I STUDIES ON VIBRATION SENSATION

AND

II HEAT PRODUCTION OF SLOW AND FAST CONTRACTIONS OF A CRUSTACEAN MUSCLE WITH DOUBLE MOTOR INNERVATION

Thesis by

Geoffrey Lorrimer Keighley

In Partial Fulfillment of the Requirements
for the
Degree of Doctor of Philosophy

California Institute of Technology
Pasadena, California
1944

CONTENTS

The literature on vibratory sensibility is largely taken up with controversies about the site of the receptors which are responsible for its appreciation. Recently Geldard (1940) has published an extensive review in which he points out that the controversies have been almost continuous, and new facts as discovered have favored now one side, now another. Zotterman (1941) agrees with this statement.

The arguments and discussions, and the experimental evidence supporting them, fall into the following classes. There are those workers who are of the opinion that the sensation of vibration is elicited by stimulation of receptors in the skin; this group can again be divided into those who believe that the sensation is aroused by interrupted or varying stimulation of the receptors for pressure, and those who believe that it is aroused by stimulation of specialized receptors which have nothing to do with pressure. There is another group of workers who hold the opinion that the sensation of vibration comes from stimulation of deep receptors; this group is also divided into those who believe the receptors are closely associated with the bones, and those who believe the receptors lie in the muscles.

Many of the earlier authors took it for granted that vibration is a tactile sense. This conception was extended and supported by von Frey (1915), who did much to develop the technique of exploring the cutaneous sensations point by point. For this purpose, he developed the hair aesthesiometer.

In its simplest form, this consists of a small rod, for a handle, with a projecting hair or bristle attached to one end. When applied to the skin, pressure may be increased up to the point at which the hair begins to bend, beyond this point the hair merely bends further. The point at which the hair begins to bend can be determined with a balance. By using hairs of different stiffness and length, it is possible to prepare a series, which when pressed on the skin until bending starts, produce a graded and known series of pressures. This is the device used to map out the points on the skin from which arise sensations of pressure. For the sensation of vibration, von Frey used a 100 cycle per second tuning fork with a hair or bristle attached to one tine. This tuning fork was electrically driven and so could be maintained at constant amplitude.

On an area of skin on his own arm, von Frey succeeded in identifying some 208 spots which were sensitive to pressure. He then explored the same skin area with the tuning fork and found that with small amplitudes the characteristic sensation of vibration was aroused only when the bristle on the tuning fork was placed on one of the pressure points. By using an electrical stimulus, a faradic current of 100 cycles per second, he found that temperature and pain spots gave their own sensations while pressure spots gave the same sensation as did mechanical vibration. He also found that areas over bone proved unusually insensitive to electrical stimulation so he felt certain that vibration is not a bone sense. Its close association on the skin with the points most sensitive to pressure convinced him that the pressure receptors are responsible for the sensation of vibration.

Katz (1923) was one of those who maintained that the sensation of vibration is aroused by stimulation of the skin, but through special sense organs responding to vibration only.

The arguments for separate sense organs in the skin for vibration can be summarized, along with the objections to them. It has been said that vibration is a distant sense, like hearing, whereas pressure is not, also that vibration is a dynamic, alive sense, and pressure is not; it does not seem likely that experiments can be contrived which will give answers to questions of this sort.

It was once believed that vibratory movements applied to the skin, which were much smaller in amplitude than the movements necessary to excite pressure, would be large enough to excite the sensation of vibration; however, the most careful measurements, made by various workers, show that the amplitude necessary to arouse a sensation of vibration is only slightly less than the amplitude necessary for pressure.

It was claimed that vibration, unlike pressure, does not exhibit the phenomenon of adaptation - this has been disproved.

If vigorous vibration is applied to the elbow, vibration may be felt in the hand, where presumably there is no pressure stimulus. The observation seems to be unquestioned. However, vibration may spread extensively and vibrations on the skin may be seen and picked up some distance from the point of application, so that these localizations may be puzzling; but they throw no light in themselves on the site of the organs which are responding.

Some points of the body are relatively sensitive to pressure but relatively insensitive to vibration, and this is believed to point to separate sense organs. Arguments of this sort must be accepted with care, as not only can vibration spread on the skin, but its spreading may vary from tissue to tissue and according to the physical state of the tissue; differences of this sort cannot be completely accepted unless these objections are met. The tongue has been much discussed as a test organ for this difference; it is said to be sensitive to touch, to the tines of a tuning fork which vibrate with considerable amplitude, but insensitive to the base which vibrates with smaller amplitude.*

Geldard (1940) has done more work which bears on this problem. Using as a stimulus a needle 0.17 mm diameter, he confirmed von Frey's findings that there is a punctate distribution of the sensitivity to vibration. He points out, however, that a mere mapping of these spots against a similar mapping of pressure spots proves nothing. The effective area of both kinds of stimuli will depend on the magnitude of the pressure and vibration and an apparent coincidence of the two types of spots might be an accidental result of this spreading of the stimuli. Therefore, he attempted to push the analysis further on the following basis. If spots highly sensitive to pressure are similarly highly sensitive to vibration, and if spots which are insensitive to pressure have high thresholds to vibration, at least there would seem to be an intimate relation between the two, or a common dependence on some other cause. He found that the two kinds of pressure spots

---

*After seeing such statements, it was surprising to find that if the base of a vibrating tuning fork is placed on the tongue, the vibration can be felt. This has occurred with all the people tested, and with forks of different frequencies.

do occupy different positions on the scale of vibratory sensitivity. At pressure insensitive spots, the threshold amplitude necessary to elicit vibration was about eight times greater than the amplitude needed at pressure sensitive spots. In his opinion these results indicate that vibration is merely interrupted or varying pressure.

Geldard has also determined the thresholds for the two types of spots over a range of frequencies from 64 to 1024 cycles per second. At the pressure insensitive spots he found, as was stated above, that the thresholds are high but they are also unreliable, and he was unable to determine with any certainty the relationship between the frequency of stimulation and the threshold. But at the pressure sensitive spots he found that the thresholds were low, were reliable, and moreover uniform for all the frequencies which he tried. This last result is a rather strange one, as all other workers have found the threshold to vibration to be lowest in the region from 100 to 200 cycles per second, increasing on both sides of this region at lower and higher frequencies.

Gilmer (1937), using a fine needle and a method similar to Geldard's, partly confirms Geldard's results. He found not much difference in the threshold to vibration between pressure sensitive and insensitive spots on the dorsal side of the arm, but on the ventral side he found a marked difference in vibration sensitivity between the pressure sensitive and insensitive spots.

Weitz (1939) was well aware that in all tests of vibration sensation the spread of the applied vibration must be taken into account. In fact, he demonstrated conclusively that the vibration does spread. Previously it had been noticed that when the amplitude of vibration was great enough, a considerable area of skin around the point of application can be seen in movement. Weitz, using a vibration pick up, that is, an instrument similar to a microphone which is designed especially to receive mechanical vibrations, showed that vibration could be picked up from the skin at points distant from the site of stimulation. Using a small needle and a method similar to that of Gilmer and Geldard, but confining himself to a frequency of 256 cycles per second, he determined the thresholds at a number of spots on the arm. He then applied cocaine to this area and found a marked rise in the thresholds to vibration and pressure. On recovery, the sensitivity to pressure and vibration returned together.

Békésy (1939-1940) has attempted a more precise mapping of the points of sensitivity to vibration, especially in the neighborhood of the hairs. He says that while, in general, the thresholds to touch and vibration vary together over the body, at individual points in one area they may vary relatively. He found that on exploring the thresholds to touch and vibration in the neighborhood of the hair root, points of maximum sensitivity are separated by a small distance, about 0.5 mm., and both these points lie over the hair root. He argues that both touch and vibration are mediated by separate sense organs. The endings for the sensation of pressure lie in line with the sebaceous gland and the endings for vibration lie in a line which corresponds with the position of the hair papilla. Békésy, then, though he believes the end organs for vibration lie in the skin, unlike many other workers who have used a stimulus applied to a small area, believes that vibration and pressure have separate end organs.

Adrian, McKeen Cattell, and Hoagland (1931) have demonstrated the type of action potentials which may be picked up from cutaneous nerves when the skin of the frog is stimulated by an intermittent blast of air. Such a blast will produce synchronized discharges of long duration and high frequency with a single impulse in response to each brief puff of air. The frequency in a single nerve may be as high as 200 to 300 cycles per second, which approaches the maximum frequency which frog nerve fibers can carry. The discharges could follow the frequency of stimulation up to this rate. They also showed quite clearly that the end organs responding are in the epidermis, for when it was scraped away high frequency discharges could no longer be obtained.

In addition to the above, there are those who hold that vibration sensibility arises from deep receptors. These workers nearly always confine themselves to the sensation as elicited by the application of the base of a vibrating tuning fork, and not a vibrating hair or needle or other stimulator of small contact area.

These deep receptors were often said to be closely related to the bones. This belief arose from the fact that the sensation of vibration is most distinctly felt when the tuning fork is placed over a bony prominence or near a joint. However, there is no derangement of the sensation of vibration in cases of fractures, dislocations, and splintering of bones, even with gross separation of the fractured ends. (Geldard 1940). And there is no doubt that the sensation may be felt when a tuning fork is applied to the breasts, to the abdomen, or other fleshy parts.

