

AN INVESTIGATION INTO THE SENSORY MECHANISMS
UNDERLYING THE TWO POINT THRESHOLD, WITH
PARTICULAR REFERENCE TO THE PRACTICE EFFECT.

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INTRODUCTION.

The two point threshold was studied extensively by the psychophysical experimenters of the last century. More recent formulations in signal detection theory have suggested that the statements of these workers about absolute thresholds should be viewed with caution.

This study investigates the two point threshold in the light of these formulations, and has two main aims:-

(I) To state and deal with the problem of relating a limitation in perceptual ability, such as that which is represented by the two point threshold, to the receptor organisation of the body.

(2) To demonstrate a practice effect on the two point threshold, and to consider this in the light of (I) above.

To fulfil these two aims, a model of the neural mechanisms underlying the discrimination of two points applied to the skin is proposed, and this is able to accommodate what is known of the two point threshold. Although the model is simple it explicitly accounts for size transfer and the practice effect, and provides some clues as to the type of neural mechanism capable of producing them. The practice effect is demonstrated experimentally, and the results are then referred to the model proposed.

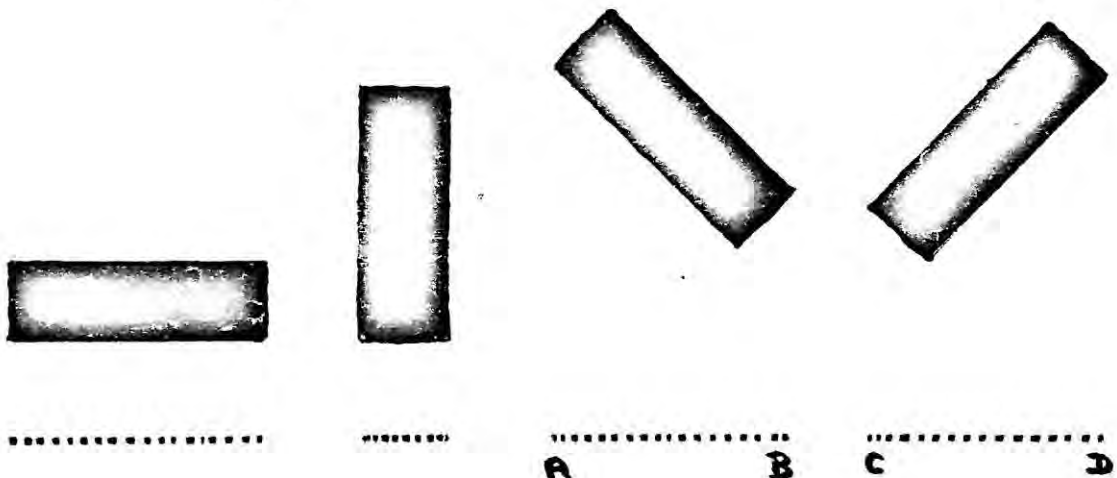
The physiology of an organism sets the limits for its behaviour. The first aim is thus an important one, in that it considers a specific case of this general problem. And secondly, the practice effect on the two point threshold is typical of a number of fairly simple "learning" phenomena, which are part of the psychologists' study of learning.

Section I. Chapter I.

RECEPTIVE FIELDS.

A general problem in sensory analysis is that of relating a discrimination ability to receptive field organisation. In an attempt to relate visual shape discrimination to receptive field organisation in the visual system, Sutherland (1957) suggested that in the octopus's visual system, shapes were converted into their horizontal and vertical projections. It was known from behavioural work (Sutherland 1957), that vertical and horizontal rectangles are very readily discriminated by the octopus, but two oblique rectangles are not.

Sutherland suggested that a "counting" of the horizontal projections of these shapes in neural terms formed the basis of the octopus's discrimination ability, and this would explain the observed findings. The horizontal projections of the two oblique rectangles are the same ($AB = CD$).



However, this early suggestion was not able to deal with later behavioural work (reviewed by Boycott - 1965), so that Sutherland (1963) suggests an "open - closed" dimension on which the octopus discriminates shapes. This later suggestion is more consistent both with what is known of the receptive field organisation of the octopus's visual system, and with what is known of the animal's discrimination abilities.

