it. The dotted line shows this heat represented by a "block" of uniform height over the whole interval, as would be obtained by using a control with time of heating equal to the interval. This block is, on the whole, too late, and better remainders after an analysis would probably be obtained with a little more than 2 units between 0 and 1, and a corresponding little negative between 1 and 2; the remainders could not be expected to be very small in either case.

The large dots show the same heat represented by "lumps" $1\frac{1}{2}$ and $\frac{1}{2}$ at 0 and at 1 respectively, as would be obtained by using a control with instantaneous heating; these have the advantage of giving the heat, on the whole, at the right time.

Now it obviously will not do to join these dots and say that the inclined line gives the estimated heat rate during the interval; such a line is much too low as the area below it only gives *half* the total heat. The important point which has not been taken into account is that if there is no heat before 0 and the analysis closes at 1 the curve showing the estimated heat rate should have vertical tangents at these points. A curve of the kind has been sketched in, having its area about right; the shape is arbitrary but, as a matter of fact, the peak should be higher and more to the left to make the centre of gravity of the curve agree with that of the dots.

In the second case, B, two units of heat occur in the second half of an interval. The dotted line, as before, shows the same heat by blocks over the first two intervals, having on the whole the right position in time; and a curve similar to that in case A has been drawn to show the result obtained from the dots. Notice now, firstly, if the blocks be replaced by single lumps of heat at their centres, as shown by the small circles, and these be joined by a straight line, the heat under the line only does not represent the whole process, giving in fact only half the total heat; secondly, that the method of blocks does not even give the best estimate of the heat occurring *during each interval* since, when a considerable part of the heat occurring during an interval happens to come near the end of an interval, part of it is necessarily attributed by the analysis to the next interval; and, thirdly, that the "block" method (*i.e.* the use of a control curve with time of heating equal to the interval of the analysis) cannot give such a good approximation to a varying heat rate as can be given by using a control curve with instantaneous heating, since the curves drawn give a closer approximation to the assumed heat than do the dotted lines. But, of course, if the heat through each interval happens to be of uniform rate, a better solution could not be given than that shown by blocks.

APPENDIX IV.

On the sharpness of an analysis.

The *sharpness of an analysis* no doubt principally depends on the quickness of rise of the control curve soon after the start. So, firstly, the time of heating for the control curve should be as short as possible.

Secondly, the thermopile junctions should rise in temperature as quickly as possible, so the insulation should be very thin. Assuming that, soon after the start, the E.M.F. produced by the thermopile rises in an exponential manner, when a dead muscle on it is instantaneously heated, it is proportional to $(1 - e^{-t/T})$, where T may be called the time-lag of the thermopile. Note that when t is very small this becomes t/T of its maximum.

Thirdly, the galvanometer should act as quickly as possible under the conditions that it must be critically damped and that it must give a certain maximum deflection (according to the size of the photographic paper used) when the muscle produces a certain amount of heat H. The larger is H and the larger the sensitivity S of the thermopile (E.M.F. it produces per degree), the smaller need the sensitivity of the galvanometer be to give the required deflection; thus, since the period of a galvanometer of the type used varies as the square root of its sensitivity, its quickness, which is proportional to the reciprocal of the period, varies as $(SH)^{\frac{1}{2}}$.

Now the deflection of a critically damped galvanometer, at time t after a constant E.M.F. has been applied to it, is proportional to

$$1 - (1 + t/T_1)\, e^{-t/T_1},$$

where T_1 may be called the time-lag of the galvanometer, and so is proportional to $(SH)^{-\frac{1}{2}}$. Note that when t is very small this becomes $t^2/T_1{}^2$ of its maximum. Thus with both thermopile and galvanometer in action the deflection for the control curve (with the above assumptions) at very small time t after the start is $t^3/TT_1{}^2$ of the maximum.

It is evident from this that the galvanometer lag is much more important than the thermopile lag, any small diminution of galvanometer lag having twice the effect of the same diminution of thermopile lag on the quickness of rise of the control curve.

Also, since the above expression is proportional to $(t^3SH)/T$, it is clear that the thermopile sensitivity is just as important as thermopile quickness. The above important results were first pointed out by Prof. A. V. Hill, to whom I am indebted for the substance of this note. He further remarks that since the time interval for a definite analysis is determined by the time required for the control curve to reach a given height, the last expression given above shows that the interval for a definite analysis is proportional to $(T/SH)^{\frac{1}{3}}$, which shows the small effect of altering any one of the quantities concerned unless this alteration is of large amount, and this can only be done at present by using larger quantities of heat than those used in the present paper, which usually referred to a very short stimulus.

The above consideration is not quite complete since no account has been taken of the resistances of the thermopile and galvanometer. However, since it is best to have the resistances of thermopile and galvanometer approximately equal, the above results hold good for a given galvanometer when using a thermopile of resistance made to suit it.