THE CUTANEOUS SENSATIONS
AND
SENSORY REFLEX ACTION.

BY

P.A.MACDONALD

Submitted to the University of Manitoba
as a Partial Requirement for the Degree
of
MASTER OF SCIENCE.

INTRODUCTION.

This paper deals with an investigation conducted with the hope of revealing the principal laws governing the behaviour of the temperature sensation, and with the hope of connecting these laws to the hypothesis of Sensory Reflex Action, put forward by Dr. Frank Allen, Professor of Physics, University of Manitoba.

The problem was suggested by Dr. Allen, who gave a great deal of stimulating constructive criticism during the progress of the work.

It is also my privilege to acknowledge financial assistance from the Honorary Advisory Council for Scientific and Industrial Research in the Dominion of Canada.

SECTION 1.

The Present State of Knowledge of the Cutaneous Sensations.

As throughout this paper we shall be dealing with the interpretation of known facts, relating to the cutaneous sensations, we shall first present in a tabulated form, the more outstanding of these facts, a number of experiments, many of which lack direct interpretation, and the more generally accepted theories presented in the modern texts (ref. 1,2,3,4,5.).

A.

1. There are three anatomically distinct classes of organs of sensation, that may be aroused by stimuli applied to the surface of the body. Before the discovery of these distinct classes, sensations aroused in this manner were feferred to as"Cutaneous Sensations". This now becomes a misnomer,for it has been shown that we deal with:-

a. Subcutaneous or Deep Sensation.

b. True Cutaneous Sensations.

a_1. Subcutaneous sensibility is mediated through sensory fibres contained in the nerves of the muscles.

b_1. True cutaneous sensibility has two anatomically distinct systems;Protopathic and epicritic. The protopathic system is the more primitive and common to the whole body. It comprises three qualities of sensation, pain, heat and cold. It is not as sensitive as the epicritic,but when excited gives rise to a more powerful sensation.

b_1^1. It is characteristic of this sensation that the reception organs are distributed in "Spots". When we stimulate a very small surface of the skin and arouse, say a touch sensation, we are said to have stimulated a "Touch Spot", the conclusion being drawn that a single end-organ of the touch sensation has been stimulated.

b_1^2. Stimulation reveals four distinct types of spots:-

1. Warm
2. Cold
3. Touch
4. Pain

b_1^3. When any of these "spots" are stimulated approximate localization is present.

b_1^4. All protopathic sense organs have a high threshold.

b_1^5. The epicritic organs are not distributed in spots, are much more sensitive to external stimulus, have a relatively low threshold, true tac--tile sense, localized pain, power of discrimination and ability to react to temperatures ordinarily met with by the body, and their sensitivity depends greatly on its adapted state.

b_1^c. The epicritic system of fibres is only found in the skin and thus is the real cutaneous sensation.

c . In the central nervous system, nerve fibres from the different systems of excitation unite in some manner, with a result that under ordinary conditions the brain does not recognise the difference in consciousness.

2. "When for any cause, one or other of the cutaneous sensations is depressed in a given area, stimulations in this region may give sensations which are referred to the symmetrical area on the other side of the body."

3. Special receptors are much more sensitive to their adequate stimulus than to any other.

B.

Individual Characteristics.

1. Touch.

a. Touch spots are stimulated both by pushing and pulling.

b. They are smarter in response than any other of the sense organs.

c. Energy of stimulus seems to be the criterion.

d. Induced currents evoke a distinctly intermittent sensation at a frequency of 130 per second.

e. Shocks individually too feeble to give sensation eventually give rise to sensation, when repeated.

f. A rotating toothed wheel gives a continuous sensation of pressure when the teeth make contact with the skin between 480 and 640 times a second.

g. There is some histological evidence of two kinds of organs.

2. Temperature Sensation.

a. Temperature sense much less marked on the exposed surface of the body.

b. Acuteness varies considerably with the condition of the skin.

c. Shows adaption to a marked degree.

d. Acuteness varies considerably with the temperature, most acute about ordinary skin temperature, 27°C.to 32°C. Can appreciate a difference of 1/5°C. at this temperature; when very hot or cold not nearly so sensitive.

e. Ability to distinguish small differences in temperature varies over the body.

f. "Fechner found the minimal perceptable difference smallest with the stimuli between the temperatures of 12.5°C.and 25°C. Using water and the skin of the finger, he discovered that when the finger had been allowed sufficient time in the first specimen of water for, as would now be said, some 'adaption'of its end-organs to the temperature of that water it could detect differences of temperature to a degree which did not affect his thermometer, although graduated in twentieths of Reaumur units.The range of temperature (12.5°C.-25°C.) between which Fechner found the liminal difference smallest must have applied entirely to the 'cold' sensation,since the skin of the hand has normally a temperature ranging between 27°C. and 29°C. Alsberg, however, found the threshold difference smallest with stimuli (water) between the temperatures of 35°C. and 39°C., a range which, as the highest skin temperature is about 32°C., must have applied to the 'warm sensation'. It might have been expected that the range of temperatures at which the threshold difference was smallest would have lain close above and below the 'adequate temperature'. Some observers have indeed obtained this result, notably Nothnagel, who found the range lie between 27°C. and 33°C."

g. "There is much evidence that the excitability of a sense organ is at any time partly determined by antecedent stimulation."

h. Long application of heat or cold greatly damages the discrimination.

i. Mean Reaction Times

	Cold Almost Painful		Warm Almost Painful		Warm Weak	
Intangible Stimuli.	.227	.035	.507	.070	1.160	.104
Tangible Stimuli	.137	.018	.162	.17	.129	.012

j. Localization somewhat finer for cold than for warmth.

k. Two stimuli, when applied to surfaces near together, mutually reinforce each other more than when farther apart.

l. Very excessive heightning of warm stimulus gives rise to cold sensations for a short time.

m. Sensation of cold may be caused without contact, by increasing radiation.

n. Cold stimulus seems dependent on the amount of heat extracted from the skin in unit time.

o. Facile evocation of positive after-images characteristic of both.

p. Warmth stimuli may evoke cold sensation on cold spot, but not reverse.

q. Heat spots do not react to temperature below 37°C. and cold to temperature above 26°C.

r. Epicritic responds to temperatures between 26°C. and 38°C.

s. Weber concluded that change of temperature and not absolute temperature was the cause of stimulus.

t. Herring produced a theory that leads to the conclusion that each end-organ has a physiological zero temperature, at which no sensation is produced. Raising above this temperature gives warmth, cooling below it, cold.

3. Pain.

a. Pain spots are far more numerous than cold and possess widely different thresholds.

b. Threshold is much higher for pain than pressure.

c. Sensitivity of spots varies from time to time.

d. Histological evidence shows no special end-organs, stimulus taking place on the free endings of the nerve fibres.

e. Cutting off of the blood supply stimulates pain, but depresses the other sensations.

f. $\frac{\text{Touch Limen}}{\text{Pain Limen}}$ varies from 1/3 in forearm to 1/100 in finger tips, with Faradic stimulation quotient altered to more than unity, pain threshold lying lower than touch.

g. Intermittent electric stimulation at a frequency above 20 shocks per second gives a continuous sensation. Touch is discontinuous at 130 per sec.

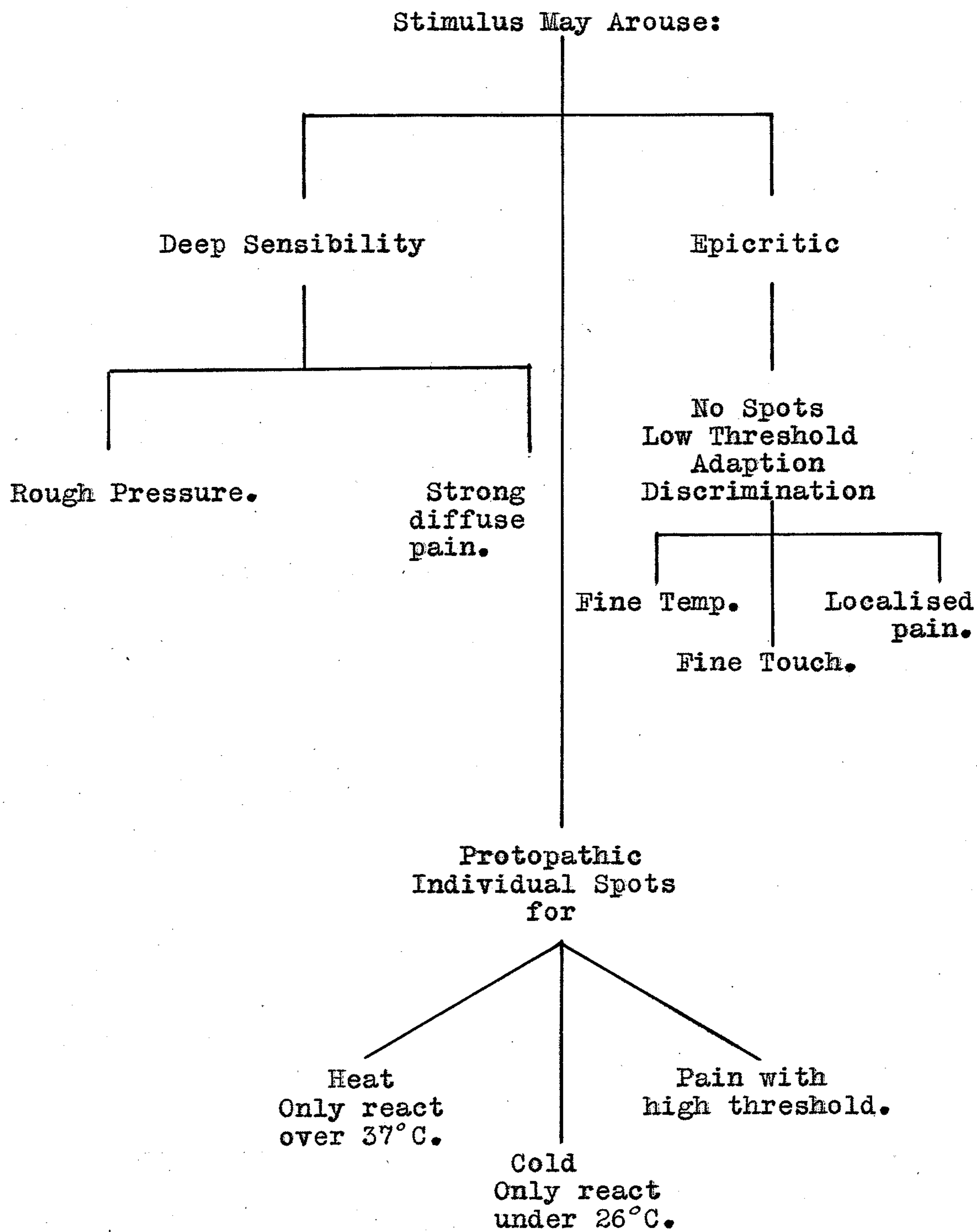
h. The liminal intensity for electric stimuli (break induction shocks) is higher for touch than pain.

i. The temperature at which the skin begins to evoke pain (48° C.) is that at which nerve substance begins to suffer injury.

k. "Is cutaneous pain the product of a specific sense of pain? Data for complete satisfaction of this problem seem still insufficient." (ref. 6.)

C.

Graphical Recapitulation.



D.

EXPERIMENTS.

A. Patient could feel no sensation of touch or temperature below 27°C. Contact with objects between 27°C. and 60°C. felt, and the degree of warmth readily estimated; no loss of pain.

B. If a metal disc, a little above 0°C. be applied to forehead for 30 seconds, the resulting cold sensation persists fully 20 seconds after the removal of the disc.

C. Nipples are very sensitive to warmth. Cool A and then apply same warm stimulus to both A and B; A feels warmth less than B.

D. A finger of one hand (A) is held in water at a temperature of 32°C. and the corresponding finger of the other hand is held, at the same time, in water at 15°C. Both are then placed in water at 40°C. A feels more warmth than B.

E. A mercury bath is heated until it is of a temperature that evokes neither a warmth nor a cold sensation when the finger is immersed. The finger is then put in mercury at room temperature. Half a minute later, when the first bath is tested with the same finger, a warm sensation is evoked.

F. When one finger is held in water at 15°C. and the corresponding finger of the other hand in water at 35°C. and then both are placed in water at 25°C. the water is felt warm by one finger, and cold by the other.

G. From granulating surfaces of wounds thermal stimuli evoke no sensation of cold or warmth, but if strong may produce pain.

H. Cold metal 2°C. to 8°C. is held against the palm for 20 sec. The temperature of the skin falls 5°C. to 8°C. and a pain sensation is evoked. After the removal of the metal the skin gets warmer again; after 8 minutes time, however, it has not reached its previous temperature, and a cold sensation is clearly felt. The period is quite too long for after-images.

I. We may sit before the fire for hours and still feel a warm sensation.

J. Metal at a temperature of 45°C. to 50°C. when held against the skin causes a cold sensation. In the case of the nipple, a temperature of 40°C. will suffice.