The frog has the ability to catch flies and insects with its tongue, and to avoid predators by jumping into the water. In his phototactic jumping experiments at Oxford, Muntz (1962) showed that frogs will jump towards blue light and avoid green light. He had already established that frogs have true colour vision in the sense that the frog's visual system is capable of wavelength discriminations, and this ability is not simply "colour dependence or spectral sensitivity" (Muntz 1962).

The fibres from the frog's retina pass along the optic nerve to the optic tectum, but the frog also has a rudimentary thalamic visual system. Muntz studied these retinal projection fibres, and found that they were sensitive to blue light to a surprising degree. Yellow or green light of up to ten times the intensity did not elicit as much response in these fibres as did even a dim blue light. This was so even when the green light contained as much blue light (mixed in it) as did the

pure blue light.

The positive phototactic jumping response to blue light is thus found together with a greater retinal projection sensitivity to that wavelength. The two are not necessarily connected, but Muntz suggests that it is possible that the greater sensitivity to blue light found in the visual system is important in the phototactic response. In the natural environment, the light above the water will be bluish, while that above the grass verges round the pond will be green. When a predator startles the frog, it is important that the frog jumps towards the blue and not the green.

Lettvin, Maturana, McCulloch and Pitts (1959) placed fine electrodes in the retinae of excised frogs' eyes, and analysed receptor activity at that level. When a small moving shadow falls on the retina, a particular set of fibres fires and elicits a reflex movement of the tongue. These are probably the fibres subserving food detection (flies and small insects) in the frog's visual system. These cells do not respond to anything but small moving objects - "a frog would probably starve to death if surrounded by dead flies only" (Muntz 1962). There are also fibres which fire only to a general dimming of illumination. These are probably the fibres which subserve the frog's ability to escape large predators.

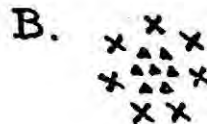
When a bird of prey flies overhead, the shadow could cause such a sudden dimming of illumination.

Receptive fields for cells in the visual system of the cat have been mapped by Kuffler (1953). At the retinal ganglion cell level, Kuffler found that he could distinguish two types of cell according to their receptive fields. The first of these had an "on" centre with an "off" surround. The centre of the receptive field was such that when a spot of light was switched on and shone into it, the cell fired a sensory volley up the optic tract to higher visual centres. But in the outer areas of the receptive field, the spot of light inhibited the firing of the cell.

In the second type of retinal ganglion cell, the centre of the receptive field was inhibitory while the surround was excitatory. These receptive fields are always concentric in shape, and fire maximally to spots of light placed over the excitatory areas and not spilling onto the surround. These receptive fields may be represented diagrammatically thus:-