In the papers of Head and his collaborators (1905-1906), on the changes in cutaneous sensation in man following section and regeneration of afferent nerves, there is almost no mention of the use of the tuning fork. They say that deep sensibility was not disturbed by the operation and that as the vibrations of the tuning fork were felt from the beginning of the period of regeneration they no longer used this test in their investigations. It should be remembered that the vibrations from a tuning fork can spread considerably and could, perhaps, reach sensitive areas outside the ones they believed they were testing.

Trotter and Davies (1909), repeated the experiment of Head more than once, and as a result of the repetition were led to conclusions which differed from Head's on nearly every point. They say, however, that they found no evidence that sensibility to heavy pressure and to vibrations is in any way affected by loss of sensibility confined to the skin.

Echlin and Fessard (1938) led off the action potentials from various nerves in the hind limbs of cats and rabbits and frogs while vibrating tuning forks were applied to the bones and tendons of the limbs. They obtained a series of discharges which were synchronized with the vibrating stimulus up to frequencies of 400-500 cycles per second. They were unable to find any synchronized responses by applying vibration to the skin of the limbs unless the tines were applied, the base of the fork was ineffective. The synchronized responses remained when the skin was removed. These responses, they believe, arise in the stretch receptors in the muscles; for when the tuning fork is applied while a muscle is under some tension, the asynchronous discharges from the stretch receptors disappear and are replaced by the discharges which are synchronous with the fork. They indicate that these responses are responsible for deep vibration sensitivity.

These experiments taken with those above of Adrian, McKeen Cattell and Hoagland show that the evidence obtained from action potentials in afferent nerves instead of deciding in favor of one side or the other of the question of cutaneous versus deep sensibility, suggest rather that receptors in both cutaneous and deep tissues may participate.

The commonly accepted conception of the pathway for the sense of vibration is that it is by the deeper sensory nerves to the posterior roots, then up the posterior columns of the same side of the spinal cord to the medulla, then across to the thalamus.

The upper frequency limit for the sensation of vibration in man is generally found to be in the neighborhood of 1200-1500 cycles per second.

The lower limit has not been much explored. At frequencies below about 50 cycles per second the sensation becomes rather vague, that is to say, there is an indeterminate region in which vibration passes over into a series of individual impacts and the quality of the sensation appears to change. At the upper frequencies most observers have failed to get results beyond the range of 1000 to 2000 cycles per second. As the frequency is increased, the amplitude of vibration from tuning forks or any other vibrator of limited power grows less and there is always the possibility that responses might be obtained at higher frequencies if the amplitude of vibration could be further increased. No one has yet made observations with devices capable of generating at these high frequencies vibrations of greater than ordinary amplitudes.

Skolnick (1938) with rats trained by the choice and reward method involving platforms which could be vibrated, found that rats could make discriminations up to an upper frequency limit of approximately 1800 cycles per second.

This study of vibration sensation is part of a survey of wider scope carried out on employees at the Lockheed Aircraft Corporation at Burbank, and at the Los Angeles County Poor Farm, Rancho Los Amigos, Hondo, California.

The purpose of the work at these two places was to see what effect adding large amounts of vitamins to the otherwise unchanged diets of the employees might have on the incidence of illness, accidents and absences, and to find out if this treatment would produce any changes in the men which could be measured by the procedures commonly used in surveys of nutritional status.

At Lockheed the men who took part were all white males. They constitute a fairly young age group. These men volunteered and came for the examinations on their own time. These examinations were conducted at the beginning and at the end of the experimental period which lasted for about one year. The first examinations were made from November, 1941, to February, 1942; the second examinations from December, 1942, to April, 1943.

The men who volunteered were divided into two groups, one of which received therapy in the form of vitamins and minerals; the other group received placebos or dummy tablets of similar appearance. All of the men were originally on the swing shift which works from 4:00 in the afternoon until 12:30 A.M. The control and experimental groups were equally divided in the major departments where they worked. The therapy and dummy tablets were given to the men twice in each shift, once in the first half and once in the second half, five days a week.

The therapy, in the form of capsules or tablets, was as follows:

	Per Day
Vitamin A	50,000 International units
Vitamin D	800 International units
Vitamin B_1	10 mg.
Vitamin B_2	10 mg.
Niacinamide	100 mg.
Vitamin C	250 mg.
Calcium	0.5 gm.

Of the group studied at the Rancho, no patients, only male employees have been included. The procedures and examinations carried out at the two places were the same, and both the Lockheed and Rancho experimental groups received the same therapy. However, the Rancho men are older.

In the course of the first examination of Lockheed men, a fairly large number, approximately 25%, were found to have loss in their toes of vibration sensation to a tuning fork of 256 cycles per second (C.P.S.). It seemed that a more thorough investigation of this sensation might be of value.

Between the first and second examinations, the apparatus described in this paper was designed and built and at the time of the last examination, this apparatus was used to test all the subjects over the whole range of frequencies in which they could feel vibration.

Apparatus and Methods

The vibrator used was electrically driven. A variable frequency audio oscillator generated the needed frequencies, the output from the oscillator was fed into an amplifier in which was incorporated a volume control. The output of the amplifier was fed into the vibrator unit which transformed the electrical oscillations into mechanical movements. A voltmeter was used to measure the strength of signal supplied to the vibrator unit and an oscillograph was used as a check when necessary on the frequency of the oscillations by comparison with the frequency of the 110-volt input to the apparatus.

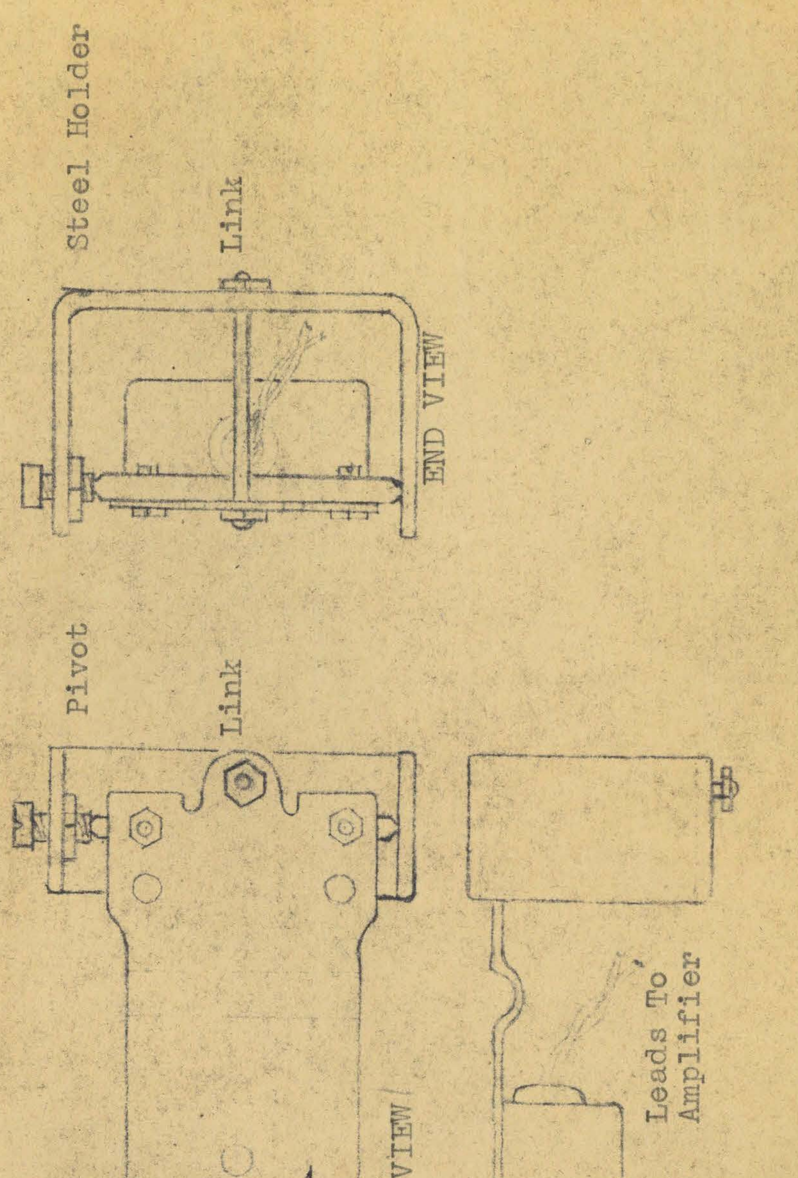
The audio oscillator was one with a range from 20 to 24000 cycles per second. Only the lower ranges from 50 to 1500 cycles per second were used. The oscillator was of the type in which the frequency is determined by a resistance capacity network, and was found to be very stable. The warming up period is short, a matter of only two or three minutes, and there is very little subsequent frequency drift. After several months of operation, of several hours a day, it was found that the calibration had not changed appreciably.

The amplifier was a commercial model, Clarion Model A3. A volume control was used to regulate the strength of the signal fed into the vibrator unit and so the strength of the stimulus applied to the subject.

The vibrator unit consisted of an Astatic M 41, magnetic, cutting head mounted in a special holder. This cutting head is one which is manufactured and sold for making gramophone records.

The design of the holder is illustrated in the drawing on page 18. Fixed to the cutting head in a transverse position, with two small machine screws, is a brass pivot with pointed ends. One end of the pivot works in a hole drilled in the "U" shaped steel holder, the other end in a similar hole drilled in the end of the 6-32 machine screw; the screw is adjusted to the proper position and locked in place with the jam nut. The holder is a piece of 3/32" x 3/4" steel bent to shape. There is also a link passing through the hole in the end of the cutting head and a hole drilled in the steel holder; it is a loose fit, and has 4-40 nuts threaded and soldered to each end.