K. Apply to the inner side of the elbow, or the front of the thigh, a silver plate 25μ thick, heated to 100°C. A short cold sensation is immediately felt, succeeded by a hot sensation and sometimes by a painful one. With thicker plates the final sensation of pain always occurs.

L. A piece of metal 52°C. to 54°C. is laid on the forearm. A hot sensation is first evoked; this decreases and a cold sensation is felt pricking through.

M. After a bath 37°C.-39°C. of some duration, the foot is passed quickly through hot water: a pure cold sensation results, subsides and a pain is felt.

N. A stimulus affecting a large area evokes more sensory reaction than one affecting a small area.

O. "It is an important observation of Weber's that the reinforcing influence which one thermal stimulus, e.g. of cold, has upon the intensity of another (of the same species) simultaneously applied, is greater when the places of application of the two stimuli lie nearer than when they are far apart. For instance, the difference between the temperatures of two equal surfaces can be distinguished with greater nicety when the surfaces are large than when they are small, but when the two smaller surfaces are applied not far apart from one another, the discrimination is more exact than between the larger surfaces if the latter be applied a considerable distance from one another." (ref.11.)

P. Water, at 29.5°R. tested with the whole hand feels warmer than water at 32°R. tested with one finger. Finger can be kept in water at 48.7°C., but the whole hand kept in the same water soon experiences a very painful sensation. Similarly, with water at 6.2°C.

Q. "Goldscheider considers the sensation ordinarily evoked by contact with an object hot enough to be 'painful', to be compound of (1) warm sensations of high intensity, due to strong adequate stimulation of the 'warmth spots'; (2) tactual sensation evoked by contact.....; (3) pain sensations evoked by the physical heat exciting pain-nerves and their endings, in virtue of its property as a general nerve stimulus. The 'burning' painful sensation of a hot body, on this view, owes its painful quality, not to over-excitation of the 'warmth spots', but to concomitant excitation of pain nerves by heat." (ref. 6.)

SECTION 2.

The Flicker Phenomenon and Reflex Action.

A method of investigating the behaviour of the special senses that has proved very fertile,is that of the critical frequency of flicker.The particular case of vision demonstrates clearly the method. A light of definite intensity is viewed through a slowly rotating fan. On increasing the velocity of the fan,a critical velocity is reached at which the light just ceases to flicker. An alteration in the intensity of the light is found to require an alteration in the velocity of the fan to keep the light just continuous. The measurement of the velocity of the fan, at this point, yields information from which the duration of a single stimulus may be obtained. This duration is taken to be a measure of the sensitivity of the eye. The flicker method has been extended to touch,(ref.7,8)using as the stimulus a jet of air at known pressure.This jet is allowed intermittent play on the touch receptors, by using a rotating segmented disc,placed immediately in front of the air jet, the air striking the skin through this. The duration of a single stimulus for a definite air pressure is obtained, and taken as a measure of the sensitivity of the receptors. Similar apparatus is used to investigate the sense of sound, replacing the air jet by air waves of different frequencies (ref.9.). To investigate taste, an electric current of known strength was allowed to electrolyse the saliva on the surface of the tongue, the current being interrupted at the definite frequency, which yielded a continuous sensation of taste (ref.10.).

In all cases the values of the time during which the stimulus acts at the critical frequency of flicker, when plotted against the logarithms of the intensities of the stimuli, yield a straight line. The equations of these lines take slightly different forms in the various senses.

$$\frac{1}{D} = k \log I + C \qquad \text{(Vision)}$$

$$\frac{1}{D} = -k \log I + C \qquad \text{(Taste)}$$

$$D = k \log I + C \qquad \text{(Sound)}$$

$$D = -k \log I + C \qquad \text{(Touch)}$$

In these equations, D is the time during which the stimulus acts at the critical frequency of flicker. I is the intensity of the stimulus employed, K and C are constants, which depend on the nature of the sense and the stimulation.

The investigations carried out by this method have shown most striking similarities in the behaviour of the nervous actions involved in the various senses. Among them are the phenomena of depression and enhancement of sensitivity of the receptors, and the reciprocal influence of portions of the sense organ, or of groups of receptors, upon each other. Perhaps the most conspicuous feature of the identity of sensory actions is the similarity of the above equations.

As a result of this work, Allen has suggested an hypothesis dealing with the action of the sensory system, known as the principle of Sensory Reflex Action "......a stimulus applied to any sensory receptor arouses a sensation in the corresponding central organs, and in addition evokes simultaneously two sets of efferent impulses, one of which enhances, and the other depresses the sensitiveness of the whole sensory system, the degree of enhancement or depression being the measure of the excess of one process over the other."

The uniformity found to exist in the four senses mentioned indicated the probability that all sensory actions followed the same laws. Both on this account, and in order further to test the hypothesis of Sensory Reflex Action, it seemed desirable to investigate the various cutaneous sensations using, if possible, the same general method.

SECTION 3.

Experimental Work

A.

The first attempt to investigate the temperature sense was to use, with slight alterations, the touch apparatus of Weinberg (ref.2), substituting heated air for that obtained from the air main. Air of measured pressure was delivered through a nozzle placed directly behind a sectored metallic disc mounted on the axle of an electric motor. The velocity of the motor could be varied by a rheostat, and a hand brake, and determined by a tachometer operating a chronograph. The lower lip of the observer was placed in line with the nozzle of the air pipe, but on the other side of the sectored disc and protected from it by an aluminium shield. It was almost certain that the touch phenomena would confuse any heat effects that might be obtained by using heated air in this apparatus, and it was thus considered advisable, before attempting work on the temperature sensation to become thoroughly familiar with the touch sensation.

Attempt was made to obtain a normal curve similar to that of Weinberg, but the results were considered, at the time, very poor. Readings at one pressure did not always come out the same and the slope of the curve finally obtained was not nearly as great as that of Weinberg. However, as our major interest was in the temperature sense, we let this problem stand, and having become thoroughly familiar with the pressure sensation, did not spend time attempting to obtain an accurate normal curve, but commenced temperature observations. The only change in the apparatus necessary to commence work on the temperature sense was substitution of an electric heating element in the compressed air circuit. The sensation of warmth was readily evoked by allowing the warm air to play on the lip, as in touch, but even a temperature as high as 80°C.with a duration of .25 second failed to make the sensation flicker. We attributed the failure to four causes;-

1. When the warm air was prevented from playing on the lip by the interception of a segment of the rotating disc, the heat was not immediately dissipated from the lip, thus while the rotation of the

disc caused an intermittent air supply, we were not obtaining intermittent heat on the surface of the lip.

2. If the flickering were present it might easily be masked by the touch sensation.

3. The receptors might be so deeply embedded in the skin that the rate of change of the temperature at the receptors, due to external stimulus would be modified by the laws of heat conduction, the time required for the heat to reach the skin being so great that the periodic impulses, originally sharply defined, would become fused before they reached the receptors.

4. The heat nerves may not react with sufficient rapidity to exhibit the phenomenon of critical frequency of flicker.

We obviated the first two difficulties by substituting for the old disc, a doubly sectored disc and by using two jets of air, the second being cooled by passage through a tank filled with freezing mixture. The hot air played through one of the sectors of the disc. As the disc rotated, the second sector uncovered the cold jet, at the same time covering the hot one. By having these two jets focused on the same portion of the lip, the flickering of the touch sensation was overcome and the lip made alternately hot and cold. Under these conditions we were still unable to obtain any flickering, and after thorough trials on different parts of the body, were forced to the conclusion that flickering could not be obtained as with the other senses. Either the action of the thermal end-organs was too sluggish, or the change in temperature was prevented ready access to the receptors, or the combined effect was preventing the flickering.

B.

Electric Stimulation.

We then turned our attention to the possibility of obtaining electric stimulation of the thermal nerves, and after various trials, succeeded in stimulating, with an intermittent direct current, heat, cold, pain and touch spots and obtaining the sensation characteristic of each. Under no circumstances were we able to obtain a flickering by interrupting the current after the manner employed in Taste (3). It should be remembered however, that in taste, the current did not directly stimulate the nerves, but produced, by electrolysis, chemicals, which acted as true adequate stimuli, Thus the action that we were seeking was not similar, but consisted of an intermittent inadequate stimulus which was not of necessity stimulating the end organ itself, but possibly the nerve fibre between the end organ and the brain (ref.12).

C.

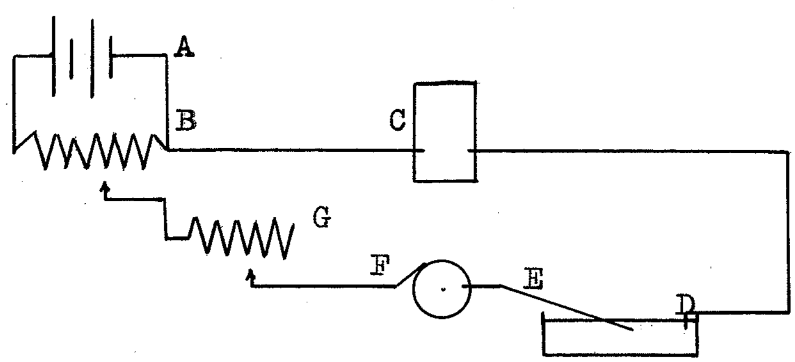
A New Principle.

Having given up hope of obtaining a critical frequency of flicker,we turned our attention to the possibility of using, as a means of measuring the sensitivity of the nerves, a fact we had previously noted, that there is a definite frequency of interruption of the stimulating current above and below which a sensation is not elicited. Experiment soon showed that this frequency varied with the voltage so we at once attempted to obtain a curve measuring the frequency necessary to cause sensation at a definite current strength.

D.

The Apparatus.

A continuous electric current was supplied by a large storage battery, A, with a maximum electromotive force of 110 volts. Any desired fraction of this voltage was obtained from a rheostat, B, and the current was conducted through a millivoltmeter, callibrated as an ammeter, C, through the metal water-basin, D, into the arm of the experimenter, E, then through the interrupting disc, F, which made the current intermittent, and finally through another controlling rheostat, G. The interrupting disc was that used in the investigation on taste, (ref. 10).



Its angular velocity and thus the duration of the interrupted pulses of current, was measured by a chronograph.

E.

The Cold Sensation.

In using the apparatus to investigate the cold sensation a small metallic electrode, approximately one centimetre in diameter, was covered with blotting paper moistened with ordinary tap water and held against the back of the right hand near the wrist-joint. The hand was immersed in water in the metal basin, thus completing the circuit. The water was at a temperature of about 23°C. When the temperature was below 20°C. there did not appear to be sufficient contrast between the temperature of the water and the sensation of cold evoked by the current to enable accurate measurements to be made.

When these arrangements were completed the motor was brought to its maximum speed, the circuit through the hand was closed, and the rheostat adjusted to give any desired current. The speed of the motor was then gradually reduced by the brake until at some critical value a sensation of cold suddenly appeared under the small electrode. The chronograph circuit was then closed and the speed of the motor recorded. The measurements were repeated at intervals for as many different current-strengths as the physiological conditions permitted. The sensation of cold does not cover the whole area of the skin under the electrode, but is localised at one pθint.

The readings obtained on the arm are given in Table 1.,and are shown graphically in figures 1 and 2. The abscissae are logarithms of the current-strength, and the ordinates are the corresponding values of the duration of one current impulse at the critical frequency of interruption at which the sensation of cold appears. The figure contains eleven graphs determined by various small numbers of measurements. These were obtained on different days and doubtless on different nerves.

A similar series of measurements of the cold sensation was made upon the right leg, the electrode being placed some distance above the ankle. A wet bandage placed just above the ankle was, in this case, substituted for the basin as the second electrode. The measurements are given in Table 11., and are shown graphically in figures 3 and 4. The seven graphs are of the same character as those for the arm; but while the time-intervals are about the same, the current-strengths are only about one-half of those in the arm. In the figure, two of the graphs,marked D and E,show distinct second branches at durations lower than the measurements obtained on the nerves in the arm. Further, it seems likely that the two lowest graphs, F and G, consist of lower branches without the upper.

F.

The Pressure Sense.

By varying the experimental conditions, the pressure sense could also be evoked by the same method. For this purpose a wet bandage placed around the wrist served as one electrode, and one finger, the second on the left hand, dipped in the water in the metal basin, was the other. With a high-frequency of interruption of the current no sensation was perceptible. On decreasing the speed of the motor, however, a point was reached at which a sensation of pressure was felt. With further decrease in speed this sensation ceased, but still further decrease caused the sensation to be renewed. The sensation produced feels as if the immersed part of the finger were being squeezed with an even pressure on all sides. There is also experienced at the same time a tingling sensation similar to that obtained when the ulnar nerve at the elbow is sharply struck. The motor was incapable of giving sufficiently high speeds for measurements on the first sensation, so all readings were taken on the second, and plotted in the graph in fig.4, which has two branches. It will be seen that the graph is identical to that obtained in touch, where the pressure of the air was used instead of the electric current.

It is noteworthy that the value of the duration of the stimulus at the critical frequency of interruption is of the same magnitude as that obtained in the experiments on touch; and that with higher values of the stimulating current the duration decreases, just as the duration of the adequate stimulus decreased in touch (ref.8.). From these similarities, we feel justified in concluding that this system of electrical measurements is a measure of the sensitivity of the nerves stimulated.