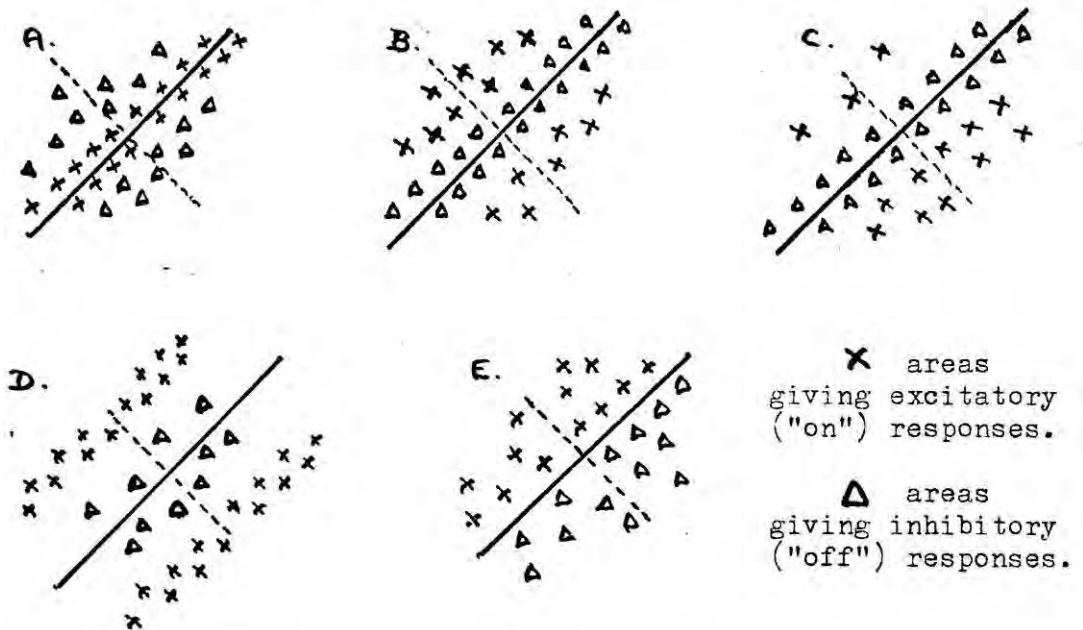


"ON" CENTRE, "OFF" SURROUND.
RECEPTIVE FIELD.



"OFF" CENTRE, "ON" SURROUND.
RECEPTIVE FIELD.

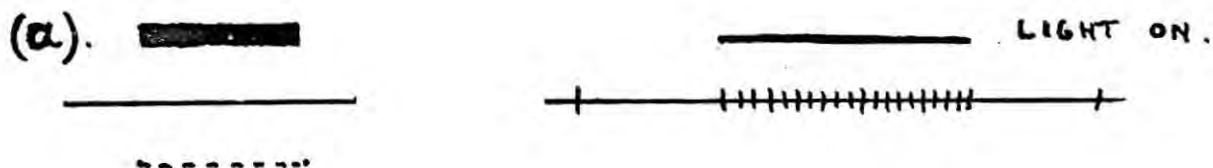
These findings have been confirmed by Hubel and Wiesel (1961, 1962) and Hubel (1960, 1963) and others. Hubel and Wiesel mapped receptive fields for retinal ganglion cells, lateral geniculate body cells and striate cortex cells by shining stimulus spots or bars of light onto the stabilised retinae of anaesthetised cats, and recording the responses of these cells through microelectrodes. Apart from confirming Kuffler's findings at the retinal ganglion cell level, Hubel and Wiesel have found the same type of cells at lateral geniculate body level. And in the visual cortex of the cat, they have discovered receptive fields which have quite specific shapes, as shown in the diagram:-