In some preliminary experiments it was found impracticable to have the cutting head held in any fixed type of holder. The time of adjustment is too long, and it was found to be very inconvenient when moving the vibrator from one toe to another or from one foot to another. Furthermore, the subjects will occasionally move their feet or toes, and there were difficulties in maintaining anything like a constant pressure on the



VIBRATOR UNIT. SCALE FULL SIZE.

needle. With the arrangement described above and with a needle fixed on the vibrator unit the whole arrangement can be conveniently held in one hand in such a way that the weight is suspended on the pivot and by the link at the back. When the needle is placed on the subject's toe and the hand is lowered a little so that the link at the back is free, all the overbalanced weight of the cutting head is supported on the toe. This weight of course is constant. Used in this way the instrument can be very rapidly moved from one toe to another with one hand, leaving the other hand free to operate the volume control and to make records of the readings obtained.

The needle was made of a piece of music wire .036" in diameter, 1" long, with a flat brass button .080" diameter soldered to the end. When in the operating position, pressure on the button was 80 gm.

All parts of the apparatus were well grounded.

The vibrator as produced by the maker was designed to have a fairly flat frequency response over the audio range. That is to say, with constant input the amplitude of the cutting stylus or needle was very similar at different frequencies. However, in place of the regular short needle, we used a somewhat longer one as explained above.

The amplitude of the vibrations actually applied to the subjects' toes has been measured in the following manner. A small mirror was fixed to the needle and with the vibrator in place on a toe in the ordinary manner the mirror was illuminated in such a way as to reflect a spot of light on a screen some distance away. Then with equal strength of signal applied to the vibrator the movement of this spot of light was measured over the whole frequency range which was used. The results, as relative amplitude of movement, are given in Table 1.

It can be seen that from 150 cycles per second to 600 cycles per second, the amplitude of the vibrations is relatively constant. At lower frequencies the amplitude increases, and above 600 cycles per second the amplitude decreases. The irregularities are probably less than the figures indicate.

Vibration sensation was explored on the toes because it was on the toes that the observations with the 256 tuning fork were made in the first examinations, and because the toes are less sensitive than the fingers.

The tests were always conducted in rooms which were adequately heated, and it was found best to insure that the subject's feet were not cold. This was of particular importance as many of the tests were conducted during cold, rainy weather and some of the subjects had come in from working outside. To guard against cold the subject's bare feet were routinely warmed over a small electric heater for a few minutes before the test was begun. Feet which felt cold to the touch were found to give irregular, unreliable responses. Experiments on two subjects showed that while cooling the skin with cold water raises the threshold to vibration, warming it does not lower the threshold below normal.

The apparatus was arranged along the front of a table of normal height, and the subject was seated on the table at one side of the apparatus. The feet were supported on a low stand; part of the top of the stand facing the subject sloped down, the rest was flat. The feet were placed so that the toes more or less curled over the break between the sloping and horizontal portions.

Seated on a low stool, it was possible to hold the vibrator unit in one hand, and resting the hand on the flat part of the stand, the button of the vibrator could be placed on any of the toes.

The first part of the test was conducted with two tuning forks, one of 128 C.P.S. and one of 256 C.P.S. Each tuning fork in turn was started and the subject allowed to feel the vibrations on a finger of one hand. He was then told that the tuning fork was to be applied to his toes and he was to say, "Yes" if he felt any vibration. He was instructed to close his eyes. All toes of both feet were tested in this way and the results entered on a form.

Because of the large number of men, and the number of examinations to which each man was subjected, there was only a limited amount of time for each test. Consequently, it was not always possible to examine with the electrical vibration apparatus the toes of both feet. Also in nearly every case the fifth or small toe was not tested at all. In a great many people this toe is so curved that it was not possible to place the vibrator on the toe in the proper position.

In those cases in which the response to the 256 tuning fork was not positive for every toe, the foot with the fewer positive responses was selected for testing with the electrical vibrator.

Tests with both the tuning forks and the electrical vibrator were made on the skin over the nail bed.

The procedure with the electrical vibrator was similar to that used with the tuning forks. The subject was first allowed to feel vibrations of one or two frequencies upon a finger. He was instructed to keep his eyes closed throughout the test. With the volume control turned down, and so, no signal in the vibrator, the vibrator was placed on one of the toes. Then, at the frequency which had been chosen, the volume control was turned up until the subject reported that he felt vibration by saying, "Yes." This was repeated with the other toes of the foot at various frequencies, choosing the toes at random, and varying the frequencies irregularly. The usual procedure was to quickly and rather roughly map out the higher frequency limits, then determine the limits more carefully and fill in the intermediate frequencies.

It was soon found that the chief likelihood of error was one caused by the subject trying to do well, and saying, "Yes" when no signal was given or one so weak that previous tests had indicated it should not give a positive response. At the beginning of the tests the subjects were warned that sometimes they would not feel any vibration but only the pressure of the instrument. Throughout the test "blank stimuli" were given -- that is, the vibrator was placed on a toe and left there for the usual interval but the volume control was not turned up. Most subjects, of course, made no response to this procedure. This method we believe to have been effective in ruling out false responses. There are, however, a not inconsiderable number of people who persist in giving a positive response to this "blank stimulus" and one is forced to conclude that either they were lacking in vibration sense under conditions of the test or they so easily confused the touch or pressure of the instrument with the sensation of vibration that they could not distinguish between the two. All these cases were marked as unreliable and have been rejected.

On the average it took about 15 minutes to complete the test on one person.

The results were entered on the form on the next page.

Name:_______________ Age:____ Survey No:______
Date:_______________ Sex:____ By:______________

VIBRATION SENSATION DETERMINATION

R. injuries:

L. injuries:

	128	256	50	100	150	200	250	300	350	400	50
R 5											
4											
3											
2											
1											
L 1											
2											
3											
4											
5											

	600	800	1000	1500			REMARKS
R 5							
4							
3							
2							
1							
L 1							
2							
3							
4							
5							

ADAPTATION

One question to be settled is whether, with the type of stimulus used, adaptation would be great enough and rapid enough to interfere with the performance of the test.

Cohen and Lindley (1938), claim to be the first to have studied the effect of continued vibratory stimulation. With a stimulus of 60 C.P.S. they found the effect of a supra-liminal stimulus is to raise the threshold. Stimulation at or near threshold strength had little effect on the threshold unless continued for some time.

Evidence has been obtained that adaptation may be excluded under the conditions, and with the methods, used in this work. Three subjects were used who were not members of either the Lockheed or the Rancho groups.

The vibrator, clamped by its holder in a stand, was placed on the right big toe of each of the subjects. The threshold at a frequency of 200 C.P.S. was determined by obtaining three consistent readings. The vibrator was then turned on at a little above threshold strength and kept in action. At intervals the input to the vibrator was shut off and a threshold on the same spot, without moving the vibrator, was again quickly determined with three consistent readings. The vibrator was then turned on again, usually with an increase of strength to take care of the increase in threshold which was found. Of the three cases tested, two were quite reliable and one was somewhat uncertain in his responses.

In all three cases, the threshold rose somewhat during the first fifteen or twenty minutes and then reached a plateau which remained the same until the end of the test which all together lasted not over thirty minutes. This is about as long as anyone cares to stand the application of the vibrator to one spot. In two cases, the threshold was finally raised about 50%, and in one case, about 100%. At the end of the period of almost continuous stimulation the vibrator was shut off. Following this, the threshold was tested both at the same spot and at neighboring spots at frequent intervals. The threshold at the adapted spot returned to its original value in one case in four minutes, in one case in five minutes, and in one case in eleven minutes. In all cases the thresholds at points about 5 mm. away from the adapted spot were raised by about the same amount as the one where the vibration had been applied. Although the threshold rises most in the first few minutes, the rise in the first few seconds is too small to be determined with any certainty.

As continuous vibration, except for short intervals for testing the threshold, took several minutes to raise the threshold, and as the return to normal was much shorter than this, it is unlikely that adaptation interfered in any way with the thresholds which have been determined. In the regular routine, the application of the vibrator to any one toe lasted only a few seconds following which there was an interval while other toes were being tested. The tests were done with the vibrator starting at rest, by increasing the strength of stimulus until the threshold was reached, so that the period during which vibration was appreciated was only a brief portion of the total time the vibrator was applied.

RESULTS

The results of testing four toes on one foot with the tuning fork of 128 C.P.S. are shown in Table 2. The table gives the number of experimental and the number of control cases for both the Lockheed group and the Rancho group. Of 618 men tested, 615 were positive on all 4 toes, only 1 was negative on all 4 toes, and 1 was negative on 3 toes and 1 negative on 1 toe. The response to a tuning fork of this frequency is almost 100% positive.

Table 3 shows a similar tabulation of the responses to a tuning fork of 256 C.P.S. In this case there are many more negative responses.

Of the total number of men, 252, or approximately 41% had one or more toes which were unresponsive to this stimulus. The distribution, by number of toes failing, is as follows:

In the experimental group, of the 138 cases

35.5% gave negative responses on 1 toe
29.7% gave negative responses on 2 toes
16.7% gave negative responses on 3 toes
18.1% gave negative responses on 4 toes

In the control group, of the 114 cases

42.1% gave negative responses on 1 toe
28.9% gave negative responses on 2 toes
15.8% gave negative responses on 3 toes
13.2% gave negative responses on 4 toes

The initial observation which suggested that a more thorough investigation of vibratory sensation than could be accomplished with a tuning fork would be useful was made at the time the group of men at Lockheed was examined for the first time. Of the 1153 cases observed then, 996 were tested with a tuning fork of 256 C.P.S. 256 of these men, or 25.7%, failed to respond.