G.

The Sensation of Pain.

Sensations of pain may be evoked in the same manner as sensations of cold. On decreasing the speed of the motor the cold sensation appears first at a certain critical frequency of interruption of the current, and with further decrease the pain sensation is produced. It is thus evident that the receptors of the latter sensation are not quite so responsive to this type of intermittent stimulation as the former. Two sets of readings have been obtained, one for the hand, and the other for the leg. A wet bandage was placed on the left wrist as one electrode, and the second finger partially immersed in water in the basin was the second. The cuticle was pulled away from the base of the nail, leaving only a very thin layer of skin covering the flesh. In this sensitive area a superficial pain sensation like a sting may be evoked, which is localised in an area about the size of the head of a pin. That this is due to individual pain spots, there is little doubt, judging from the character of the sensation. Better results were obtained on the front of the leg than on the wrist. The electrode is fastened just above the ankle over the shinbone. From the sensation evoked, we would say that the stimulation was some distance under the skin, probably at the surface of the bone. The sensation is extremely painful and not sharply defined, as if kicked on the bone.

H.

The Sensation of Warmth.

It should be remarked that no sensation of warmth, which permitted measurement was evoked by the method of stimulation described above.

I.

Nerves of Unknown Name.

Certain nerves of unknown name, running to the hand near the surface of the skin on the wrist, may also be stimulated in the same manner as the cold sensation. These do not give rise to any ordinary sensation, but at a certain critical frequency of stimulation, the impression is given that they have started to vibrate under the skin. A series of measurements was obtained for this phenomenon, which are given in Table 6, and are shown in figures 11 and 12.

J.

Stimulation of Individual End-Organs.

By using a fine platinum wire in a drop of water for one electrode, and the hand immersed in the water in the basin for the other, individual points of all kinds may be examined by this method of intermittent stimulation.The electrode in a drop of water around each hair invariably evokes a pain sensation of the same type as that obtained at the base of the nail. Cold, warm, and pressure spots may also be found accompanied by most decided sensations. The first time pressure was evoked,the sensation was so realistic that for a moment it seemed as if a solid object were being forced against the surface of the skin. Attempts to obtain series of measurements with this method were unsuccessful, as the current rapidly destroyed the skin, and it was impossible to maintain it long enough to obtain readings.

K.

Conclusions.

The graphs for the four kinds of cutaneous sensations discussed above are all of the same type, consisting in their entirety of at least two branches. These correspond exactly to the first and second branches of the graphs obtained for the tactile sensations by Allen and Weinberg (ref.8). Possibly if the measurements could have been extended over greater ranges of current-intensities a third branch would have been found, as in the senses of vision, touch,,and taste. The graphs all conform to the same equation found for the sense of touch.

The order of magnitude of the times of duration of the stimulus at the critical frequency of stimulation is also the same for all the sensations discussed in this paper, and for touch. We may conclude, therefore, that all the cutaneous sensations obey the same fundamental laws. In the equations to the graphs the constants k and C have different values for the two, or more, branches, and they are different for the different sensations.

The measurements obtained in these investigations, as far as we can judge, are the normal values for the receptors indicated. No measurements under the conditions of depression and enhancement of sensitivity seemed possible, as there was no certainty that the same receptors were stimulated on different occasions. The interpretation of the two-branched graphs most probably rests upon the functions of the sensory reflex actions involved. In other researches on the sensations of vision, touch, and taste, experiment justified the conclusion that in each sense, reflex actions of two kinds existed, one of which depressed and the other enhanced the sensitiveness of the receptors. It is a sudden change in the ratio of these two processes that causes a corresponding alteration of the sensitivity of the receptors and thereby of the slope of the graph.

In the sense of touch it was found that stimulation of low intensities corresponding to the uppermost branch of the graph elicited enhancement in excess of depression, while higher intensities of stimulation caused the reverse. Since the other cutaneous sensations are found to conform to the same equation, it might be inferred that the result of stimulation would also be similar.

SECTION 4.

Further Experimental Work.

While the previous experimental work has been of value in revealing the nature of the laws controling the temperature and pain sensations, it has not shown the presence of sensory reflex action save for a change of slope in a few of the curves. Some of the standard experiments already mentioned however, (Section 1, D), are readily interpreted assuming the hypothesis of sensory reflex action,so we adopted a standard method of experimentation in an attempt to show the presence of enhancing and depressing influences having their origin in the central organs.

The Apparatus.

Three two-litre wide-mouthed gas jars were placed side by side. Ordinary centigrade thermometers, calibrated in units of 1 degree, were suspended in the two outer jars, while the centre jar was equipped with a centigrade thermometer calibrated in tenths of one degree. This jar was also equipped with a small water heater, composed of three carbon rods, placed at the bottom of the jar, between which the electric lighting current was allowed to pass through the surroundung water. This jar will in future be referred to as Jar B. The jar on the right was reserved for cold water, that on the left for warm. These will be referred to as Jar C and Jar A.

Experiment 1. Jar B was filled with water at room temperature and on placing the hand in this water a cold sensation was evoked.

Experiment 2. The temperature of the water was raised to 45°C., and immersing the hand evoked a warm sensation which gradually weakened, until, at the end of two minutes, we were certain that the temperature of the water had dropped. This was found not to be the case. During the immersion, a warmth sensation was distinctly felt creeping up the under surface of the arm. In two minutes, it had almost reached the elbow.

Experiment 3. Experiment 2 was repeated, and at the end of two minutes the hand was placed in Jar C, which had previously been made neutral (32°C) This evoked a cold sensation.

Experiment 4. Jars B and C were filled with water, the former at 32°C and the latter at 6°C. The hand was placed in Jar B, where the water felt neutral; then in Jar C, where the hand felt cold, but this sensation lessened gradually. On moving the hand back and forth in the water, however, the sensation was renewed the instant the hand started to move. A deep pain sensation was aroused shortly after the hand had been placed in the water. The motion of the hand also caused this to become intense. It required a great effort on the part of the will to keep the hand in the water, there being a strong desire to remove it. A sensation also was experienced at the back of the head, which could be expressed better as agony rather than pain. The stronger this sensation grew, the greater was the impulse to remove the hand. The hand was kept in this jar for two minutes, then placed in Jar B which aroused a distinctly warm sensation.

Experiment 5. The fingers of one hand were placed in Jar B, at 45°C. which felt warm. Lowering the whole hand into the water caused the sensation to become much stronger.

Experiment 6. The hand was placed in Jar B, the water in which was gradually raised in temperature. At a point, about 48°C., a pain sensation was aroused. This point seemed to be fairly sharply defined, so we attempted to determine a critical point at which pain was aroused. This point was not, however, readily determined, for pain was found not to be aroused immediately on placing the hand in the water, but after a wait of some seconds. The period of waiting depended on the temperature of the water. Being afraid of obtaining enhancement that would raise the minimal value, we altered our objective, and attempted to find a point at which the pain became strong enough to cause the hand to be jerked out without conscious action. This was found to be at 49.5°C. The water was brought to 49.5°C. and the heat turned off. The hand was immersed, and during the wait for the pain to set in, the temperature dropped a few tenths of a degree, but no attempt was made to keep the temperature constant by closing the heater switch, for we were afraid that the hand might be quicker than the thermometer in response to temperature change.

Experiment 7. The hand was placed in Jar A, with water at 44 to 45°C., until the warm sensation was quite fatigued. Then it was placed in Jar B, with water at 49.4°C.and it was found that the pain sensation had not been affected.

Experiment 8. The right hand was placed in Jar C, with water at 6°C., for two minutes and then in water at 49.4°C.It was found that the pain sensation was not evoked. Then the left hand was placed in water at 49.4°C., and it was noticed that the pain did not seem to react as readily as usual.

Experiment 9. The hand was immersed in Jar B, with water at 49°C., and the pain sensation carefully examined. This sensation seemed to increase with time, and then decrease, only to re-appear stronger than it had been originally. This may take place four or five times. There seem to be individual points on the surface of the skin that are particularly active, stinging in a painful manner, similar to the sensation aroused in determining the date for Table 3. There is also a strong sensation underneath the base of the nail. One observer described it "As if the nails were going to drop out". Repeating observations a number of times, it was found that sometimes the rise and fall was not as clearly defined as at others, and that the rise and fall seemed to be a property of the deeper sensation. The sensations due to single spots on the surface of the skin also rose and fell individually, but one would start to increase as another was decreasing. When the mind ceased to focus attention on the individual spots and attempted to estimate the resultant effect on the whole skin surface, it was concluded that the sensation rose continually with time, showing no depressions. The lower sensation could be felt underneath and seemed to be oscillating continuously, the amplitude increasing with time.

Experiment 10. The hand was placed in water not quite hot enough to evoke pain. The hand was moved about, and pain was aroused.

Experiment 11. An observer placed his hand in water about 49°C and we noted, in seconds, the time of rise and fall of the pain sensation. The temperatures given are those at which the test was started, the water having lost a few tenths of a degree at the end of the measurements. The final time is that at which the hand was withdrawn owing to the intensity of the pain. Results follow;-

Temperature	Time, in Seconds, of Rise			
	1	2	3	4
48.9	6	25	35	45
49.0	4	20	35	50
49.0	3	14	35	50

Experiment 12, Normal readings were taken for the right hand as above. Then the hand was fatigued by holding it in water at 6°C until the pain became so strong that the hand had to be removed. The left hand was then placed in water at 49.4°C, and time readings taken. In this case the rise and fall of the sensation was not nearly as clearly defined as when the other hand had not been fatigued, and the sensation did not seem to be as strong.

Time of Rise in Seconds.

	1	2	3	4
Normal	4	17	35	
	4	17	33	
Fatigue	4	19	50	
	4	14	37	

Experiment 13. The right hand was placed in Jar B at 47C. for two minutes. Then both hands were placed in Jar C at 37°C. The right hand felt colder than the left.

Experiment 14. The right hand was placed in water at 37°C. for one minute, then both hands were placed in water at 47°C. They both felt the same sensation.

Experiment 16. The right hand was placed in Jar B ar 32°C. A trace of cold was perceptible, but at the end of five seconds, the bath felt natural. The hand was dried, and water tested again in one minute, when it felt distinctly warm. The hand was again removed and dried. At the end of another minute the water was tested again, when it felt warm.

Experiment 17. The left hand was placed in Jar A, with water at 44°C., for two minutes; then the right hand was placed in Jar B previously neutral at 32°C. This felt cool.

Experiment 18. The first two fingers of one hand were placed in Jar A with water at 49.5°C., for two minutes. Then the other two fingers of the same hand were placed in the neutral bath. This at first felt a little cool. Then warmth came in, and the resultant sensation was warmth. The corresponding fingers of the other hand were also placed in the neutral bath. These felt the water as cool and served to emphasise the warmth sensation of the first fingers.

Experiment 19. The hand was placed in water at 37°C.and allowed to remain. The warmth sensation did not seem to be fatigued, but on testing the neutral bath, it was found to evoke a cold sensation.

Experiment 20. The hand was placed in water at 37°C., and kept in motion, but this did not seem to affect the strength of the sensation.

Experiment 21. The first and second fingers were allowed to stand in water at 37°C., and after one minute the neutral bath was tested with the other two fingers of the same hand. The bath was possibly a little cooler, but the effect was so small that it may not have been due to a transferred effect, but to a repetition of Experiment 16.

Experiment 22. One hand was allowed to stand in water at 37°C., and after a suitable wait, the neutral bath was tested with the other. There seemed to be a small cold sensation, but, as above, we did not feel justified in attributing it to a transferred effect.

Experiment 23. The right hand was placed in a bath between the temperatures of 6 and 10°C., and allowed to stand for about 20 seconds, then being placed in a bath at 50°C. A pure cold sensation was at first evoked, rapidly disappearing, and being followed by a warm sensation. This experiment was repeated, with the second bath at 47°C., the same result being obtained. Using the second bath at 41°C. also seemed to give a light effect; similarly with the second bath at 37°C.

Experiment 24. The above experiment was repeated with a second bath about 47°C., but the hand was allowed to remain in the cold bath until a strong pain sensation was evoked. The warm bath was tested, and the cold effect was found to be greatly diminished.

Experiment 25. The first two fingers of one hand were immersed in water at 3°C., and allowed to remain until the pain could no longer be stood. Then on testing the neutral bath with the other two fingers of the same hand, the bath was still found to be neutral. Testing the fingers that had been placed in the cold water, with the neutral bath gave rise to a sensation of warmth.

Experiment 26. The above experiment was repeated, substituting a cold bath of 15°C. for the 3°C. bath, and the same result obtained.

Experiment 27. One hand was placed in water at 7°C., and allowed th remain as long as the pain could be endured. On testing the neutral bath with the other hand the bath was still neutral. Placing the fatigued hand in the neutral bath however, first elicited a slight cold sensation, then a prickling pain, followed by a warmth sensation.

Experiment 28. The first two fingers of one hand were kept in a cold bath, until the pain became intense. On testing the remaining fingers of the same hand in water at 49.4°C. pain was evoked. The amount of pain compared with the amount normally produced was hard to estimate. The result we shall consider indefinite.

