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# EFFECTS OF STRETCH ON MUSCLE RESPONSES IN THE EARTHWORM

## (*HELODRILUS CALIGINOSUS*)

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Much investigation has been done on the physiology of the muscles of the vertebrates as compared with that of the invertebrates. Buddington[1] ('02) brings together the bibliography bearing on this problem, and shows that with increasing temperature Lumbricus muscle shows little constancy in changes of tone below 15° C and the first uniform result is a gradual loss of tone beginning at 20° C; rapid loss of tone occurring between 30° and 40°; an improvement from 42° to about 55° when rapid relaxation sets in, this changing to final heat rigor at about 65°. Eddy and Downs[2] ('21) showed that the gastrocnemius muscle of the frog when stretched by a weight of 100 grams for one-half to three hours can be completely fatigued in 85.98 per cent of the time required in the case of an unstretched muscle, when both were stimulated by the same strength induced current. Harrison and Baldwin[3] ('21) obtained definite qualitative differences in responses in earthworm muscle in concentrations of alcohols, ranging in ethyl alcohol from 40 to 1.56 vols per cent, and in propyl alcohol from 10 to 0.5 per cent. In general, the higher concentrations are toxic, the lower have no noticeable effect, while between the two extremes are concentrations of decided sensitization.

## APPARATUS AND METHOD

The apparatus used in this series of experiments was the same as described in a previous paper by Harrison and Baldwin[3] ('21). A more detailed description of a part of the apparatus is given by Harrison[4] ('23). A tetanizing electric current was employed for stimulating, strengths of 6 and 8 volts were used as subsequently described. The secondary coil of the inductorium was set at 4½ centimeters from the primary, where it was maintained throughout the entire series of experiments. The kymograph was adjusted to make one revolution in one hour. The inductorium was adjusted so as to give thirty-eight to forty make and break stimuli

per second. Forty to forty-five of these make and break shocks constituted the stimulus after each time interval through the entire series of experiments. The solutions in which the muscles were immersed were drained off and replaced with fresh solution after each series which ran thirty-five minutes or more, and after every second or third where each ran fifteen or twenty minutes. In each case where there was a change made in the kind of solution used, the glass tube which was to contain the muscle was thoroughly rinsed with the solution next to be used. The earthworms used in these experiments were *Helodrilus caliginosus* var. *trapezoides* (Duges). These were collected in the field, placed in jars with moist earth, and kept at room temperature, sometimes for several days before being used, with a variation of only two or three degrees from 70° F. All the experiments were performed at room temperature, the variation of which was so slight that the resulting effects on the muscle may be considered as being practically negligible. Sections of ten somites of the earthworm constituted the unit of muscular tissue used in each case and were taken from behind the clitellum as it was found that these were more easily standardized. The sections were mounted and stimulated as previously described in the paper mentioned above.

Figures 1 to 5 inclusive are records of typical experiments indicating the effects of variation in length of time of stretch upon the responses of the muscle when immersed in normal sodium chloride solution, the time varying from ten minutes to three hours. Each muscle was mounted as previously described and given thirty-five to forty stimuli with one minute intervals. Figure 1 of Plate I shows what may be considered a typical record of responses without stretching. The type of the curves is uniform, varying principally in the heights of contraction, indicating the gradual onset and progression of fatigue. The relaxation or loss of tonus begins with the initial stimulus and continues uniformly to the later part of the series where the sodium chloride is removed and .12 per cent amyl alcohol is added which immediately sensitizes the tissue to a greater height of contraction and a rise of tonus. The progressive inhibitive effects of the alcohol are shown in the last few curves of the series. In the first few curves of each of the series, 2, 3, 4, and 5, the tissue was stimulated immediately after mounting and before stretching, following this a ten gram weight was added to each for ten minutes, twenty minutes, thirty minutes and two hours, respectively. The