In this, the second examination, 252 out of 617 cases, or 40.8%, gave negative responses on one or more toes. This discrepancy can be explained by the more careful attention which was paid to this examination the second time and the fact that on each person more toes were tested, so it is possible that some men originally classified as being positive would have given a negative response on one toe if all the toes had been tested.

Table 4 shows the relation between testing the toes with a tuning fork of 256 C.P.S. and with the electrically driven vibrator at 250 C.P.S. As all four toes were tested it was thought better in arranging this table not to take any arbitrary figure of, say, three toes positive and call such a case positive or to adopt any other measure to divide positive from negative cases, but rather to make a tabulation of the whole number of toes tested, which gives a figure four times the number of cases. As can be seen from the totals at the bottom of the table, 76% of the toes of men in the experimental group and 79.8% of those in the control group were positive to both the tuning fork and the electric vibrator at these frequencies. 3% and 3.5% respectively were negative to both the tuning fork and the electric vibrator. Less than one per cent in each group were positive to the tuning fork and negative to the vibrator. 20.4% and 15.8% in the two groups were negative to the tuning fork and positive to the electric vibrator.

It should be noted that the electric vibrator is capable of giving a somewhat stronger stimulus than the tuning fork so that some cases in the last classification of negative to the tuning fork and positive to the electric vibrator are to be expected.

Individuals vary as to the highest frequency they are able to feel. When, on increasing the frequency of stimulation, a frequency is reached to which the subject no longer responds with all four toes, all the toes do not cease to respond together. There is a scattering in the number which drop out together. In table 5 are tabulated the results from all the groups.

The table shows that for all cases just over 50% first indicated that they had reached the frequency which they cannot feel on all toes by failing to feel that frequency on one toe only. Only a very small number (the average for all cases is 4% of those tested) fail with four toes at a time when they are tested with a frequency which is too high.

More than 25% of the cases tested, first failed to respond to increasing frequency on two toes, and approximately 12% failed with three toes at a time.

The preponderance, over 50%, of cases dropping out with one toe, is explained when an examination is made of the extent to which the different toes of the foot participate. If the different toes, first, second, third, or fourth, were equally sensitive it might be expected that one would occur as often as another. This was not found. Actually, in the class which drops out one toe at a time, the first toe occurs about twice as often as might be expected. The second, third, and fourth toes are about equally represented.

The numbers failing to respond to increasing frequency by one toe at a time or two toes at a time together amount to over 80% of all the cases. In determining the highest frequency to which any one man was found responsive, this point, that is the highest frequency to which two or more toes respond, has been taken.

From the data obtained, tabulations were made showing the highest frequencies to which each man responded. These were arranged by age groups and by experimental and control groups. The group of cases from the Rancho included in this tabulation were especially valuable because most of them are older persons and they provide figures in higher age groups where the

Lockheed group gives only a few cases. Although in the original tabulations the age groups chosen were 20-24 years, 25-29 years, 30-34 years, 35-39 years, 40-50 years, 50 years and over, the final tables have been prepared on a broader basis with the following age groups: 20-29 years, 30-39 years, 40 years and over.

The first two of these tables, No.'s 6 and 7, show the Lockheed and Rancho cases arranged according to the highest frequency felt. One table includes the cases in the experimental group; the other, the cases in the control group. In each age group in both tables the first line gives the number of persons under the highest frequency they were capable of feeling. The second line gives under each frequency, the percentage of the men in the group who responded to that frequency or a higher one.

It can be easily seen from inspection of the tables that one of the features of the younger age groups is an ability to perceive higher frequencies than persons in the older age groups. The difference between the age groups 20-29 years and 40 years and over is most marked; as can be seen by comparing these two age groups in their response to a frequency of 500 C.P.S.

The next table, No. 8, includes only the cumulative percentages from the two previous tables, for ease of comparison between the experimental and control groups. There has been added a line which shows, for each age group, the difference, D, between these percentages. A positive difference indicates that at that frequency the experimental group surpassed the control group, and vice versa.

In the first age group, 20-29 years, most of the differences are small; they are also both positive and negative.

In the second age group, 30-39 years, the differences are all positive, but too small to be significant.

In the third age group, 40 years and over, the differences are again all positive, and they are larger. The standard error of the differences between the percentages, σD_p, has been calculated for the frequencies from 300 to 600 C.P.S., and also the ratios of the differences to the standard errors. They are as follows:

C.P.S.	300	350	400	500	600
σD_p	.093	.108	.113	.106	.074
$\frac{D}{\sigma D_p}$	1.1	1.4	0.9	0.4	2.0

It is customary to regard a ratio $\frac{D}{\sigma D_p}$ as significant when it is 3 or greater. None of these differences between experimental and control, in the age group 40 years and over are significant, nor are any of those in the other age groups.

As both experimental and control groups are so similar, they have been added together for the purpose of constructing table 9. In this table, the numbers of men are again arranged according to the highest frequency to which they responded, and are divided only into the three age groups. Lines 1, 2, and 3 show, under each frequency, the percentage of the men in the group who responded to that frequency or a higher one.

This table also includes the results of calculating the ratio of the difference (D) to the standard error of the difference (σD_p). At the lower frequencies the ratios have not been determined beyond the point at which they become insignificant; at the higher frequencies they have been carried out to the end, except for the entries under 1000 C.P.S. where the difference is negative.

Between the groups 20-29 years and 30-39 years, the differences are below the level of significance. Between 30-39 years and 40 years and over the differences are greater, at 5 frequencies out of 7 the ratio $\frac{D}{\sigma D_p}$ is greater than 3, and between the groups 20-29 years and 40 years and over the differences are still larger.

Table 10 gives the age distribution of the men included in tables 6, 7, 8, and 9. The experimental group has a smaller proportion of younger men, and a larger proportion of older men than the control group. This would tend to make the performance of the experimental group poorer.

The numbers entered on the form at the time of the examination were measures of the threshold of the subjects to the frequency used. As was mentioned in the description of the apparatus, this value was observed by taking a reading from the voltmeter across the output of the amplifier. The voltmeter was supplied with a multiplier switch with six positions. Each range of this switch represented twice the voltage of the range below it. In any particular case after the correct range had been found, the output was increased while watching the needle of the voltmeter and its position noted at the time the subject said, "Yes", indicating when he felt the vibration. Consequently, the entries consisted of two numbers, the first one indicating the range of switch used and the other the reading on the meter. As often as possible, the readings on the meter were confined to the central part of the dial.

All these readings converted to whole numbers and fractions expressed as decimals have been tabulated on the basis of four toes on one foot for all the subjects in the two groups (excluding the unreliable ones), and divided into age groups and into experimental and control groups. In any one group all the readings at one frequency have been averaged. From these averages, it is possible to construct a table representing the change of threshold with frequency. This has been done in Table 11. In this table all values representing less than 20 cases have been omitted.

The table shows, following it from side to side, that there is a regular variation of the mean thresholds with respect to frequency of stimulation, except at 400 C.P.S. The reason for the drop at this frequency is undetermined.

It should be remembered that the characteristics of the vibrator unit are such that the amplitude of the vibration delivered at 50 and 100 C.P.S. is greater than the relative voltage readings indicate, so that the thresholds at these two values are higher than the figures show.

After dropping to a low value at 200 C.P.S., the thresholds rise throughout the range of increasing frequency.

In the age group 20 - 29 years the differences between the experimental group and control group are variable. At three frequencies, 200, 500, and 600 C.P.S. those in the experimental group have lower mean thresholds than those in the control group; the differences are positive. At four frequencies, 50, 100, 350, and 800 C.P.S. the differences are negative. At three frequencies there is no difference.

The differences between the mean thresholds in the next age group, 30-39 years, are positive at three frequencies, 200, 250, and 600 C.P.S., negative at three frequencies, 50, 350, and 400 C.P. S., and at three there is no difference.

In the last age group, 40 years and over, at two frequencies, there is no difference between the experimental and control groups; at the other four frequencies the differences are all positive, and are larger than similar differences in other age groups. The differences, D, for this age group only, are entered in the next to last line of the table.

The standard errors of the means, σ M, for both experimental and control groups have been calculated for this age group, from the data from which table 11 is derived, and from these the standard error of the differences between the means, σ D. The last line in the table shows the ratio, $\frac{D}{\sigma D}$, between the difference and the standard error. All these ratios are less than 3.

For purposes of comparing the thresholds at different ages the experimental and control groups have been combined. The new mean thresholds for the three age groups are entered in the first three lines of table 12. The rise in the threshold with increasing age is quite clear.

The standard errors of all these means, σ M, have been calculated from the original data, and from these the standard error of the difference of the means, σD. The ratios of the difference between the means to the standard error of the difference, $\frac{D}{\sigma D}$, have been entered on the last three lines of the table.

The ratios, except for the two underlined in the table, are all greater than 3. The differences between the age groups are then significant.

The variation of the threshold to vibration with frequency, exhibited in tables 11 and 12, is similar to previously reported results. Other workers have generally determined such thresholds by investigations on a few people. The present investigation is less intensive, but included a large group, over 600 cases in all.

The increase of the threshold of vibration with increasing age is one of the most striking features of this work, and was one of the first effects to be noticed. Newman and Corbin, (1936) seem to have been the first to measure this quantitatively, finding the chief increase at 50 years of age and over. They measured the threshold at one frequency, 60 C.P.S.