Interpretation of These Experiments.

Experiment 1. That the sensation aroused by the temperature end-organs is not only a function of the applied temperature.

Experiment 2. That the warmth sensation evoked above 38°C.(sec 1,B,2,Q) is readily fatigued; that there is an enhancing influence started when fatigue sets in and that this enhancing influence communicates itself throughout the neighbourhood in which the sensation is aroused.

Experiment 3. That fatiguing the warmth sensation above 38°C. enhances the cold sensation.

Experiment 4. That the cold sensation is aroused as long as the rate at which heat is being lost from the skin is changing. Symbolically; $ds = \frac{d^2H}{dt^2}$ The intense sensation which Experiment 8 shows to be pain, is accompanied by an instinctive desire to remove the exposed organs from the stimulus, and also that the cold sensation is fatigued and the warm sensation, at the same time, enhanced in the region of stimulation.

Experiment 5. That the amount of sensation evoked varies as the area of the surface exposed, that is, is a function of the number of the end-organs stimulated.

Experiment 6. That the well marked transition point from the warm to the hot sensation is an indication that there is a new set of end-organs coming into use at that strength of stimulation; that this sensation is accompanied by the same impulse to withdraw the organ exposed that was present with the cold sensation and that the sensations were in both cases very similar.

Experiment 7. That any warm sensations existent below 49°C. do not give rise to a pain sensation when strongly stimulated.

Experiment 8. That the pain sensation evoked at 6°C. and the pain sensation evoked at 49.4°C.are one and the same sensation; that this sensation is due to a specific sense of pain; that it is capable of fatigue, and that this fatigue is due to some impulse having its origin in the central nervous system, its effect being transmitted to the corresponding nerves on opposite sides of the body, but to a lesser extent, with the organs that are not stimulated.

Experiment 9. That there are two principles acting on the pain sense, one tending to enhance and the other to depress it. These two neutralise each other under normal conditions but on lightly stimulating the nerves, the enhancing principle is first aroused, enhancing the nerves and continuing to do so until the end-organs are sufficiently sensitive to give rise to sensation. At this point the depressing principle commences to act, reducing the sensitivity of the system. This is followed again by enhancement and these two oscillate. That this effect is found in both pain sensations, but that the pain sensation having its origin on the surface of the skin, is aroused by stimulation of pain spots of different sensibility; and that the period of oscillation of each spot is dependent on its sensitivity, so that the resultant sensation felt on the skin is one of continuously rising sensation, the enhancing principle in this particular experiment being stronger that the depressing. Also that the deep sensation is of uniform sensitivity, at least over any small area.

Experiment 10. That the pain sensation when stimulated by heat also conforms to the equation;

$$ds = \frac{d^2H}{dt^2}$$

Experiment 11. That on a curve, showing the variation with time of the pain sensation evoked by light stimulus, there would be a well defined maximum at the point $t = 35$ seconds.

Experiment 12. That fatiguing the pain sensation of one hand alters the position of the maximum point $t = 35$ seconds of the other hand, giving strong evidence of the presence of Sensory Reflex Action.

Experiment 13. That fatiguing the warm sensation which reacts to temperatures above 38°C. does, at the same time, fatigue the warm sensation which reacts to temperatures below 38°C. and thus the sensation aroused at temperatures above 38°C. is a combination of these two individual sensations.

Experiment 14. That fatiguing the sensation that reacts to warmth below 38°C. does not fatigue the sensation that reacts to warmth above 38°C. and that this is evidence in favor of a set of end-organs that react to warmth stimuli, only when they exceed the temperature of 38°C. in still water.

Experiment 15. That the warm sensation for stimuli over 38°C. enhances the cold end-organs on the opposite side of the body, possibly also the warm to a lesser extent.

Experiment 17. That fatiguing the warm sensations of one hand with temperatures above 38°C.

enhances the cold sensation of the other hand, possibly also the warm, but as the amount of enhancement is small, only the enhancement of the more sensitive cold sensation is noticed.

Experiment 18. That fatiguing two fingers on the same nerve with warmth causes enhancement of the warmth sensation of the neighboring two fingers also the cold to a lesser degree.

Experiment 19. That the warmth sensation between 32°C. and 38°C. does not show appreciable fatigue,but with its stimulation the cold sensation is enhanced.

Experiment 20. That the warm sensation between 32 and 38°C. is not sensitive to small changes of temperature.

Experiment 21. Results not decisive enough to be reliable.

Experiment 22. Results not decisive enough to be reliable.

Experiment 23. That with cold stimuli the cold sensation at first is enhanced. That the cold sensation is stimulated by warmth, and the cold sensation is quicker to react than the warmth.

Experiment 24. That after considerable exposure to cold, the cold sensation ceases to be enhanced and becomes fatigued.

Experiment 25. That stimulating cold end-organs on one part of the body does not appreciably affect the cold end-organs in the neighbouring regions, but does enhance the warm end-organs in the same region.

Note.

The results of the experiments relating to modification of the sensation felt by previous stimulation of other parts of the body should be accepted with some reservation, as we knew beforehand what result was expected on the hypothesis of Sensory Reflex Action, and, as the resultant modification of the sensation is small, it is extremely difficult to give an unprejudiced opinion.

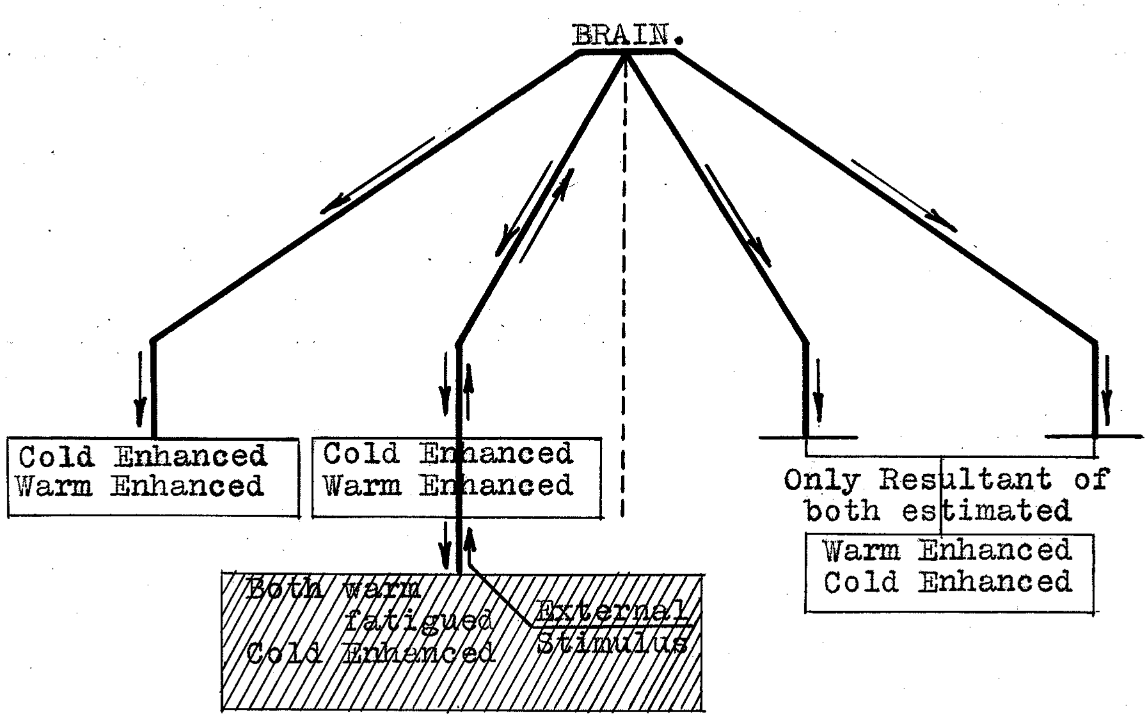
Experiment 16 might also alter the findings.

Diagrammatic Representation of Results.

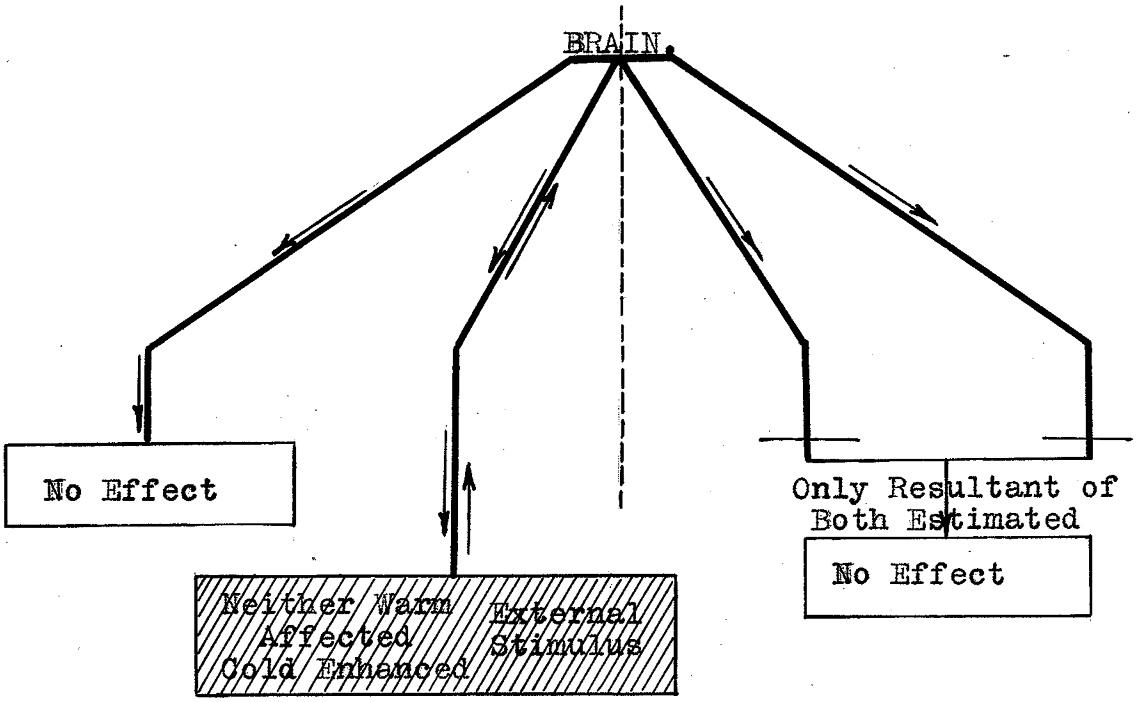
The results of the experiments just described lend themselves to diagrammatic representation and this method of presentation readily shows the presence of Sensory Reflex Action.

In these diagrams the vertical dotted line represents the vertical bisector of the body, the black squares, groups of receptors, while the shaded square shows the group of receptors stimulated. Heavy black lines show the path of the nerve fibres between the receptors and the brain.

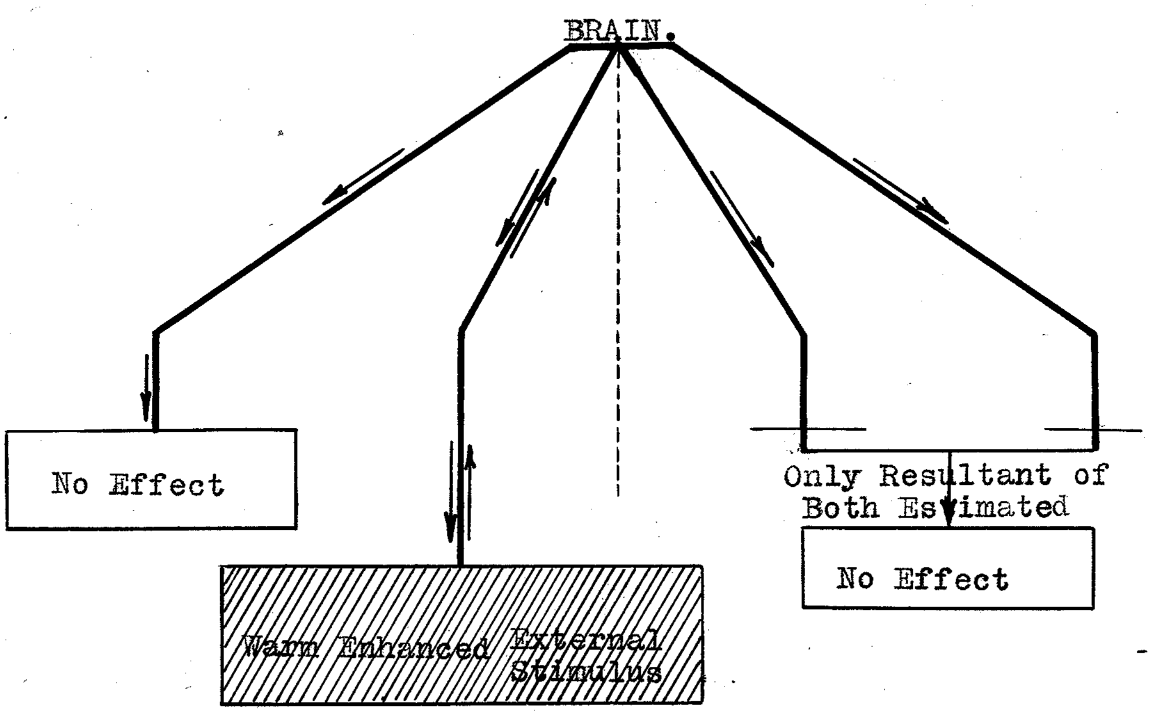
Warm Sensation Over 38°C.