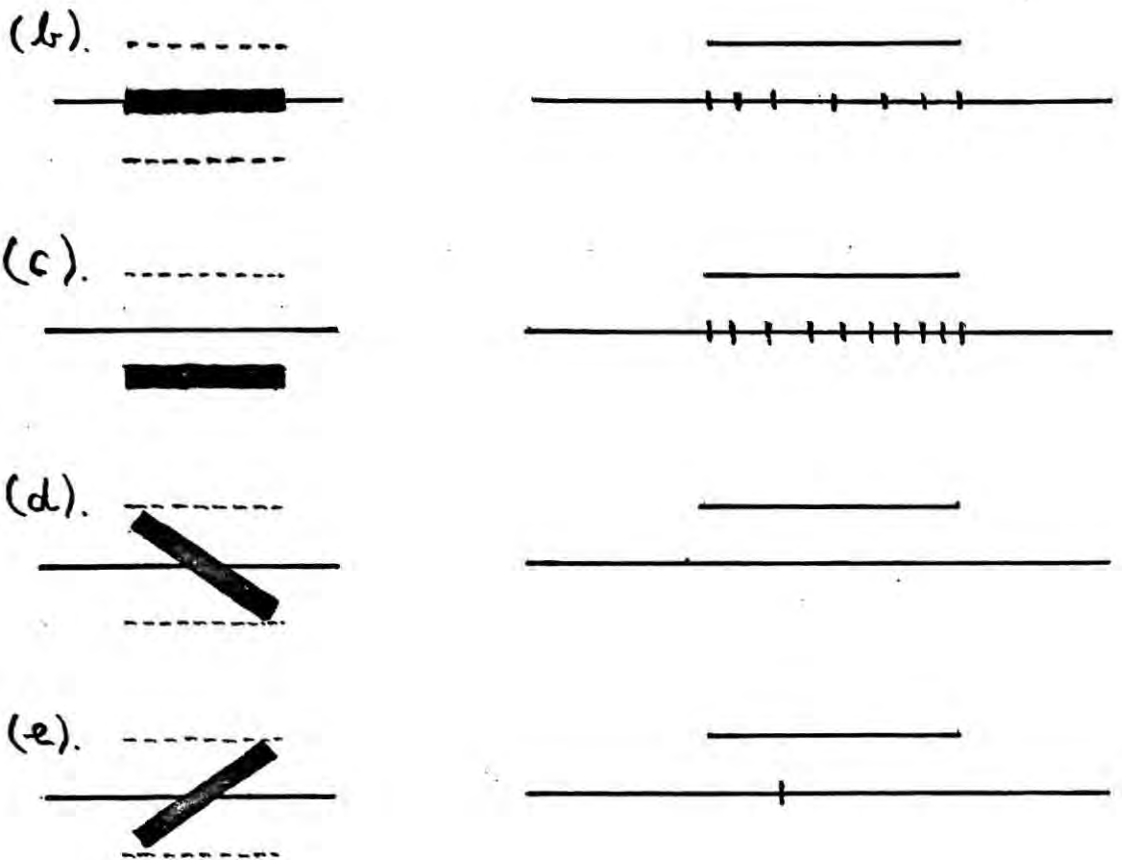


(Adapted from Hubel D.H. and Wiesel T.N. (1962) Journal of Physiology Vol. 160 page III.)

The shapes shown here are the actual maps of points on the retina which were found to affect the firing of a single cortical neuron. A typical field is elliptical, having a narrow band of excitatory points running longitudinally, flanked by two wider longitudinal inhibitory strips, or vice versa.

From the shape of the receptive field of a cortical neuron, as mapped by a spot of light, Hubel and Wiesel found that they could predict what stimulus shape would give a maximal response from the neuron. In the case of diagram (A) above, this would be a rectangle of light laid along the length of the receptive field covering only the excitatory centre band. A small twisting of the orientation of the rectangle would probably be enough to do away with the response, since it would now cover both excitatory and inhibitory areas, and the response would thus be something less than maximal. An example of this is given by Hubel and Wiesel in the diagram below. On the left is the position of the stimulating rectangle and on the right are the number of spikes fired by the cell. Notice how tilting the stimulus abolishes the response in diagrams (d) and (e).





(Adapted from Hubel D.H. and Wiesel T.N. (1962) Journal of Physiology Vol. 160 page 114.)

Uniform stimulation of the whole field (without any contours at all) would leave the neuron unaffected. Thus each neuron has a particular shape and orientation of contoured stimulus which will elicit a maximum response.

In the cat's visual cortex, Hubel and Wiesel have found cells having receptive fields much more complicated than these. These cells probably give "a further stage in the analysis

of information in the visual system" (Sutherland 1963). For instance, some cells fire maximally to a straight edge. Others fire maximally to rectangular bars of light in a particular orientation, as noted above, but moving in a certain direction. Yet others were affected not only by shape, orientation and direction of movement, but also by the speed of movement of the stimulus across the visual field. This was so for large parts of the retina: in extreme cases, the receptive fields of the cells involved could be the whole half of the retina.

Again, it is known that cats can discriminate various shapes. This work is an attempt to relate that ability to receptive field organisation.

Roughly, the receptive field of a cell at any point in a sensory system, is the area of receptor surface over which the firing of that cell can be influenced by stimuli. Thus Gordon and Jukes (1962) speak of receptive fields on the cutaneous surface of the body of cats when dealing with the excitatory and inhibitory influences on cells in the nucleus gracilis of the hindbrain. And Gordon and Paine (1960) showed that cells in the middle 3 mm. of the long axis of the nucleus gracilis of the cat have receptive fields on the cutaneous surface which are much smaller than those lying on either side of them.