This work, based on a larger number of men, shows in tables 9 and 12, increases of thresholds with age at all the frequencies used, which are significant for the two older age groups, and probably significant for the interval between the two younger groups.

Because the thresholds are higher at the upper frequencies, and because any instrument used as a source of vibrations will have a maximum output beyond which it cannot go, older men will often fail to respond to the highest frequencies.

If there is any difference between the experimental group which received the therapy and the control group which did not, tables 8 and 11 show that there is little difference to be found in the thresholds of the two younger age groups. In the age group 40 years and over the differences, though larger, are below the level which is commonly considered significant. If these differences were sought in a similar group and under comparable conditions, it might be advisable to use a population of older persons.

The lowest thresholds found in this study correspond to a power input to the vibrator of approximately 0.008 watt. The efficiency of the vibrator unit is unknown; but at least these low thresholds correspond to a power level applied to the skin of less than 0.008 watt.

The sensation aroused by contact with a vibrating object may be of use to an engineer, or anyone who might wish to know by applying his hand whether, for instance, a piece of machinery is running smoothly or not. The need for this sort of information is a relatively recent one.

A few experiments have suggested that the sensation of vibration may be of assistance in the appreciation of that quality of a surface which is spoken of as texture. If two objects with surfaces which are not visibly of a different roughness or smoothness are presented to a person with the request that he express an opinion as to which is the smoother or which is the rougher, he will rub his fingers over the two surfaces in order to compare them. By passing a finger across the proper kind of surface it is easy to obtain impressions which do not seem to differ greatly from those received from an object which is vibrating. With surfaces which are not too coarse-grained it is difficult and sometimes impossible to make judgments about their texture by merely placing a finger on them without moving it about. Even with movement, it is difficult to make decisions about this quality of surfaces, if they are applied to an area of the skin which is relatively insensitive to vibration.

Though the sense of vibration may assist in judgments of texture, other sensations may participate, such as touch and the compass sense----that is, the ability to perceive as separate two closely spaced points which are pressed on the skin.

TABLE 1

AMPLITUDE OF VIBRATION AT DIFFERENT FREQUENCIES WITH NEEDLE IN PLACE ON A TOE AND CONSTANT INPUT TO VIBRATOR

	Frequency, cycles per second												
	50	100	150	200	250	300	350	400	500	600	800	1000	1500
Amplitude (relative)	14	14	8	8	7	8	8	8	9	8	5	4	3

TABLE 2

RESPONSE TO TUNING FORK 128

TABULATION FOR 4 TOES OF 1 FOOT

		No. of cases	4 toes positive No.	4 toes positive %	Fewer than 4 toes positive
LOCKHEED	Experimental	299	297		2
	Control	275	275		0
RANCHO	Experimental	23	23		0
	Control	21	20		1
TOTAL, ALL CASES		618	615	99.5 %	3

TABLE 3

RESPONSE TO TUNING FORK 256

TABULATION FOR 4 TOES OF 1 FOOT

		No. of cases	4 toes positive No.	4 toes positive %	Fewer than 4 toes positive No.	Fewer than 4 toes positive %
LOCKHEED	Experimental	298	170	57.0	128	43
	Control	275	169	61.5	106	38.5
RANCHO	Experimental	23	13	56.5	10	43.5
	Control	21	13	61.9	8	38.1
TOTAL, ALL CASES		617	365	59.2%	252	40.8%

TABLE 4

RELATION BETWEEN TESTS ON 4 TOES WITH A TUNING FORK AT 256 C.P.S.

AND WITH ELECTRIC VIBRATOR AT 250 C.P.S.

	No. of toes tested	256 tuning fork + / 250 vibrator +	256 tuning fork + / 250 vibrator -	256 tuning fork - / 250 vibrator -	256 tuning fork - / 250 vibrator +	
LOCKHEED						
Experimental	1180	899	6	33	242	No. of toes
		76.2	0.5	2.8	20.5	% of toes tested
Control	1096	882	10	30	174	No. of toes
		80.5	9.9	2.7	15.9	% of toes tested
RANCHO						
Experimental	92	68	1	5	18	No. of toes
		73.9	1.1	5.4	19.6	% of toes tested
Control	84	60	1	11	12	No. of toes
		71.4	1.2	13.1	14.3	% of toes tested
TOTAL						
Experimental	1272	967	7	38	260	No. of toes
		76.0	0.6	3.0	20.4	% of toes tested
Control	1180	942	11	41	186	No. of toes
		79.8	0.9	3.5	15.8	% of toes tested

TABLE 5

EFFECT OF INCREASING THE FREQUENCY OF STIMULATION

NUMBER OF TOES DROPPING OUT TOGETHER AT POINT

WHERE FAILURE TO RESPOND FIRST OCCURS

	EXPERIMENTAL					CONTROL					
		No. of toes showing loss of sensation					No. of toes showing loss of sensation				
	No. of cases	1	2	3	4	No. of cases	1	2	3	4	
LOCKHEED	302	55.3	29.1	11.6	4.0	280	54.6	27.9	13.2	4.3	% of cases in each class
RANCHO	23	56.5	21.7	17.4	4.3	21	61.9	19.0	19.0	0.0	% of cases in each class
TOTAL	325	55.4	28.6	12.0	4.0	301	55.1	27.2	13.6	4.0	% of cases in each class

TABLE 6

EXPERIMENTAL GROUP

NUMBER OF MEN ARRANGED ACCORDING TO HIGHEST FREQUENCY TO WHICH 2 OR MORE TOES OF 1 FOOT RESPONDED

AGE GROUP IN YEARS AND NO. OF MEN	Frequency, cycles per second 150	200	250	300	350	400	500	600	800	1000	1500	
20 - 29		1	5	7	8	36	35	41	31	9	1	No. of men
(174 men)		100	99.5	96.5	92.5	87.9	67.2	47.1	23.6	5.7	.6	Cumulative %
30 - 39			4	3	12	21	24	22	10	6		No. of men
(102 men)			100	96.1	93.1	81.4	60.8	37.3	15.7	5.9		Cumulative %
40 +	1	2	4	5	11	9	5	8	2			No. of men
(47 men)	100	97.9	93.6	85.1	74.5	51.1	31.9	21.3	4.3			Cumulative %

TABLE 7

CONTROL GROUP

NUMBER OF MEN ARRANGED ACCORDING TO HIGHEST FREQUENCY TO WHICH 2 OR MORE TOES OF 1 FOOT RESPONDED

AGE GROUP IN YEARS AND NO. OF MEN	Frequency, cycles per second											
	150	200	250	300	350	400	500	600	800	1000	1500	
20 - 29	2	1	5	5	7	33	48	62	21	6	1	No. of men
(191 men)	100	99.0	98.4	95.8	93.2	89.5	72.3	47.1	14.7	3.7	.5	Cumulative %
30 - 39	1	0	4	5	8	17	17	16	4	4		No. of men
(76 men)	100		98.7	93.4	86.8	76.3	53.9	31.6	10.5	5.3		Cumulative %
40 +	0	1	7	5	6	4	7	2				No. of men
(32 men)		100	96.9	75.0	59.4	40.6	28.1	6.2				Cumulative %

TABLE 8

ACCUMULATED PERCENTAGES BY AGE GROUPS OF MEN ACCORDING TO HIGHEST FREQUENCY TO WHICH THEY RESPONDED

COMPARISON OF EXPERIMENTAL AND CONTROL GROUPS FROM TABLES 6 AND 7

AGE GROUP IN YEARS		Frequency, cycles per second										
		150	200	250	300	350	400	500	600	800	1000	1500
20 - 29	Experimental		100	99.5	96.5	92.5	87.9	67.2	47.1	23.6	5.7	0.6
	Control	100	99.0	98.4	95.8	93.2	89.5	72.3	47.1	14.7	3.7	0.5
	Difference			+1.1	+0.7	-0.7	-1.6	-5.1	0	+8.9	+2.0	
30 - 39	Experimental			100	96.1	93.1	81.4	60.8	37.3	15.7	5.9	
	Control	100		98.7	93.4	86.8	76.3	53.9	31.6	10.5	5.3	
	Difference				+2.7	+6.3	+5.1	+6.9	+5.7	+5.2	+0.6	
40 +	Experimental	100	97.9	93.6	85.1	74.5	51.1	31.9	21.3	4.3		
	Control		100	96.9	75.0	59.4	40.6	28.1	6.2			
	Difference				+10.1	+15.1	+10.5	+3.8	+15.1			

TABLE 9

ACCUMULATED PERCENTAGES BY AGE GROUPS OF MEN ACCORDING TO HIGHEST FREQUENCY TO WHICH THEY RESPOND

COMPARISON OF AGE GROUPS

	Frequency, cycles per second											AGE GROUP YEARS
	150	200	250	300	350	400	500	600	800	1000	1500	
1	100	99.5	98.9	96.2	92.9	88.8	69.9	47.1	18.9	4.7	0.5	20 - 29
2	100		99.4	94.9	90.4	79.2	57.9	34.8	13.5	5.6		30 - 39
3	100	98.8	95.0	81.0	68.4	46.8	30.4	15.2	2.5			40 +
$\frac{D}{\sigma D_p}$ of 1 & 2					0.3	2.7	2.6	2.7	1.6			
$\frac{D}{\sigma D_p}$ of 2 & 3			1.8	3.0	2.2	5.1	4.3	3.6	3.4			
$\frac{D}{\sigma D_p}$ of 1 & 3			1.5	3.4	4.5	7.1	6.9	6.6	6.3			