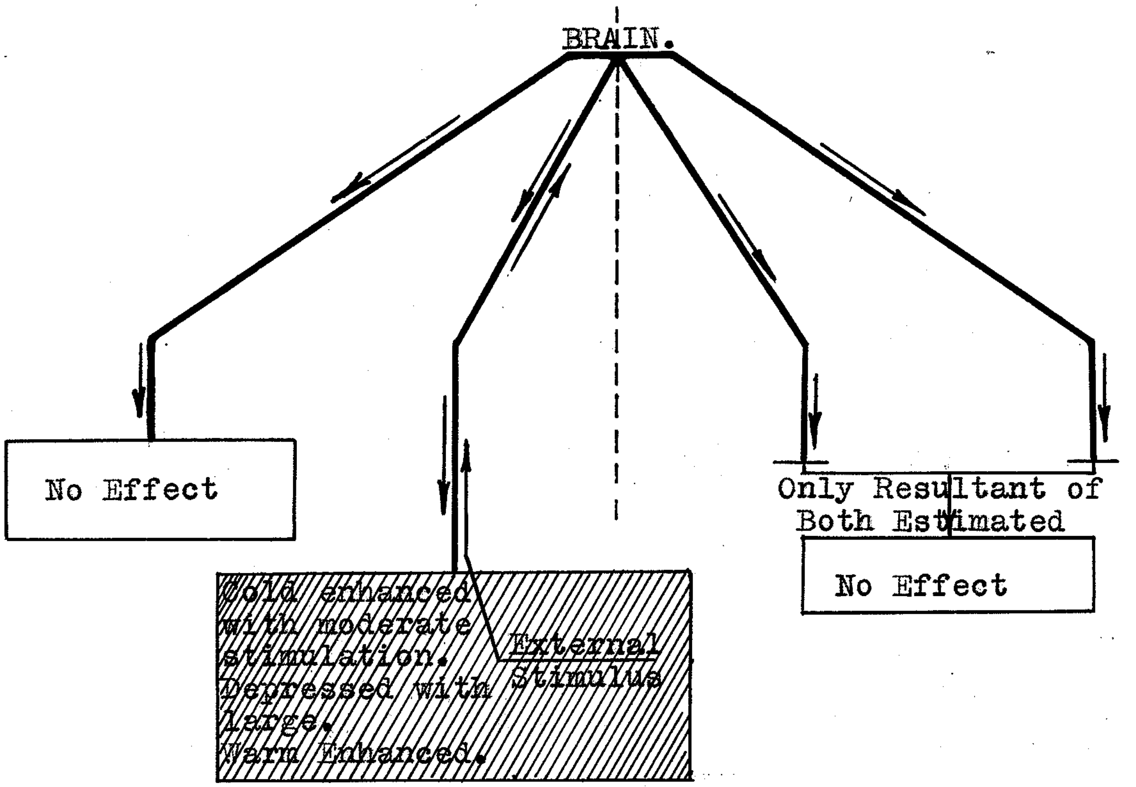
Warm Sensation Between 32°C. and 38°C.



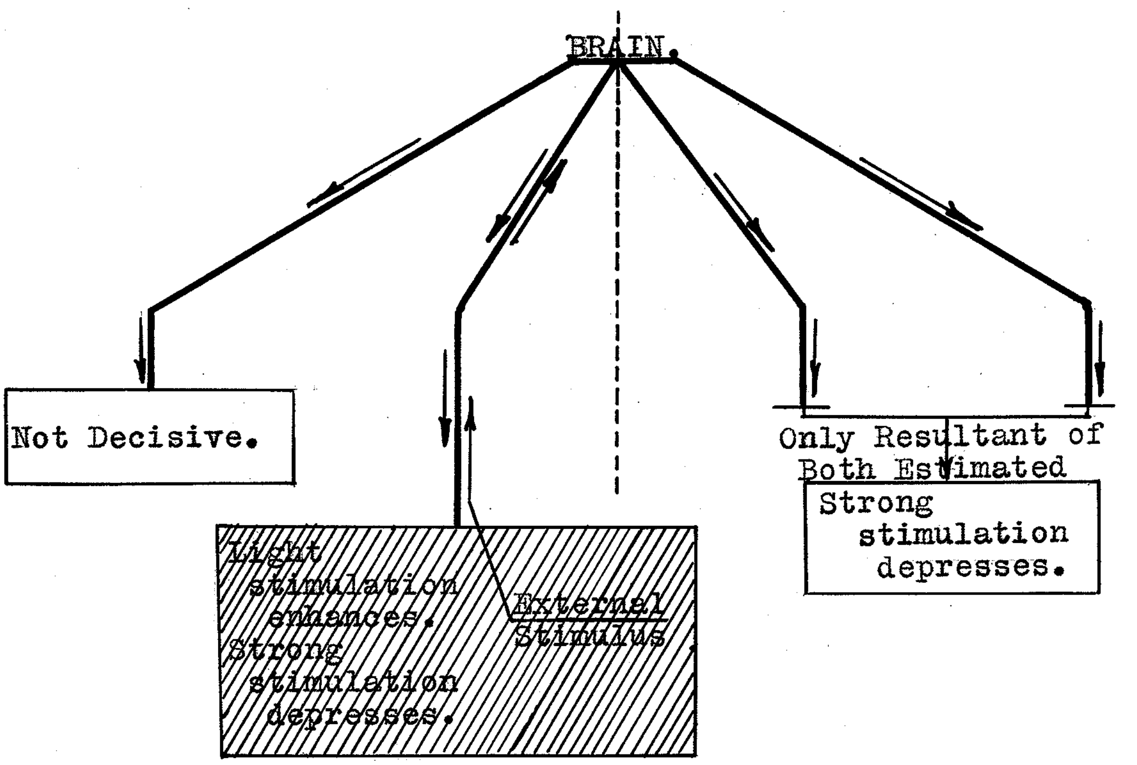
Temperature Sensation Between 26°C.and 32°C.



Cold Sensation Below 26°C.



Pain Sensation.



SECTION 5.

Summary of Conclusions.

We believe that we have shown;-

1. That all the cutaneous sensations obey the same general law.

2. That the hypothesis of Sensory Reflex Action is applicable to the cutaneous sensations, and that the behaviour of these sensations tends to confirm this hypothesis.

SECTION 6.

Remarks.

We are now in a position to offer, on the basis of Sensory Reflex Action, an explanation of the experiments in Section 1, D.

Experiment B. The metal disc lowers the temperature of the skin and twenty seconds after the removal of the disc the external surface of the skin is still drawing additional heat from the inner surface thus evoking a cold sensation; moreover, the cold end-organs have become enhanced during the short application of the disc, thus we should expect a positive after-image.

Experiment C. Cooling A enhances the cold sensation at A, also the warm. Applying a warm stimulus would stimulate the cold sensation first, it being the more sensitive, thus the observer would at once declare B to feel warmer than A. If however, the warmth sensation were continued for some ten seconds we believe that A would feel warmer than B, which is very slightly, if at all, affected by the previous cold stimulation at A.

Experiment D. The warm sensation of A is enhanced, also that of B, but not nearly as much, so that at 40°C. A feels the warmth better than B.

Experiment E. Immersing the finger at room temperature enhances the warm sensation, so that the previously neutral bath will feel warm.

Experiment F. Holding the finger in 35°C. enhances the cold sensation but not the warm; holding the finger in 15°C. enhances the warm slightly, but not the cold, so that the finger previously held in 35°C. would feel 25°C. as cold and the finger previously held in 15°C. would feel it as warm.

Experiment G. This is due to the presence of a specific sense of pain.

Experiment H. The explanation of this is the same as that offered for Experiment B.

Experiment I. The warm sensation existent for temperatures between 32°C. and 28°C, shows neither enhancement nor depression to stimuli within this range.

Experiment J. The cold end-organs are stimulated by warmth and being more sensitive than the warm end-organs will be stimulated first. This sensation would not persist.

Experiment K. The explanation is the same as that offered for Experiment J. The pain sensation also being evoked by the hot stimulus.

Experiment L. The application of the metal at 52°C. causes stimulation of the warmth sensation. This rapidly becomes fatigued and the cold end-organs at the same time become enhanced.

Experiment M. The warmth sensation has become fatigued and the cold enhanced. On putting the foot in hot water, the cold sensation is evoked and then the pain, there being little warmth due to the previous fatigue of the warmth end-organs. This bath should be over 38°C.

APPENDIX.

FIGURE 1.

Cold Sensation. Left Wrist.

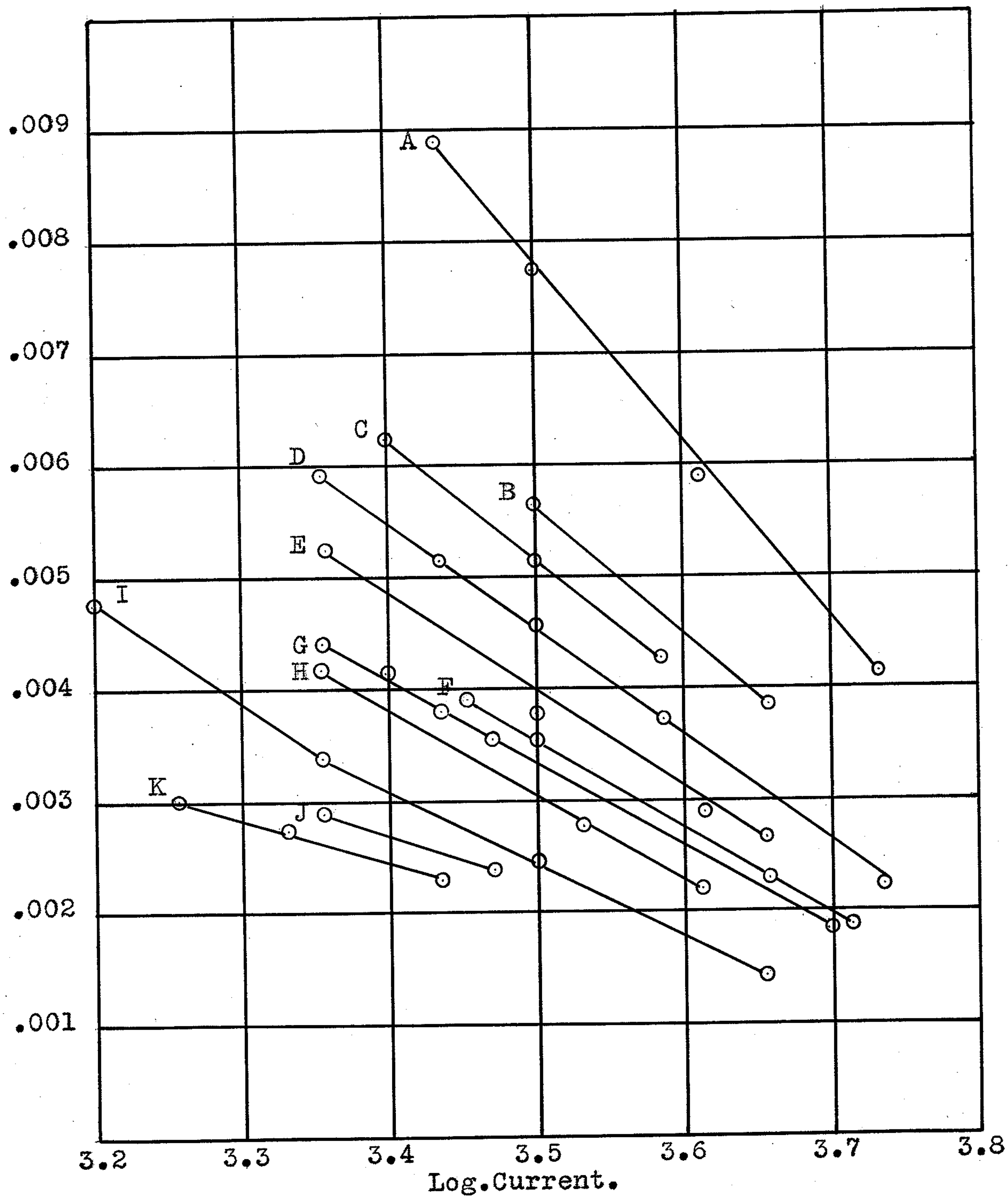


FIGURE 2.

Cold Sensation. Left Wrist.