These workers were measuring the firing responses

of nucleus gracilis cells to touch stimuli, for example, the bending of hairs or the application of pressure to the body surface. In this way they were mapping receptive fields for these cells.

J.Z. Young (1960) studied what he called "Regularities in the Retina and Optic Lobes of the Octopus", and attempted to relate these to the animal's form discrimination ability.

"He obtained evidence that the dendritic pickup fields in the optic lobe of the octopus are predominantly elliptical, and that there is a maximum number oriented in a plane which corresponds with a visual horizontal, and a second maximum number oriented in a plane which corresponds with a visual vertical, and fewer in the intermediate orientations. It is possible that Young has discovered in the octopus the anatomical basis for a coding arrangement similar to that demonstrated by physiological techniques in the striate cortex of the cat. Two simple operations which could be performed on information coded by this arrangement in the octopus are, to count the total number of receptive fields fired and to count the ratio of fields fired in one orientation to those fired in the others" (Sutherland 1963).

This may give the mechanism of shape discrimination in the octopus visual system. Such are the types of

link up between receptive field organisation and a known discrimination ability (or lack of ability), which have been attempted. This paper will attempt such a link up for the two point threshold.

Receptive fields are present on the skin for all the cutaneous senses. Thus E.H. Weber (1834, cited by E.Boring 1942) spoke of "sensation circles" on the skin:-

"If one regarded the cutaneous zone in which any given nerve fibre could be affected as a circle, the skin could be divided into a very large number of sensory circles. In Weber's "compass experiment", these sensation circles were affected by the two compass points applied lightly to the skin. If the two points were applied within the same sensation circle, they would give rise to the stimulation of only one fibre, and thus to the perception of only one point. If the two points rested on two sensation circles next to one another, the perception was of a line. Two points would be appreciated only if an unexcited sensation circle was interposed between the two excited ones" (Boring 1942).

Weber drew his sensory circles as hexagons so that they would fit together without overlap. In fact, there is overlap of innervation. Although the branches of different cutaneous fibres do not join up, they do serve overlapping areas of the skin (Morgan 1965). Weber's concept of an excited fibre next to an unexcited fibre, each with a private path to the cortex, is not correct either (T.C. Ruch, 1951).

THE CUTANEOUS SENSES.2(i) Skin Structure.

The skin is made up of two layers, an outer layer called the Epidermis and an inner layer called the Dermis. The boundary between the dermis and subcutaneous tissue is not clear cut. The epidermis itself is made up of two layers, the outer dead corneal layer and the inner malpighian layer. The corneal layer of the epidermis is made up of "flattened dead cells... because living cells cannot survive exposure to air or water" (Montagna, 1965). The Malpighian layer, however, is living tissue and is supplied with nerve endings, while the dermis is richly supplied with both nerve endings and blood vessels. The thick fibrous tissue of the dermis makes up the main bulk of the skin (Montagna 1965).

The skin is not uniformly sensitive to all sorts of stimuli but has sensory spots on it. This "punctate sensitivity of the skin" (Morgan 1965) refers to spots of high sensitivity surrounded by areas of relatively lower sensitivity. If the skin is mapped with a small stimulator at a low temperature, for example, some points respond with cold while others do not (Morgan 1965).

There is a traditional division of the cutaneous senses into four: touch, pain, warm and cold. There are a large number of derivations from these four basic qualities of cutaneous sensation, of which vibration, itch and tickle are perhaps the most common. It is just possible that there are actually three touches, two pains and two each of the temperature senses (Jenkins 1951). In any event, in everyday life one seldom experiences pain without touch, and so each cutaneous experience is the result of a combination of sensory events from two or three of the four senses.