TABLE 10

AGE DISTRIBUTION OF THE MEN

INCLUDED IN TABLES 6-7-8-9

	Age Group Years	No. of Men in Each Age Group	No. of Men in Each Age Group as % of Total No.
Experimental	20 - 24	79	24.5
	25 - 29	95	29.4
	30 - 34	58	18.0
	35 - 39	44	13.6
	40 - 49	32	9.9
	50 +	15	4.6
		Total 323	

Experimental, Mean Age 31.0 years

	Age Group Years	No. of Men in Each Age Group	No. of Men in Each Age Group as % of Total No.
Control	20 - 24	85	28.4
	25 - 29	106	35.5
	30 - 34	51	17.1
	35 - 39	25	8.4
	40 - 49	25	8.4
	50 +	7	2.3
		Total 299	

Control, Mean Age 29.6 years

TABLE 11

THRESHOLDS IN ARBITRARY UNITS AT

VARIOUS FREQUENCIES, BY AGE GROUPS

AGE GROUP YEARS		Frequency, cycles per second											
		50	100	200	250	300	350	400	500	600	800	1000	1500
20 - 29	Experimental	3.8	2.5	2.9	3.7	4.2	5.5	5.0	5.5	5.9	6.3	6.6	
	Control	3.7	2.4	3.0	3.7	4.2	5.3	5.0	5.6	6.0	6.2		
30 - 39	Experimental	4.1	2.8	3.4	4.0	4.6	5.7	5.4	5.8	6.0	6.4		
	Control	4.0	2.8	3.5	4.2	4.6	5.5	5.1	5.8	6.1			
40 +	Experimental	4.7	3.6	4.2	4.7	5.3	6.0	5.9	6.3				
	Control	4.7	3.8	4.5	5.1	5.6		5.9					
40 +	D	0	+0.2	+0.3	+0.4	+0.3		0					
	$\frac{D}{\sigma_D}$		0.6	1.2	1.4	1.4							

TABLE 12

MEAN THRESHOLDS AT VARIOUS FREQUENCIES

COMPARISON OF AGE GROUPS

	Frequency, cycles per second										AGE GROUP YEARS
	50	100	200	250	300	350	400	500	600	800	
1	3.8	2.4	3.0	3.7	4.2	5.4	5.0	5.6	6.0	6.3	20 - 29
2	4.1	2.8	3.4	4.1	4.6	5.6	5.3	5.8	6.1	6.3	30 - 39
3	4.7	3.7	4.3	4.9	5.4	6.0	5.9	6.3			40 +
$\frac{D}{\sigma D}$ of 1 & 2	5.5	4.3	3.8	4.3	4.3	<u>2.1</u>	4.1	2.4	<u>1.8</u>		
$\frac{D}{\sigma D}$ of 2 & 3	6.1	5.2	5.6	5.1	6.2	3.0	4.3	3.4			
$\frac{D}{\sigma D}$ of 1 & 3	9.5	7.9	8.9	8.3	10.1	4.8	6.7	5.4			

LITERATURE CITED

Adrian, E. D., McKeen Cattell and H. Hoagland 1931 J. Physiol., 72, 377.

Békésy, G. 1939 Akust. Z., 4, 316.

Békésy, G. 1940 J. Exptl. Psychol., 26, 514.

Cohen, L. H., and S. B. Lindley 1938 Am. J. of Psychol., 51, 44.

Echlin, F., and A. Fessard 1938 J. Physiol., 93, 312.

Frey, von M. 1915 quoted from Geldard and others.

Geldard, F. A. 1940 J. Gen. Psychol., 22, 243.

Gilmer, B. von H. 1937 J. Exptl. Psychol., 21, 456.

Head, H., W. H. R. Rivers and J. Sherren 1905 Brain, 28, 99.

Head, H., and T. Thompson 1906 Brain, 29, 537.

Katz, D. 1923 Munch. Med. Woch., 70, 706.

Newman, H. W., and K. B. Corbin 1936 Proc. Soc. Exptl. Biol. Med., 35, 273.

Skolnick, A. 1938 J. Exptl. Psychol., 22, 273.

Trotter, W., and H. M. Davies 1909 J. Physiol., 38, 134.

Weitz, J. 1939 J. Exptl. Psychol., 25, 48.

Zotterman, Y. 1941 Ann. Rev. Physiol., 3, 475.

HEAT PRODUCTION OF SLOW AND FAST CONTRACTIONS OF A CRUSTACEAN MUSCLE WITH DOUBLE MOTOR INNERVATION

The heat liberated during a contraction of a crustacean muscle was measured first by Bronk (1932), who used the adductor muscle of the claw of Maia. He measured the heat produced during contractions lasting several seconds. The claws were separated from the animal and the muscles were stimulated by small electrodes entering through holes drilled in the shell. A thermocouple was pushed into the muscle through another hole drilled in the shell.

It is likely that Bronk stimulated the whole nerve bundle. It has been demonstrated since that time (van Harreveld and Wiersma, 1936; Wiersma and van Harreveld, 1938a) that many of the leg muscles of crustaceans can contract in two ways when the appropriate, single, motor axons are stimulated. To do this, part of the meropodite is removed and the nerve exposed. The nerve can be separated into bundles and finally into single axons. As the work proceeds the bundles are tested by stimulation and the type of contraction elicited is noted; unwanted fibres are cut away.

The crayfish, Cambarus clarkii, has been used in the following experiments. In the adductor muscle of the claw of this animal a fast and a slow type of contraction may be elicited by stimulation of two single motor axons. One of these axons is thicker than the other; single induction shocks applied to it cause a quick, twitchlike contraction, and faradic stimulation a tetanus which may rise to a maximum in 1 or 2 seconds. This is the contraction referred to as the fast contraction. Stimulation of the other, thinner, fiber with single shocks causes no contraction, faradic stimulation results in a tetanus which may take 30 seconds or longer to develop its maximum tension. This is the slow contraction.

It has been shown by van Harreveld (1939a) that the nerve supply to these muscles is quite rich. There are always two nerve fibers which run together, and which branch at the same place, so that all the branches are double. This double innervation was found in the finest branches which could be seen ending on the muscle. Contractions have been observed by van Harreveld (1939b) in the same muscle fibers when the axons for the fast and the slow contractions were stimulated. It is concluded that the same muscle fibers participate in the two kinds of contractions.

In the claw of the crayfish an opportunity is provided of measuring the heat production of the two kinds of contractions, as these contractions can occur separately and in one muscle.

METHOD

In the usual method of preparing a claw so that fast and slow contractions may be obtained, the partly prepared claw is held with a clamp, in a dish of physiological salt solution on the stage of a binocular microscope. The nerve fibers are separated with fine needles, and tested by stimulation, after they are lifted above the surface of the solution on electrodes held in micro-manipulators. For the heat work it was necessary to devise some means of holding the claw and a set of electrodes, in such a way that the whole assembly, after preparation of the fibers, could be moved to a constant temperature vessel.

The claws were removed from the animal and a small hole drilled in the shell at about the center of the adductor muscle where a thermocouple could later be inserted. Part of the shell of the meropodite was cut away and the muscles in it removed. The claw was then firmly attached to a piece of bakelite slightly larger than the claw by wrapping with fine copper wire. The tip of the propodite was hooked under a metal stud in the bakelite. This stud provided solid anchorage for the claw when the dactylopodite was later caused to contract against an isometric lever.

This bakelite plate, with the attached claw, was then fastened to another heavier bakelite plate about 4" long by 2" wide by machine screws. On both sides of this large plate were pairs of platinum electrodes which could be moved in any direction. The joints were tight enough to hold the electrodes in any position they were moved to. The electrodes were connected to small binding posts in the corners of the larger plate.

This assembly was put in a dish containing physiological salt solution and the two single motor axons prepared in the usual way under the microscope. The moveable electrodes on the plate were then swung into position and adjusted to the two axons. The electrode wires, which were turned up at the ends to form small hooks, held the axons which were placed on them slightly separated from each other. It was now possible to move the claw to the constant temperature chamber and the two motor axons could be stimulated without any further disturbance or manipulation.

The constant temperature chamber was a heavy brass cylindrical vessel and cover. On the under side of the cover was a substantial bakelite frame for the claw and electrode assembly, and on the upper side of the cover another frame to hold an isometric lever. On the lower frame near the top were two large copper blocks, the cold junctions for the thermocouple. The thermocouple was made of No. 40 copper and constantan wires soldered at one end into the shape of a V, at the other end soldered directly to the copper blocks. The claw and electrode assembly was securely fastened to the lower part of this frame in a vertical position. The end of the thermocouple was inserted into the muscle through the hole in the claw and held in place with a small piece of wax. The dactylopodite was connected by a steel wire running through a glass tube in the cover to the isometric lever above. The ends of the wires from the stimulation apparatus, which came through other glass tubes in the cover, were connected to the binding posts on the claw assembly. Other tubes provided openings through which ran the connections from the copper blocks and through which physiological salt solution could be added and removed.

After the cover and the cylinder were assembled, the whole device was submerged about two inches below the surface of a large insulated water bath. The glass tubes through the cover extended well above the surface. The water bath was stirred and was kept at a temperature of 17° to 18° C. Physiological salt solution of the same temperature as the water bath was then added to the vessel to a level a little above the top of the copper blocks and a slow stream of oxygen bubbled through for stirring. Twenty-five minutes were found to be long enough to insure temperature equilibration and then all but about half an inch of the physiological salt solution was siphoned out.