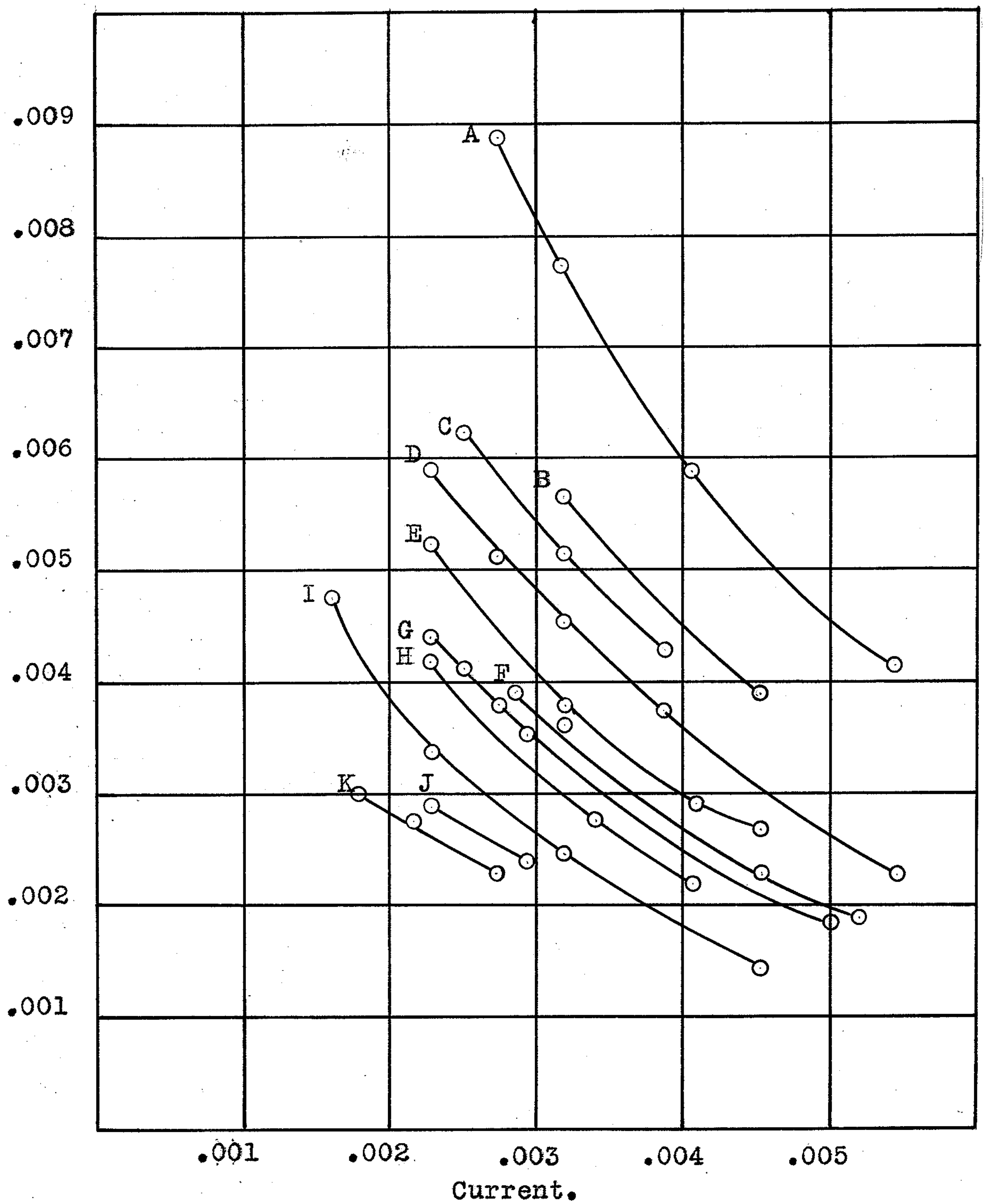


FIGURE 3.

Cold Sensation. Right Leg.

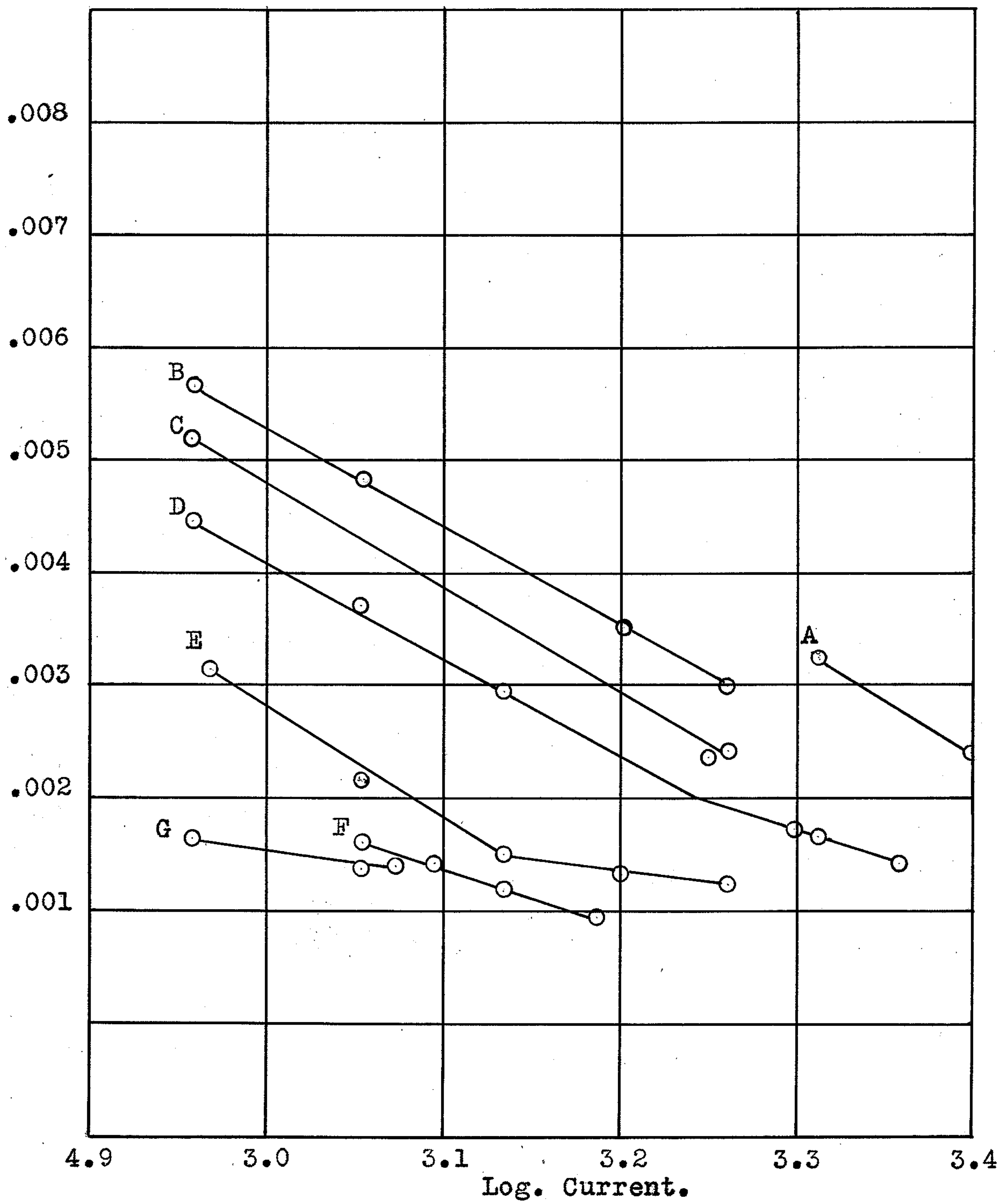


FIGURE 4.

Cold Sensation. Right Leg.

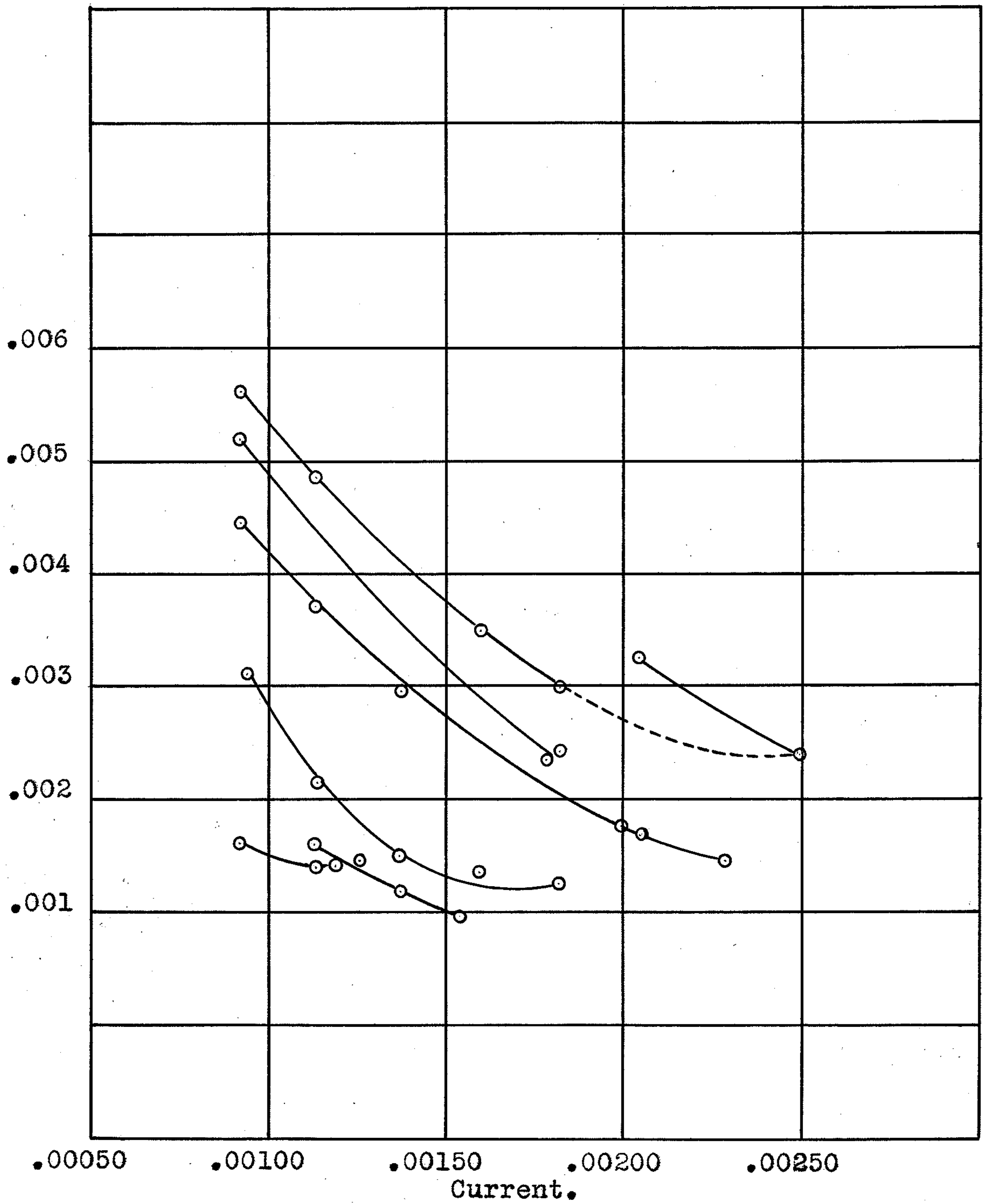


FIGURE 5.

Pressure Sensation.