kymograph was stopped and the electric current was shut off in each case during the stretching, after which the weights were removed and the muscle was stimulated as before. In figure 2 the contractions following the stretch with ten gram for ten minutes are practically twice as high as those preceding the stretch on the corresponding curves in figure 1 where there was no stretch. The increased height might be attributed to the recuperation during the time interval or rest, but in figure 6 where a ten minute rest occurred without any stretching the succeeding contractions were practically the same height as before, about the only change which is evident being a slight relaxation while the kymograph was stopped. It is interpreted that this increased sensitization is brought about by the stretching of the tissue. Little difference in the variation of tonus occurs, but the onset and progressive effects of fatigue are more definitely indicated than where there was no stretch. Figures 3, 4, and 5 also show this increase in sensitization due to the stretching. Figure 4 fits least well into the series, but taking all these series together the height of the contraction and the onset and progressive effects of fatigue are in proportion to the duration of the time of stretch. In the last of the series in figure 3, stimuli were introduced every twenty-five seconds which is equivalent to about twenty make and break shocks or about one-half the duration and strength of those just preceding. The corresponding contractions are proportional to the amount and duration of current used. Series 7 and 8 having twenty and thirty gram weights respectively, were stretched ten minutes each in order to attack this problem of stretch from another angle, and here again the initial sensitization and the onset and progress of fatigue are in proportion to the amount of stretch. Series 9, which was stretched for two hours with a ten gram weight in sodium chloride solution, was made to further analyze this increased sensitization property of stretched muscles. This series is directly comparable with series 5, the only variable being that instead of removing the ten gram weight after the two hours stretch it was allowed to remain and be lifted following the first three stimuli; after which it was removed and the muscle stimulated as usual. The muscle contracted only about one-fourth the height of the corresponding contractions in series 5 where the weight was removed. There is the immediate onset and progression of fatigue in the two cases which are practically the same. The height of the contractions following the removal of the weight are practically the same as the corresponding con-

traction in 5. It is thus evident that the amount of work done in lifting the weight is equivalent to that done in the corresponding contractions where the weight was removed. Apparently there was a certain definite amount of sensitizing material present before each of the initial contractions following the two hour stretch period, and the additional stretch due to lifting the weight liberated no appreciable additional amount. Figures 10 and 11 are continuations of series 7 and 9, respectively. In the former the muscle is only partly fatigued while in the latter the fatigue is practically complete. The sodium chloride solution was removed in each case and 0.18 per cent amyl alcohol was added, and the subsequent curves show the progressive effects of the alcohol. While these curves are not exactly comparable due to variation in the time between the introduction of the alcohol and the application of the stimulus it is quite evident from these and other experiments that the increase in sensitization by amyl alcohol in this concentration is most rapidly brought about in partly fatigued muscles.

Series 12 to 31 inclusive are records made to test the effects on the normal responses of muscles immersed, stretched and stimulated in normal sodium chloride, potassium chloride, and calcium chloride solutions. The method used in mounting and stimulating the various tissues is the same, but the length of time of stretch varies in the different series from ten minutes to three hours. The muscles are automatically stimulated with an eight volt tetanizing electric current, set to make thirty-eight to forty double vibrations each second, with intervals of twenty seconds. Each series is selected as typical among many made under the same conditions. In each solution used the most marked initial sensitization appears in tissue stretched with a ten gram weight for about one hour. Sodium chloride produced marked sensitization during the longer periods of stretch. Potassium chloride produces marked inhibition when compared with sodium, while calcium chloride brings about contracture which merges into rigor and these factors hasten proportionately comparative fatigue processes. Figure 12 is a record of a muscle when stimulated immediately after mounting and immersed in normal sodium chloride solution, without being stretched, and is a normal or standard series under these conditions. It is the same type of series as that shown in figure 1 where only six volts were used at intervals of one minute, and shows the same, in that contractions following the first ten or twelve stimuli remain prac-

tically the same, but are followed by a gradual decrease in height with the onset and progression of fatigue, and a slow relaxation or decrease of tone. Series 13, 14, 15 and 16 were made in the same way as the above, with the exception that immediately after mounting in the sodium chloride solution, each was stretched with a ten gram weight. The length of time of stretch was the only varying factor and was for ten minutes, twenty minutes, one hour and three hours, respectively. Figure 13 shows very little variation from the standard sodium chloride series. The relaxation phase is not so evident, but the evidence of fatigue is more pronounced. After a stretch of twenty minutes as shown in figure 14, the heights of the contractions are much greater and also the tonus holds up much better than in the preceding series of this group. This suggests, when compared with 12 and 13, that stretching sensitizes the muscle to greater contractions and enables it to better withstand the onset and progressive effects of fatigue. Figure 15, made after stretching one hour, shows a marked increase in the height of contraction, but fatigue begins at about the same relative time and progresses at about the same rate, and the tonus remains practically constant, all of which are important when correlated with the previous series. After three hours stretching with a ten gram weight a series is obtained as shown in figure 16. The height of contraction is not so great, the progressive effects of fatigue are more pronounced, and the loss of tone is again observed, all of which indicate that the point of maximum sensitization has been passed.