At the end of each run, after the used claw had been removed, the cover and all the parts suspended below it, and the inside of the cylinder, were washed out with distilled water; the cylinder and cover were reassembled and kept in the water bath till the next experiment. From time to time it was necessary to renew the baked-on varnish which was used for insulation.

The galvanometer was a Kipp and Zonen, type Zb, with a period of 3 seconds. The leads to the galvanometer were run through glass tubes.

This arrangement, which was arrived at after some failures, proved to be satisfactory. The electrical circuit was guarded from external leaks and stray currents, and the zero of the galvanometer was stable and constant. This was checked at intervals by runs which were complete except that the thermocouple was attached not to a claw, but inserted into a hole in a piece of bakelite. Any accidental failures during an experiment showed up as erratic excursions of the galvanometer.

The method is similar to the one used by Bronk (1932), but is more elaborate because of the arrangements necessary to stimulate single axons.

Results

The fibers of the muscle are so attached to the claws that they cannot be removed as units which will function. This is made all the more impossible by the network of nerve fibers which is inevitably damaged if an attempt is made to separate any part of the muscle. This makes it impossible to work with a muscle unit which can be calibrated in the usual way by sending through it a known amount of electrical energy while a thermocouple is in place and at the same time observing the resulting deflection of the galvonometer. As this cannot be done, the heat has not been determined in absolute units.

The loss of heat from the muscle is small, as can be seen from the character of the galvanometer deflections. As soon as a contraction takes place there is a rapid deflection, which may continue after the contraction has stopped, and the return from the maximum position lasts for several minutes. The heat capacity of the thermocouple is small. The cold junctions are some distance away and of a rather large size. Consequently, the maximum deflection of the galvonometer is a measure of the rise of temperature in the muscle. These maximum deflections have been taken as a measure of the heat. They are expressed in arbitrary units and are referred to as H.

As a rule succeeding contractions in one claw were separated by intervals of ten minutes, to allow the galvanometer to return to its zero position.

The increases of temperature which were observed ranged from 0.01° C. to 0.05° C.

The observed galvonometer deflections are not due to escape of the stimulating current because the deflections continue after the stimulation is stopped. The possibility that the deflections are due to heat or current escape from the stimuli is also ruled out by the failure to get deflections on stimulating a dead preparation, that is, a claw which failed to contract when stimulated.

The contractions were recorded isometrically on smoked paper. The initial tension on the dactylopodite was 50 gm. in all cases. The amount of shortening in these muscle fibers is more difficult to estimate than in isolated muscles attached directly to a lever. However, from the amount the dactylopodite moved, it can be stated with certainty that the shortening did not exceed 0.1 mm. The area of the recorded curve of each contraction was measured. This area, which was taken as a measure of the mechanical work done, will be referred to as M.

To compare the heat production of the fast and slow contractions the ratio H/M is used, which is taken as a measure of the efficiency with which the muscle contracts. An examination of the data shows that the values of the ratios vary considerably from claw to claw. If the values could be reduced to absolute units much of this variation might disappear. As this reduction was not possible, the ratios H/M can be compared only in a series of contractions taking place in one muscle.

In the course of preparing the nerve fibers a minimum number of test stimuli were given, and the greatest care was taken to handle the fibers as gently as possible and to avoid stretching. The fact that the claw was fastened down to the plate which had on both sides of it binding posts and electrodes, interfered somewhat with the field of work and made this task more difficult. When the prepared axons were placed on the electrodes the smallest amount of separation possible inevitably placed them under a slight tension. Many preparations were lost at this point. Mounting the claw and electrode assembly below the cover of the constant temperature chamber, fastening the thermocouple in place, making the other electrical connections, and assembling the chamber took some minutes. This was followed by a longer period which had to be allowed for temperature equilibrium to take place.

The net result of all this was that by the time the experiment was ready to be performed, in most cases the preparation was no longer active. There was only a small number of claws in which one of the two types of contractions survived long enough to give a series of contractions. The number in which both fast and slow contractions survived was even smaller, and only in about a third of these did the claw remain active long enough to give more than one contraction of each type. To obtain the results described here a very large number of preparations had to be made.

Some of the claws in which only fast or slow types of contraction survived were used to see whether successive contractions in the same claw were similar. They were stimulated at intervals of 10 minutes. In any one claw the stimulation was of the same frequency and duration. It was found that in succeeding contractions, M, the area of the curve of contraction, became smaller. At the same time, H, the heat, also became less by a proportionately greater amount. Consequently, the ratios H/M became smaller in successive contractions, indicating an increase in efficiency.

The same was observed in experiments involving both kinds of the contractions in one claw. In these experiments the two motor axons were stimulated alternately, every ten minutes. Each fast contraction was less expensive, as is shown by the ratio H/M, than experiment was ready to be performed, in most cases the preparation was no longer active. There was only a small number of claws in which one of the two types of contractions survived long enough to give a series of contractions. The number in which both fast and slow contractions survived was even smaller, and only in about a third of these did the claw remain active long enough to give more than one contraction of each type. To obtain the results described here a very large number of preparations had to be made.

Some of the claws in which only fast or slow types of contraction survived were used to see whether successive contractions in the same claw were similar. They were stimulated at intervals of 10 minutes. In any one claw the stimulation was of the same frequency and duration. It was found that in succeeding contractions, M, the area of the curve of contraction, became smaller. At the same time, H, the heat, also became less by a proportionately greater amount. Consequently, the ratios H/M became smaller in successive contractions, indicating an increase in efficiency.

The same was observed in experiments involving both kinds of the contractions in one claw. In these experiments the two motor axons were stimulated alternately, every ten minutes. Each fast contraction was less expensive, as is shown by the ratio H/M, than its preceding fast contraction. This increased efficiency in successive contractions can be seen in tables 1 and 2. As a result of these changes in the course of every experiment, other differences to be evident must be larger.

In experiments in which fast or slow contractions were produced by stimulation throughout a wide range of frequencies, no relation could be discovered between the frequency and the ratio H/M.

It has been shown (Wiersma and van Harreveld, 1938b) that on continued stimulation of the axon for the fast contraction by single stimuli at a low frequency, the contraction disappears but the muscle action potentials continue without appreciable decrease in size. Two claws were brought into this condition by stimulation once every five seconds. Though the action potentials could not be recorded in these experiments, it can be assumed that they were present when contractions were no longer visible. As the twitch-like contractions disappeared, the heat production decreased and finally ceased when no further contraction could be seen. When the stimulation frequency was then increased, no measurable amount of heat was produced until a frequency was reached which also produced visible contractions. Under the conditions of these experiments, the heat produced by the processes underlying the action potentials is too small to be measured.

In a few of the claws in which both types of contraction functioned, both axons were stimulated at the rate of 40 times per second. The fiber for the fast contraction was stimulated for 4 seconds at a time, the slow for 10 seconds. The two were stimulated alternately every 10 minutes. With these frequencies and durations of stimulation, the areas of the two kinds of isometric contraction curves are approximately equal. The shape of the curves is different, as the slow contraction develops its tension slowly. When the ratios, H/M, of the two contraction types are compared, Table 1, it is found that the slow contractions are more efficient than the fast. As mentioned above, both sets of ratios decrease in succeeding contractions; that is, each kind of contraction becomes more efficient. Nevertheless, the least efficient slow contraction is always more efficient than the most efficient fast contraction. This higher efficiency of the slow contraction is also true for contractions of other durations.

The most striking demonstration of the difference in efficiency of the two contractions was obtained in experiments in which the motor axon for the fast contraction was stimulated at the rate of 50 times per second, and the motor axon for the slow contraction was stimulated at the rate of 150 times per second. Figure 1

(Claw A of Table 2) gives part of the kymograph record of one such experiment, and shows that this produces contractions which are similar in size and shape. This was done to minimize as far as possible any differences which might be attributed to differences in the way in which the work is performed by the muscle.

Table 2 gives the results of four experiments of this kind which were successful. All the contractions were of the same duration and the kymograph records show that any two successive contractions are similar. As each experiment proceeds, the ratios, H/M, of each type of contraction get smaller. In every claw the ratios for the slow contraction are always smaller than the corresponding ratios for the fast contractions. The slow contractions even under these circumstances are more efficient, and again, in each claw, even the least efficient slow is more efficient than the most efficient fast.

Figure 1 shows also the last two contractions of Claw A of Table 2. These do not appear in the table. Number 7 is a slow contraction obtained by a stimulation frequency of 50 per second and number 8 is a fast contraction obtained by a stimulation of 25 per second. At these rates of stimulation the type of contraction can be readily identified. Whenever possible contractions of this sort were obtained at the end of the experiments and served as a check on the identity of the two types of contractions.

Table 3 shows an experiment in which fast and slow contractions were followed by contractions of a mixed type. The mixed type was obtained as follows. During the course of a 5 second stimulation of the fiber for the slow contraction at a frequency of 150 per second, the fiber for the fast contraction was stimulated for 3 1/2 seconds at a frequency of 50 per second. This imposes a fast contraction on the slow one. The curve of the contraction is double. It first rises to the height of the slow contraction, then the tension increases when the fast contraction is started. This increased tension is maintained till the fast contraction stops, when it falls again to the height of the slow contraction. At the end the curve returns to the base line when the slow contraction is over. In this way, rather than by starting and stopping the stimulation of both fibers together, it was possible to be sure that both contractions took place.