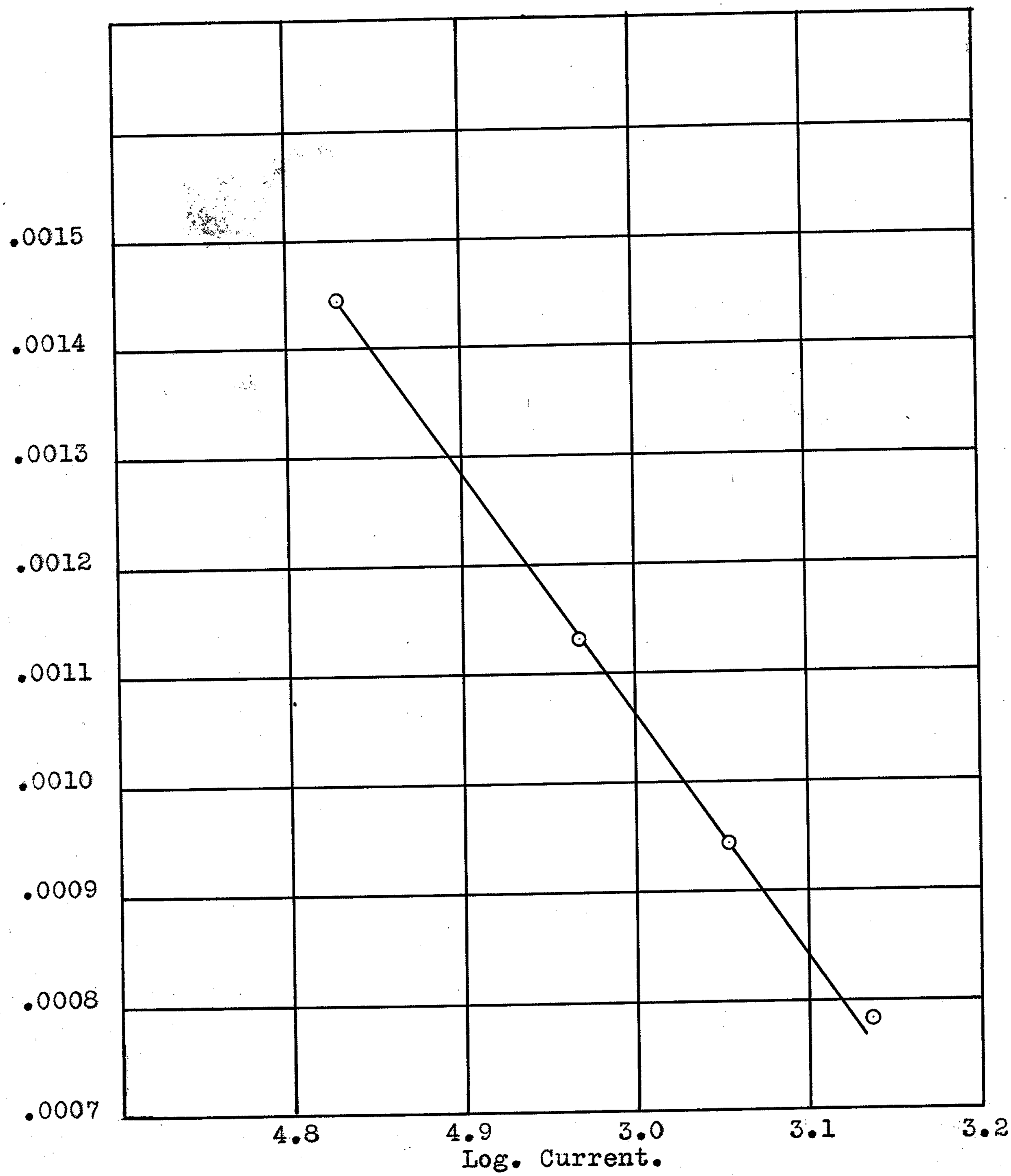


FIGURE 6.
Pressure Sensation.

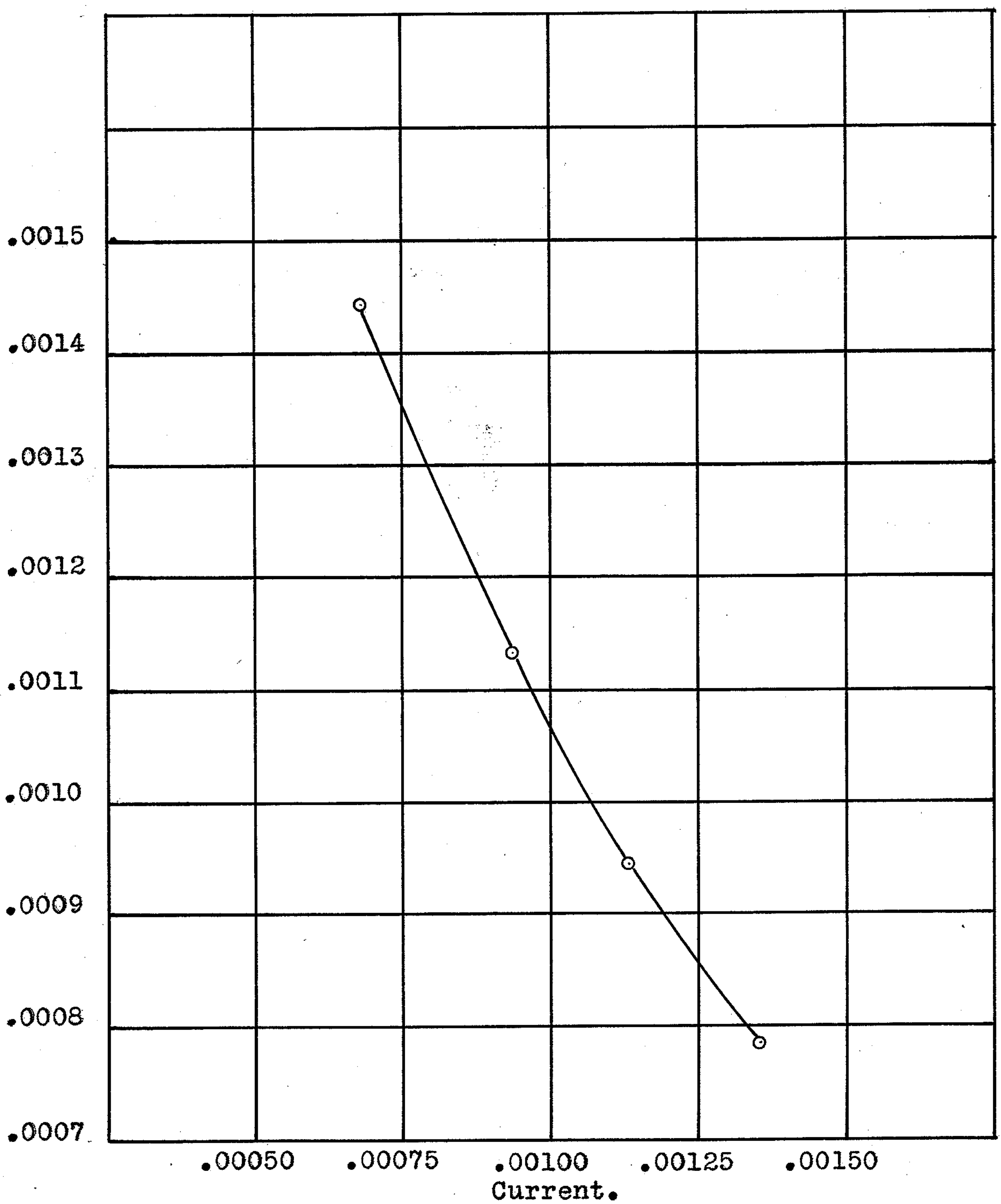


FIGURE 7.

Pain Sensation.

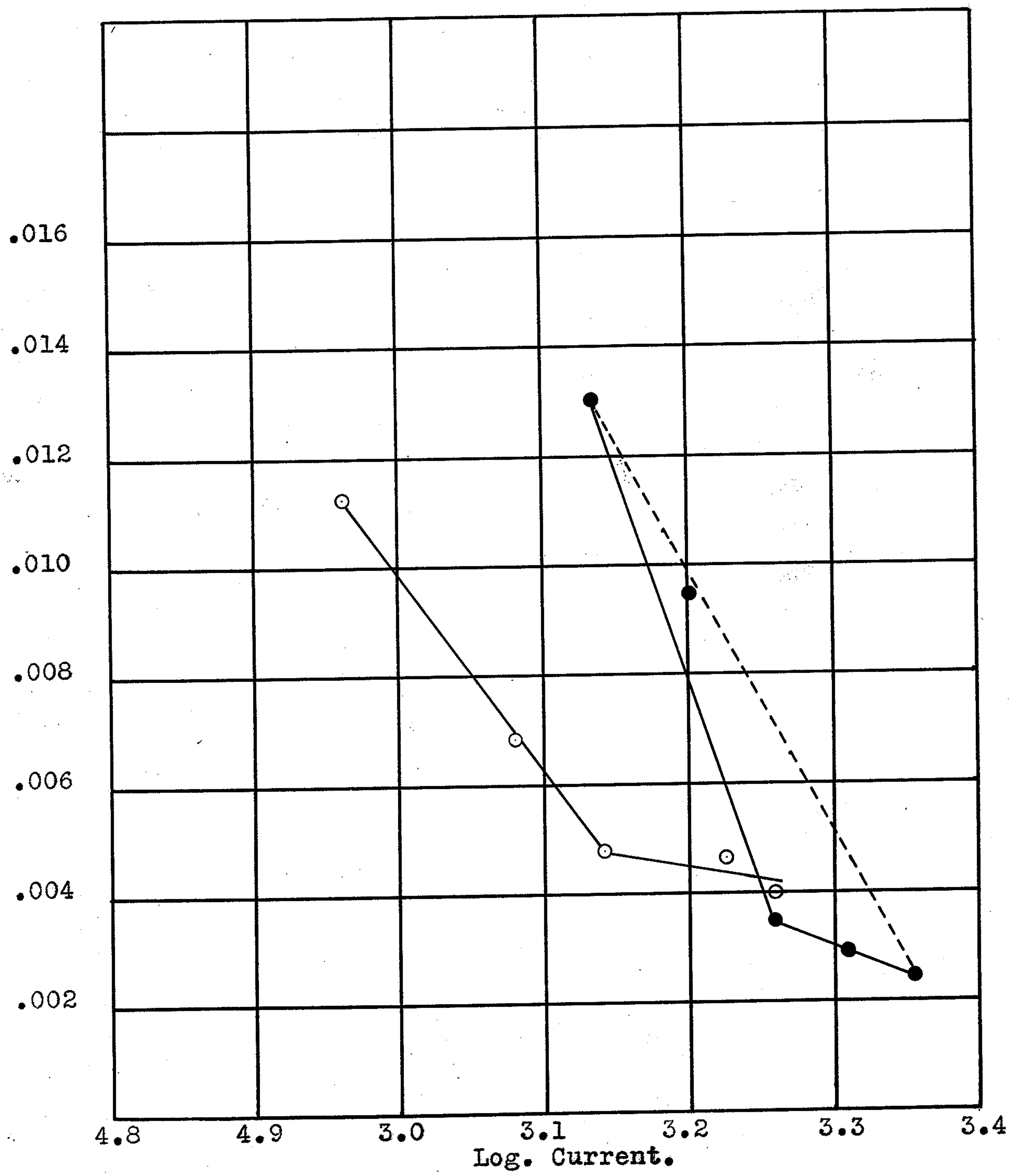


FIGURE 8.

Pain Sensation.

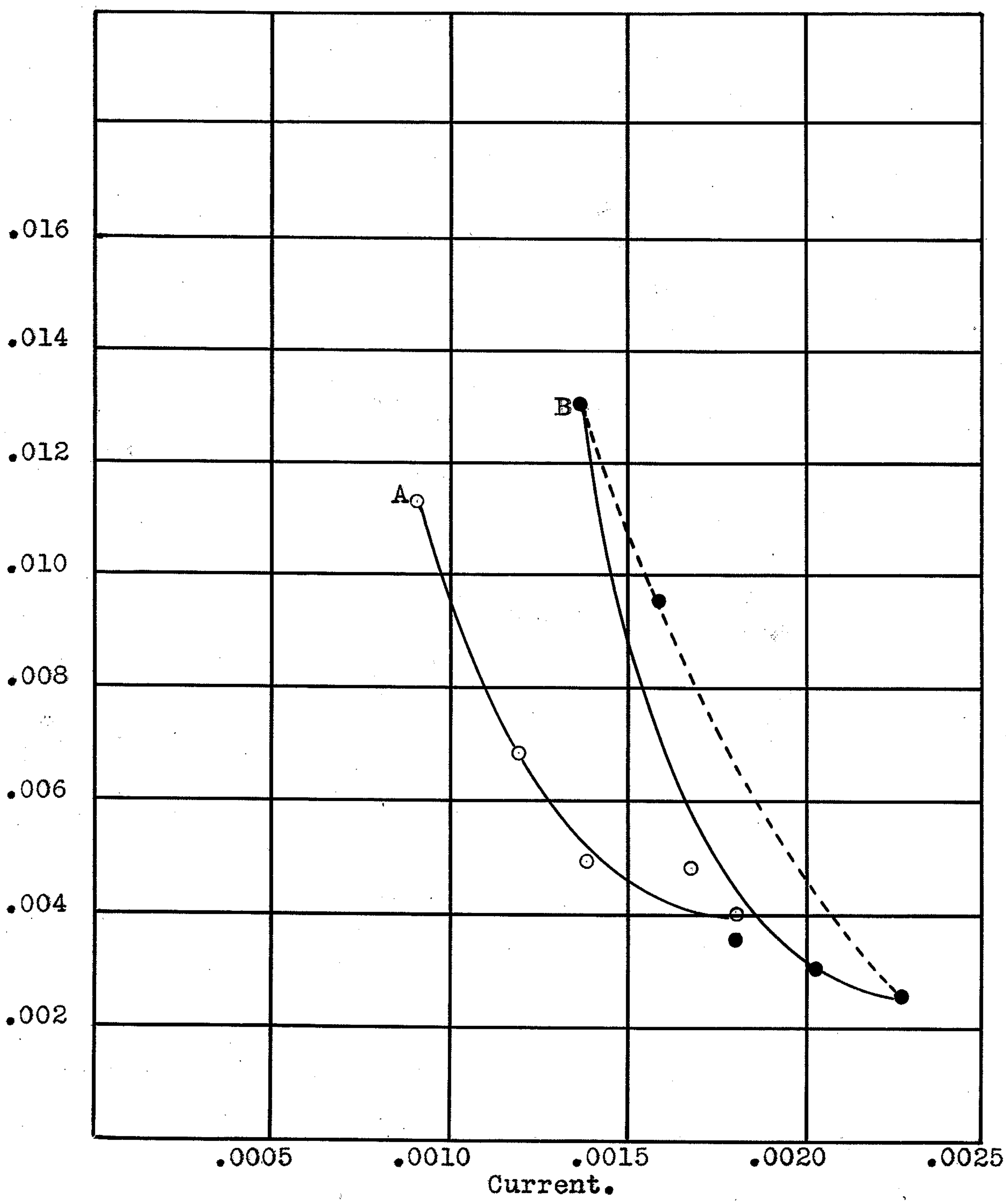


FIGURE 9.