Series 17 to 21 inclusive show the effects of stretching muscles in normal potassium chloride solution, with the same weights and the same lengths of time, as those in series 12 to 16 respectively. Each series of the potassium chloride group possesses the characteristic initial contraction, followed by a series of curves indicating marked inhibition as compared with the corresponding sodium chloride series. Figure 17 shows the typical or standard series of curves when the muscle was not submitted to previous stretching. The heights of contractions, following corresponding stimuli and the resistance to the progressive effects of fatigue are much less where potassium chloride is used. In figure 18, where stretching continued for ten minutes, the relaxation following each contraction is much inhibited and the increase in tonus continues during several stimuli, followed by a gradual loss of tonus and sensitization, reaching complete exhaustion near the end. When compared with figure 17 where no stretching

occurred, one also observes the increase in the initial contraction. Figures 19 and 20 record the effects of stretch in normal potassium chloride for twenty minutes and an hour and fifteen minutes, respectively, and show the same general effects as already mentioned but in a more pronounced way. Thus in series 18, 19 and 20 there is a progressive increase in the height of the initial contraction and also an increase in the duration of the maximum contractions following, which is similar to series 13, 14 and 15. This is interpreted as indicating that the depressing effects produced by the potassium chloride are more than counterbalanced by the sensitizing effects produced by stretching. Figure 21 records results of stretching for three hours and is strikingly similar to figure 18, the principal differences being the variation in the heights of the initial contractions and the tonicity during the latter parts of the experiments. The point of maximum sensitization has evidently been passed and the muscle is approaching rigor. This, in a general way, coincides with the results recorded in the sodium chloride series. Series 22 to 26 inclusive were performed to test the effects of variation in the amount of weight used, in stretching muscles when they were immersed in normal potassium chloride solution. The experiments were performed as in the previous potassium chloride series excepting that a twenty gram weight was used instead of ten grams for the same lengths of time as in the series 17 to 21, respectively. The maximum sensitization point was reached sooner, being most evident after ten to twenty minute stretch while in the potassium series where a ten gram weight was used this point was reached after about one hour and fifteen minutes stretch. The onset of fatigue is sooner and its progressive effects are more pronounced where the greater weight is used. Series 25 and 26 show results after stretching one hour and three hours, respectively. There is little response as compared with series 20 and 21, showing that a condition of practically complete fatigue is reached.

The records in series 27 to 31 inclusive are of muscles stretched in normal calcium chloride solutions for periods of time comparable to the sodium chloride series 12 to 16, and the potassium chloride series 17 to 21 and show that the initial contractures following the shorter periods of stretch are greater than in the corresponding series of the other solutions, while for the longer periods of stretch the reverse is true. The progressive effects of fatigue following the initial contractions are less marked during

the earlier periods of stretch than in the corresponding potassium series, while in those of the longer periods of stretch the reverse is true. Also following the initial contraction the tonus is increased during several stimuli and maintained in a comparatively striking manner throughout each series of the calcium group.

## SUMMARY

Mounts of intestine and body wall muscles of the earthworm when immersed in normal sodium chloride solution and stretched for various intervals with ten gram weights and subsequently uniformly but intermittently stimulated with a tetanizing current of known strength at successive intervals, (i. e. each minute for one-half hour) show that stretching has a sensitizing effect in the responses immediately following the treatment which is relatively proportional to the duration of the stretch up to certain limits. Noticeable relationships are found between duration of stretch and the onset of fatigue which in general seem to indicate that the greater the stretch, the greater the initial sensitization followed by rapid onset of fatigue.

Mounts stretched with different weights in normal sodium chloride, potassium chloride and calcium chloride solutions and stimulated every twenty seconds for a period of fifteen minutes show remarkable correlation between duration of stretch, intensity of stretch and the kinds of solutions used together with characteristic comparative differences in the types of curves produced. In all solutions the most marked initial sensitization appears in tissue stretched by ten gram weight for about one hour duration. Potassium chloride produces marked inhibition when compared with sodium, while calcium chloride brings about contracture which eventually merges into rigor and these factors hasten proportionately comparative fatigue processes.

These results help to substantiate a belief that stretching a muscle involves the liberation of certain amounts of energy which in turn call forth certain metabolic changes. These changes apparently produce stimulating substances, which on further transformation, by stretching yield toxic properties. Further, these inner changes can be markedly modified by environmental conditions, a point of wide significance in making physiological interpretations.

## EXPLANATION OF FIGURES

The series of curves in each of these figures was selected after eight to twenty-five had been made under exactly the same

conditions. Hence each is considered typical for a given set of conditions. The muscle of each of the series 1 to 11, was stimulated before stretching in order to see that everything was in proper working order. The kymograph was then stopped, the electrical wires disconnected and the desired weight applied on the longer lever arm at an equal distance from the fulcrum as the end of the short lever arm. Thus the muscle was stretched without removing it from the chamber in which it was immersed. After the proper time interval for stretching had transpired the weight was removed, the kymograph started and the necessary electrical connections made, otherwise there were no adjustments except in special cases which are subsequently explained. An eight volt tetanizing electrical current was used for stimulating.