As shown in Table 3, the ratios H/M again decrease in succeeding contractions of the same kind, and they are larger for the fast contractions than for the slow. The ratios for the mixed contractions have values which are intermediate between the ratios for the fast and slow. As the tension developed and maintained by the mixed contraction is greater than that of either the fast or slow contractions alone, it seems likely that both contractions do occur together. The figures do not indicate whether the mixed contraction can be considered as a slow with a small fast part added, or whether during the combined stimulation any or all of the slow contraction is suppressed.

Bronk found in his experiments that successive contractions became less expensive. The changes in efficiency were greater than any which have been found in the crayfish. He ascribed these changes to a pronounced slowing of the muscle as a result of previous activity. The contractions he obtained do show a marked slowing; at the end of a series the tension develops slowly and relaxation is prolonged. In his experiments the whole nerve bundle was stimulated. Therefore, it is possible that the first contractions he obtained from a claw were predominantly of the fast type. This contraction fatigues more rapidly than the slow, and in succeeding contractions would tend to disappear and be replaced by the slow type of contraction. This would account for the large change in shape of the contractions which he observed.

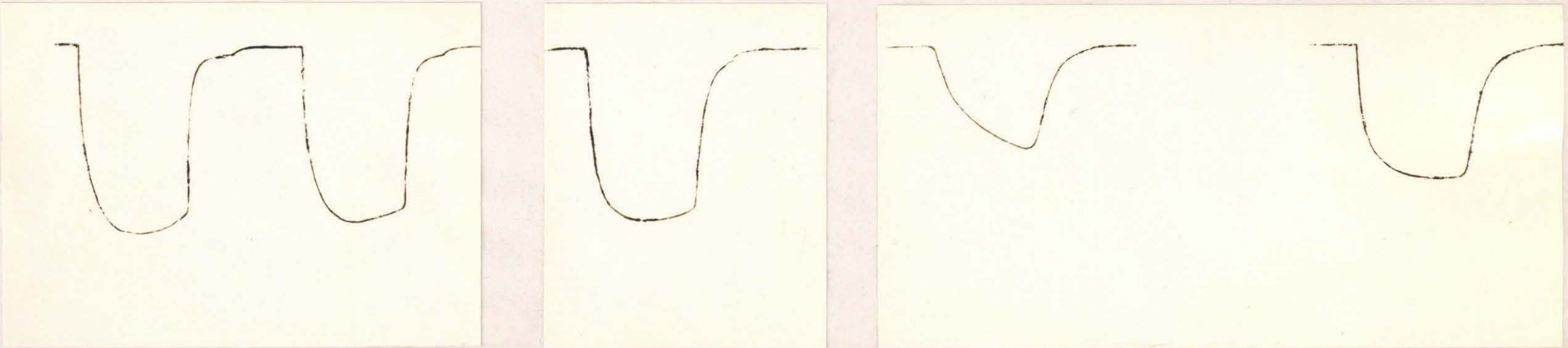
Under the conditions used in the experiments on the crayfish in which the isolated motor axons were stimulated, no such marked slowing has been seen. In figure 1, contractions 1 and 5 are both fast and are separated by one other fast and two slow contractions (only one of which, no. 2, slow, is shown). The relaxation of contraction no. 5 shows a certain amount of slowing, but not very much. In other experiments similar differences in relaxation were obtained.

That a difference in efficiency is not necessarily dependent on a widely different shape of contraction has been demonstrated (Figure 1 and Table 2). Contractions of the fast type resulting from a stimulation at 50 times per second are not obviously different from contractions of the slow type from stimulation at 150 times per second. Nevertheless, there is a consistent and considerable difference in the efficiency.

With the type of stimulation used in the experiments in Table 2, the action potentials accompanying the fast contraction are larger than the action potentials accompanying the slow. With the methods used no heat could be measured from action potentials occurring in the absence of contraction, so the pronounced differences in heat production cannot be ascribed to differences in the action potentials.

It is logical to ascribe different efficiencies to a difference in the time relations, and thus to a slowing of the muscle. Of course, even though the contractions look very much alike, the fast will always develop its tension quicker, since a response is obtained to the first impulse. Furthermore, the fact that a smooth tetanus is obtained at low frequencies of stimulation of the slow contraction, whereas, at the same frequencies the fast often shows hardly any summation of the twitches, is proof that the relaxation of the slow is indeed slower. However, the relaxations of the two contractions are under any circumstances very much alike, and it is certainly impossible to take this relaxation as a measure of the slowness of the contraction. It has been shown previously (van Harreveld and Wiersma, 1936) that in a fatigued muscle, relaxation of both contractions takes more time, but there is never a pronounced difference between the two, no matter how quick or slow relaxation is. In figure 1 the relaxation of the slow contraction no. 2 is faster than that of fast no. 5; nevertheless, the slow is more efficient.

If the difference of efficiency of fast and slow types of contractions is ascribed to slowing, it should be pointed out that this slowing seems to be of a different nature than that involved in fatigue, for it is not dependent on previous activity. The same muscle can be made to perform similar contractions with one of two different efficiencies; now one, now the other, at will. As both contractions occur in one muscle fiber, this difference of efficiency arises from some difference in each muscle fiber, not in separate and different fibers.



1 2 5 7 8

Fig. 1 Claw A of Table 2. Isometric contractions of 4 seconds duration, from one muscle: 1 and 5, fast contractions, stimulation frequency 50 per second; 2, slow contraction, stimulation frequency 150: 7, slow contraction, stimulation frequency 50: 8, fast contraction, stimulation frequency 25. Contraction downward. 3 and 4 omitted, same as 1 and 2.

TABLE 1

The Relative Heat Produced by Fast and Slow Types of Contractions. Both Types of Contractions Obtained by Stimulation at a Frequency of 40 per Second.

Contraction					$\frac{H}{M}$	
No.	Type	Duration Seconds	H	M	F	S
1	F	4	85	36	2.4	
2	S	10	70	50		1.4
3	F	4	65	32	2.0	
4	S	10	60	44		1.4
5	F	4	50	30	1.7	
6	S	10	45	36		1.3
			Average		2.0	1.3

TABLE 2

The Relative Heat Production of Fast and Slow Types of Contractions. Fast Contractions Obtained by Stimulation at a Frequency of 50 per second, Slow at a Frequency of 150.

Claw	Contraction No.	Contraction Type	Contraction Duration Seconds	H	M	$\frac{H}{M}$ F	$\frac{H}{M}$ S
	1	F	4	260	53	4.9	
	2	S	4	145	48		3.0
A	3	F	4	220	53	4.2	
	4	S	4	125	49		2.6
	5	F	4	175	52	3.4	
	6	S	4	105	49		2.1
				Average		4.2	2.6
	1	S	4	150	25		6.0
	2	*	*	*	*	*	
	3	F	4	210	28	7.5	
	4	S	4	125	27		4.6
B	5	F	4	195	27	7.2	
	6	S	4	115	25		4.6
	7	S	4	95	23		4.1
	8	F	4	145	21	6.9	
				Average		7.2	4.8
	1	F	4	130	66	2.0	
	2	S	4	80	58		1.4
C	3	F	4	115	60	1.9	
	4	S	4	60	49		1.2
	5	F	4	80	45	1.8	
	6	S	4	45	40		1.1
				Average		1.9	1.2
	1	F	4	255	52	4.9	
	2	S	4	140	52		2.7
D	3	F	4	220	48	4.6	
	4	S	4	90	38		2.4
	5	F	4	160	44	3.6	
	6	S	4	85	40		2.1
				Average		4.4	2.4

*Incomplete fast contraction omitted.

TABLE 3

The Relative Heat Produced by Fast and Slow Types of Contractions Compared with Contractions Consisting of a Fast Type Imposed on a Slow Type. Fast Contractions Obtained by Stimulation at a Frequency of 50 per Second, Slow at a Frequency of 150.

Contraction					$\frac{H}{M}$		
No.	Type	Duration Seconds	H	M	S	F	S+F
1	S	5	50	23	2.2		
2	F	3.5	90	20		4.5	
3	S+F	5 and 3.5	95	35			2.7
4	S	5	30	20	1.5		
5	F	3.5	60	17		3.5	
6	S+F	5 and 3.5	60	28			2.1

LITERATURE CITED

Bronk, D. W. 1932 J. Cell. and Comp. Physiol., 2, 285.

Harreveld, A. van 1939a J. Comp. Neurol., 70, 267.

Harreveld, A. van 1939b J. Exp. Biol., 16, 398.

Harreveld, A. van, and C. A. G. Wiersma 1936 J. Physiol., 88, 78.

Wiersma, C. A. G., and A. van Harreveld 1938a J. Exp. Biol., 15, 18.

Wiersma, C. A. G., and A. van Harreveld 1938b Physiol. Zool., 11, 75.

SUMMARY

Apparatus and a method are described for testing the responses in men to mechanical vibrations of different frequencies. This method has been applied to over 600 men. In the whole group the thresholds at all frequencies increase with the age of the subjects. Similarly the upper frequency limit to which there is a response falls off with age. Half of the men received vitamins for a period of approximately one year, half did not. In the older age group, those receiving the vitamins were found to have lower thresholds than those who did not, but the difference is below the level of statistical significance.

A method has been developed for measuring the heat produced during sustained contractions, of both the slow and fast types, of the closer of the cheliped of the crayfish Cambarus clarkii. The contractions occur in the same muscle fibers. Any heat produced by, or accompanying, the muscle action current alone is less than can be measured by the method used. On repetition, both types of contraction become more efficient. The slow contractions are more efficient than the fast, both when the mechanical effects of the contraction are dissimilar and when they are made as alike as possible.