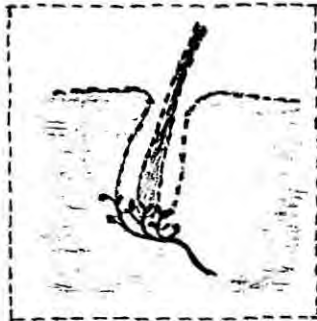
There are a number of different variations in the structure of the somatic receptors. For example, there are:-
I). FREE NERVE ENDINGS. These are widely distributed in the skin and are found in great numbers in the dermis and malpighian layer of the epidermis. They are found in the cornea of the eye, which has no blood vessels and in fact obtains its nutriments from the aqueous humor.



Free nerve endings.

(Adapted from Wyburn G.M., Pickford R.W. and Hirst R.J. (1964)
"Human Senses and Perception" Oliver & Boyd, London, p16)

2). Around each hair bulb are the BASKET ENDINGS, which are not found at all in smooth skin. Deflecting a hair is enough to innervate the fibre served by the basket ending at the hair bulb. Thus a sensation of touch can be aroused without direct contact on the skin simply by touching a hair. Stetson (1923, quoted by Jenkins 1951 on p 1177) showed that destroying the hair root endings reduces, but does not do away with the sensitivity to touch. It seems, then, that movement of the hair not only disturbs the basket endings but also distorts the surface of the skin and so affects the other touch receptors as well.



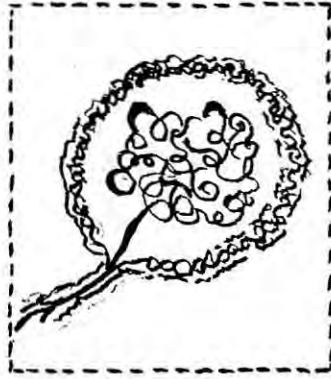
Basket ending and hair follicle.

3). ENCAPSULATED END ORGANS. The nerve fibre here ends in a shell or other structure. At least the following divisions of encapsulated end organs have been made:- Meissner corpuscles, Krause End bulbs, Ruffini cylinders, and, deeper in the body, Pacinian corpuscles and Golgi tendon organs.

All of these are illustrated in the schematic diagrams which follow:-



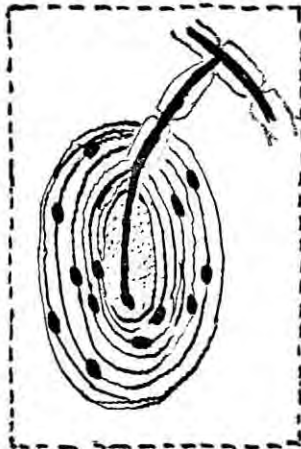
Meissner
Corpuscle.



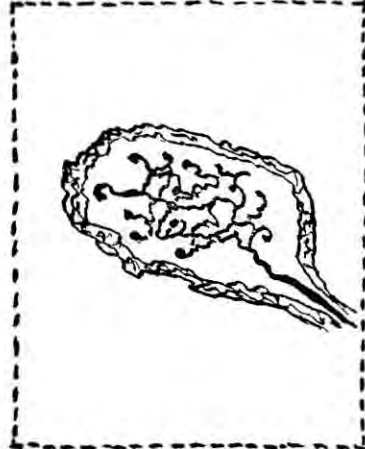
Krause End Bulb.



Ruffini
Cylinder.



Pacinian
Corpuscle.