Figure 1. This is a series of curves of the intestine and body wall of the earthworm, stimulated in normal sodium chloride solution without stretching. Observe the gradual relaxation or loss of tonus. After the fortieth stimulus the progressive effects of .12 per cent amyl alcohol are shown.

Figure 2. Typical normal curves are shown in the first few contractions followed by a stretch of ten grams for ten minutes during which time the kymograph was stopped. Observe the increased height after stretching. The amount of stimulus remains constant.

Figure 3. Curves similar to figure 2 excepting the stretch was for twice the length of time. The onset of fatigue came much more abruptly. After the thirty-second stimulus, the stimuli were made every twenty-five seconds. Observe that the extent of contraction is about one-half of the former.

Figure 4. Similar to 2 and 3 only here the length of stretch is for thirty minutes. The onset and progressive effects of fatigue are observed in a slight degree.

Figure 5. The stretching here continued for two hours but the initial contraction afterward is about the same as after the ten minute stretch. The onset and progressive effects of fatigue, however, are much more marked.

Figure 6. This series was made as a check on series number 2. After the first few contractions a rest of ten minutes occurred with no weight applied. The resulting curves when compared with those of figure 2 show that the time interval alone is not responsible for the increased contractions but, that these were due to the stretching.

Figures 7 and 8. Typical curves where muscles were stretched

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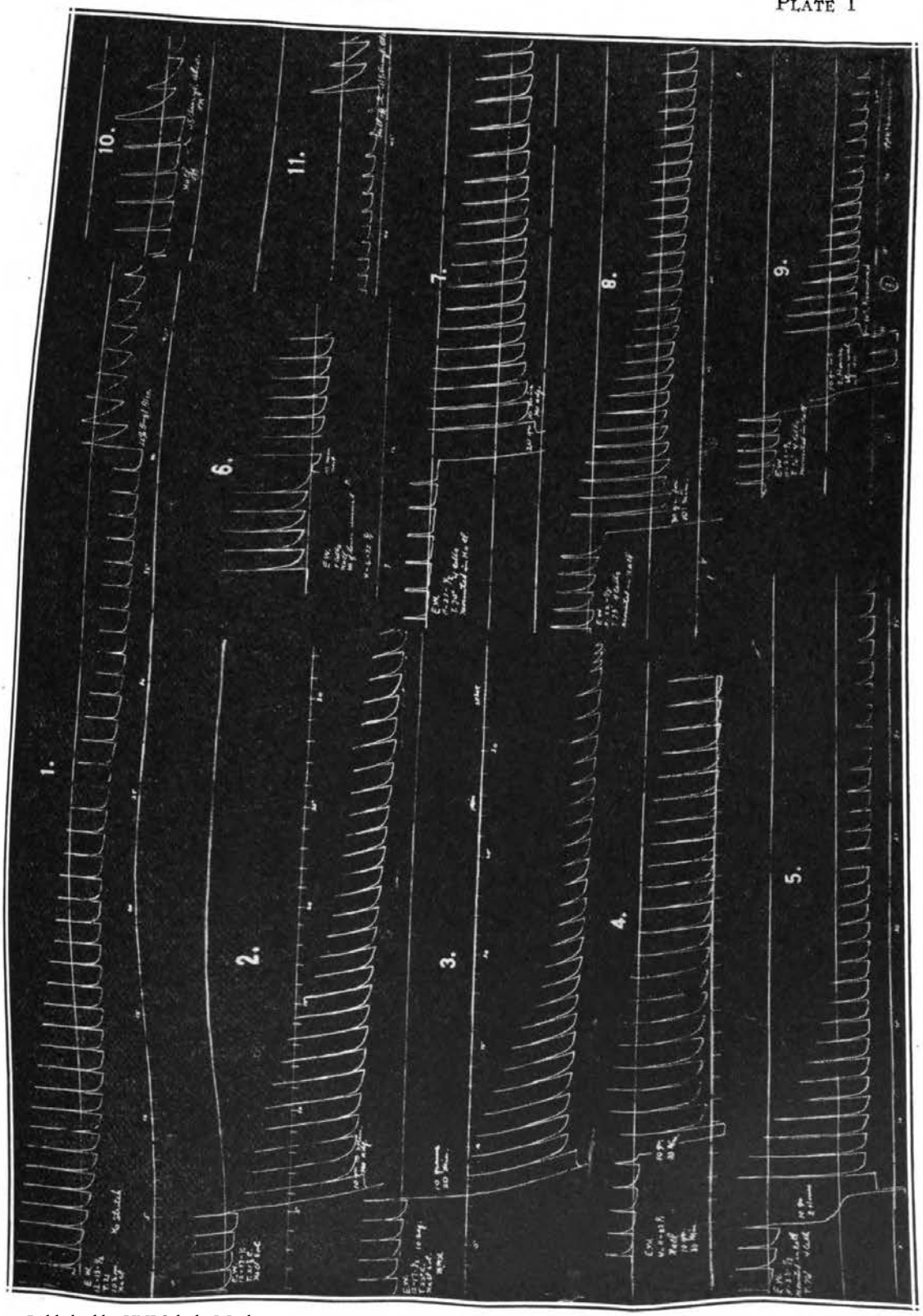
PLATE I