Unknown Nerve.

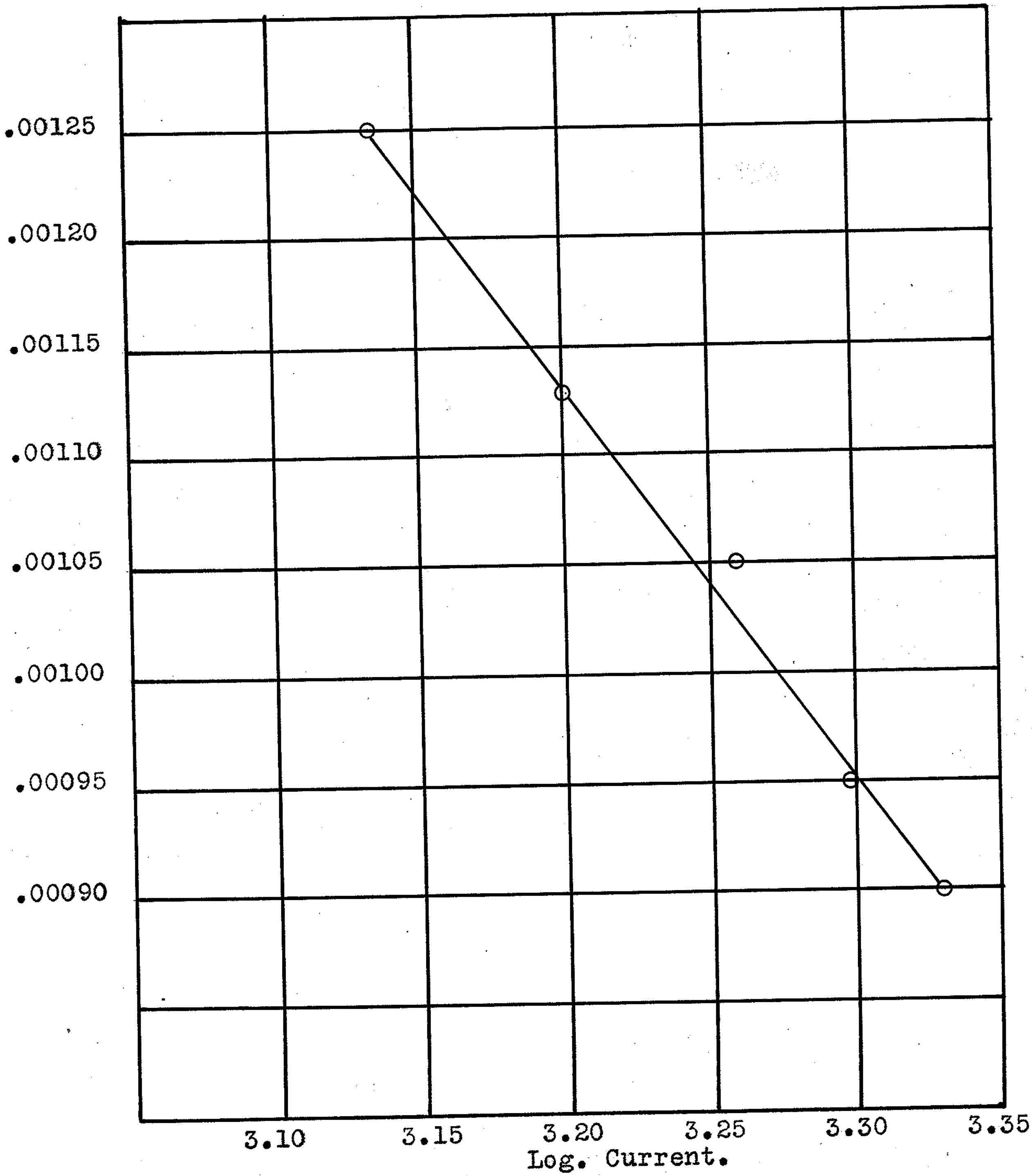


FIGURE 10.

Unknown Nerve.

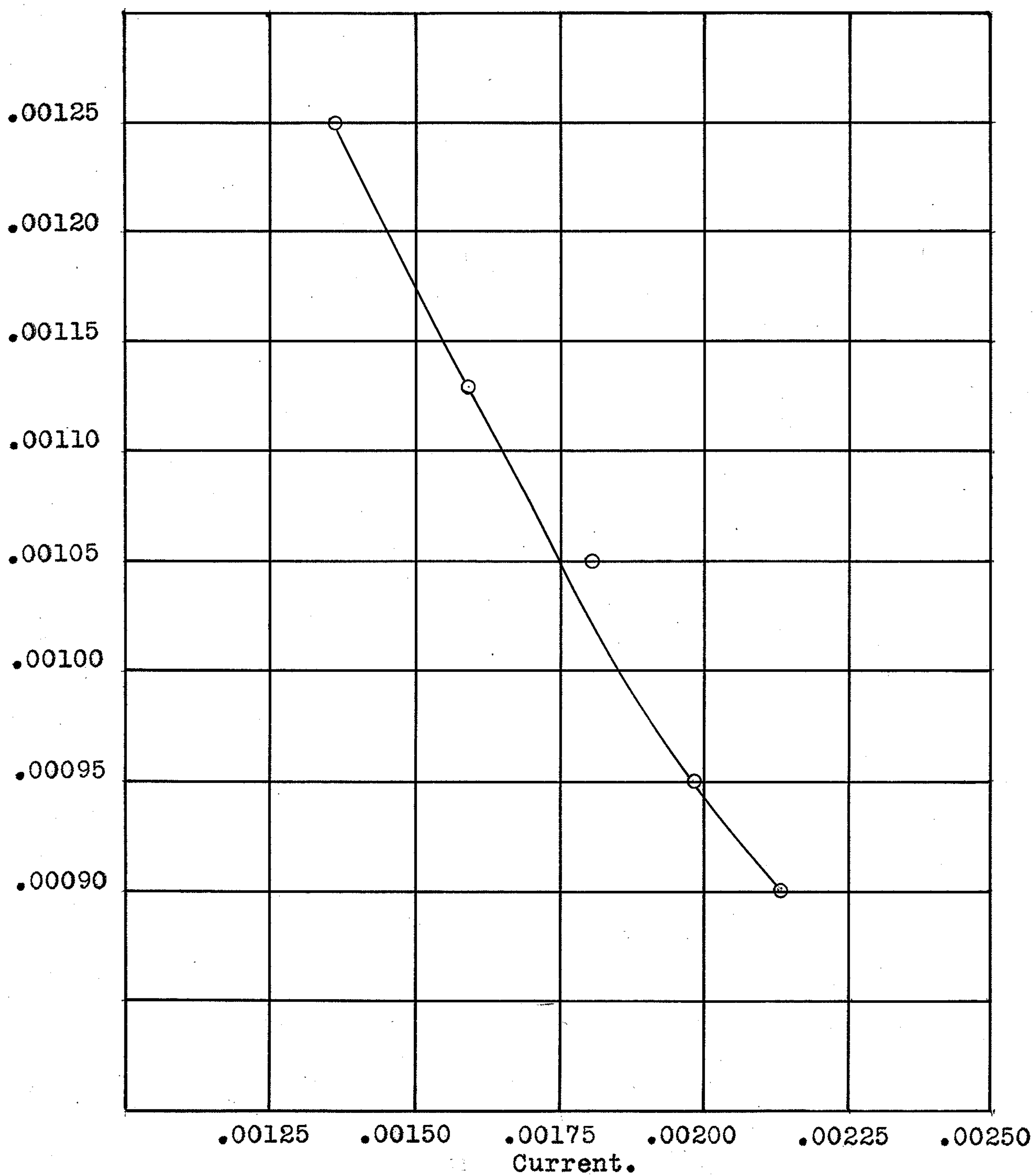


TABLE 1.

Sensation of Cold. Left Wrist.

Curve.	Current	Log. Current.	Duration.
A.	0.00272	3.435	0.00888
	0.00317	3.502	0.00755
	0.00408	3.611	0.00590
	0.00544	3.736	0.00413
B.	0.00317	3.502	0.00563
	0.00453	3.657	0.00390
C.	0.00249	3.397	0.00623
	0.00317	3.502	0.00513
	0.00385	3.586	0.00425
D.	0.00227	3.356	0.00588
	0.00272	3.435	0.00515
	0.00317	3.502	0.00456
	0.00385	3.586	0.00373
	0.00544	3.736	0.00225
E.	0.00227	3.356	0.00520
	0.00317	3.502	0.00380
	0.00408	3.611	0.00285
	0.00453	3.657	0.00268
F.	0.00283	3.452	0.00390
	0.00317	3.502	0.00360
	0.00453	3.657	0.00225
	0.00521	3.717	0.00188
G.	0.00227	3.356	0.00440
	0.00249	3.397	0.00413
	0.00272	3.435	0.00382
	0.00295	3.469	0.00350
	0.00499	3.698	0.00178
H.	0.00227	3.356	0.00415
	0.00340	3.532	0.00275
	0.00408	3.611	0.00213
I.	0.00159	3.201	0.00475
	0.00227	3.356	0.00343
	0.00317	3.502	0.00245
	0.00453	3.657	0.00135

TABLE 1. (Cont.)

Sensation of Cold. Left Wrist.

Curve.	Current.	Log.Current.	Duration.
J.	0.00227	3.356	0.00288
	0.00295	3.469	0.00238
K.	0.00181	3.259	0.00300
	0.00215	3.333	0.00275
	0.00272	3.435	0.00225

TABLE 2.

Sensation of Cold. Right Leg.

Curve.	Current.	Log.Current.	Duration.
A.	0.00204	3.310	0.00323
	0.00249	3.397	0.00238
B.	0.00091	4.958	0.00565
	0.00113	3.054	0.00485
	0.00159	3.201	0.00350
	0.00181	3.259	0.00300
C.	0.00091	4.958	0.00518
	0.00177	3.248	0.00233
	0.00181	3.259	0.00240
D.	0.00091	4.958	0.00445
	0.00113	3.054	0.00370
	0.00136	3.134	0.00295
	0.00198	3.298	0.00175
	0.00204	3.310	0.00168
	0.00227	3.356	0.00145
E.	0.00093	4.968	0.00313
	0.00113	3.054	0,00215
	0.00136	3.134	0.00150
	0.00159	3.201	0.00133
	0.00181	3.259	0.00125

TABLE 2. (Cont.)

Sensation of Cold. Right Leg.

Curve.	Current.	Log.Current.	Duration.
F.	0.00113	3.050	0.00164
	0.00125	3.096	0.00145
	0.00136	3.134	0.00120
	0.00153	3.185	0.00095
G.	0.00091	4.958	0.00165
	0.00113	3.054	0.00138
	0.00118	3.072	0.00140

TABLE 3.

Sensation of Pain. Left Hand.

Curve.	Current.	Log.Current.	Duration.
	0.00091	4.958	0.01125
	0.00120	3.080	0.00688
	0.00138	3.141	0.00475
	0.00168	3.225	0.00463
	0.00181	3.259	0.00395

TABLE 4.

Sensation of Pain. Right Leg.

Curve.	Current.	Log.Current.	Duration.
	0.00136	3.134	0.01300
	0.00159	3.201	0.00950
	0.00181	3.259	0.00350
	0.00204	3.310	0.00290
	0.00227	3.356	0.00245

TABLE 5.

Sensation of Pressure.

Curve.	Current.	Log.Current.	Duration.
	0.00068	4.833	0.00144
	0.00093	4.968	0.00113
	0.00113	3.054	0.00094
	0.00136	3.134	0.00078

TABLE 6.

Unknown Nerve.

Curve.	Current.	Log.Current.	Duration.
	0.00136	3.134	0.00125
	0.00159	3.201	0.00113
	0.00181	3.259	0.00105
	0.00198	3.298	0.00095
	0.00213	3.329	0.00090

References.

1. Text Book of Physiology - Schafer. Vol.2.

2. Human Physiology - Starling.

3. Principles of General Physiology - Bayliss.

4. Text Book of Physiology - Howell.

5. Studies in Neurology - Henry Head.

6. Page 965 of Ref.1.

7. Quart. Journ. Exper. Physiol. Frank Allen and A.Hollenberg, Col.XlV. No.4.

8. Quart. Journ. Exper. Physiol. Frank Allen and Mollie Weinberg, Vol.XV.Nos.3 and 4.

9. Phil. Mag. Vol.xlvii, Jan. 1924

10. Quart. Journ. Exper. Physiol. Frank Allen and Mollie Weinberg, Vol. XV.Nos. 3 and 4.

11. Page 956 of Ref.1.

12. Page 986 of Ref.1.