with twenty and thirty grams respectively for ten minutes, which show when compared with 3 and 4 that where the minute-gram unit is constant the sensitizing effect produced is practically the same.

Figure 9. The muscle in this case was first stimulated after stretching without removing the ten gram weight, which counteracted the sensitizing properties so that when the weights were removed and the muscle was then stimulated the contractions were much lower. Compare with figure 5. The tissues used in 5 and 9 were taken from the same specimen.

Figures 10 and 11. These are continuations of figures 7 and 9, respectively, the latter being almost completely exhausted. Each was treated with 0.18 per cent amyl alcohol. The curves show its progressive effects.

The muscles in each of the series 12 to 31 were stimulated with a six volt current every twenty seconds. In figures 12 to 16, the muscles were immersed in normal sodium chloride, in 17 to 26, in normal potassium chloride and in 27 to 31 in normal calcium chloride. In each case where stretching occurred the weight was removed before the muscle was stimulated.

Figure 12. A typical normal series obtained after mounting and stimulating without stretching.

Figure 13. Similar to 12 except that the muscle was stretched with a ten gram weight for ten minutes. The onset and progressive effects of fatigue are indicated by the rapid decrease in the heights of contraction.

Figure 14. The muscle in this case was stretched with a ten gram weight for twenty minutes, and is to be compared with 12 and 13. The sensitization of the muscle is indicated by its increased and sustained contractions.

Figure 15. In this case the ten gram weight was applied for one hour. The sustained heights of the contractions which immediately followed indicate the maximum sensitization of the muscle. The tissues used in 14 and 15 were taken from the same specimen.

Figure 16. The ten gram weight was applied in this case for three hours. The rapid decrease in the height of contraction and its early depletion indicate the progressive effects of fatigue.

Figure 17. This shows a typical series when immersed in normal potassium chloride without stretching.

Figure 18. A series made from a muscle treated the same as

17 except it was stretched with a ten gram weight for ten minutes before being stimulated.

Figures 19, 20 and 21. These are series treated the same as 18 except that the ten gram weight stretched the muscles for twenty minutes, one hour and fifteen minutes, and three hours, respectively. When compared with the corresponding sodium chloride series, 14, 15 and 16, they show the inhibiting effects of potassium chloride on the contraction of the tissues.

Figures 22 and 23. The former is a record of an unstretched muscle in normal potassium chloride while the latter is comparable with it. The only difference is that in 23 a twenty gram weight was applied for ten minutes. Figures 23 and 18 are also similar, the only difference being that the former was stretched with twice the amount of weight as the latter. The greater sensitization is much more apparent where the stretch was greater.

Figures 24, 25 and 26. These series are comparable to 19, 20 and 21, respectively, differing only in being stretched with twice the amount of weight. The onset of fatigue is sooner and its progressive effects are more pronounced where the greater weight is used.

Figure 27. In this series normal calcium chloride was used and the series is comparable to 12, 17 and 22. The initial contraction is much greater, showing that the process of sensitization has taken place more quickly.

Figures 28, 29, 30 and 31. This series is similar to 27 and comparable with series 13, 14, 15 and 16, respectively, and also with 18, 19, 20 and 21, respectively. The only difference in the treatment is in the kind of solution in which the tissues were immersed.

## BIBLIOGRAPHY

1. Buddington, R. A., '02, Am. Jour. Phys., Vol. VII, page 155.
2. Eddy & Downs, '21, Am. Jour. Phys., Vol. LVI, page 182.
3. Harrison, B. M., and Baldwin, F. M., Proceedings of the Iowa A ademy of Science, Vol. 28.
4. Harrison, B. M., '23, Science Jan. 19, page 87.

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