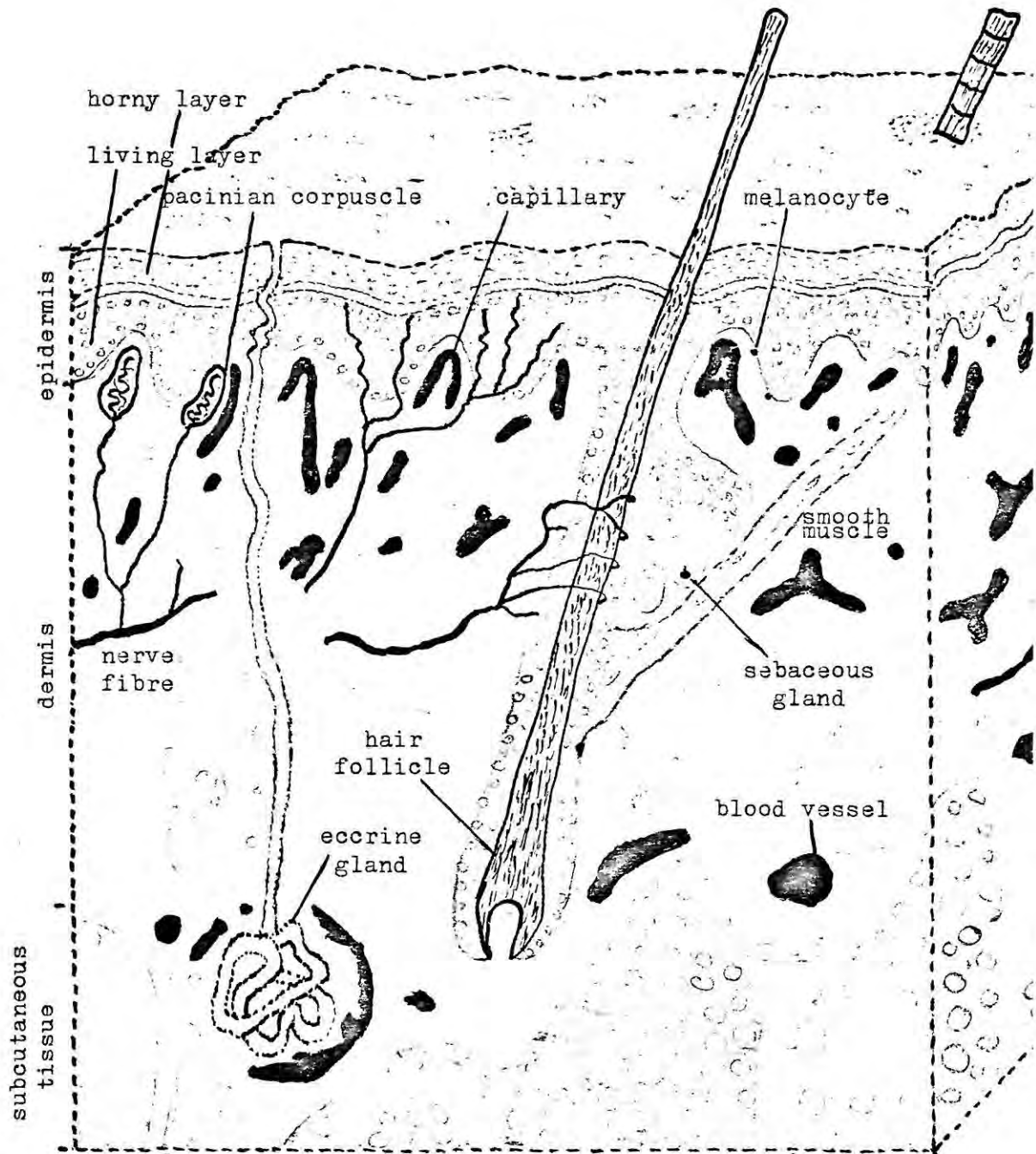


Golgi Tendon Organ.

(From Morgan C.T. (1965) "Physiological Psychology" McGraw-Hill, PP244 - 245, and Wyburn G.M., Pickford R.W., and Hirst R.J. (1964) "Human Senses and Perception" p16)

In many parts of the body there are found in addition to the glomus bodies, which are direct connections to the veins and arteries, and are larger than simple capillaries (Jenkins 1951)

The relative sizes and positions of the various skin structures may be seen in the idealised section given below:-



(Adapted from MONTAGNA W. (1965) Scientific American vol. 212 p 60)

In this idealised section of the skin, it is seen that:- "The underlying dermis is supported by a fat - rich subcutaneous stratum. Intermingled with the cells of the dermis are fine blood vessels (colour), tactile and other nerves, the smooth muscle that raises the hair when contracted and a variety of specialised glands. Above the dermis are the twin layers of the epidermis ..." (Montagna, 1965 p 60)

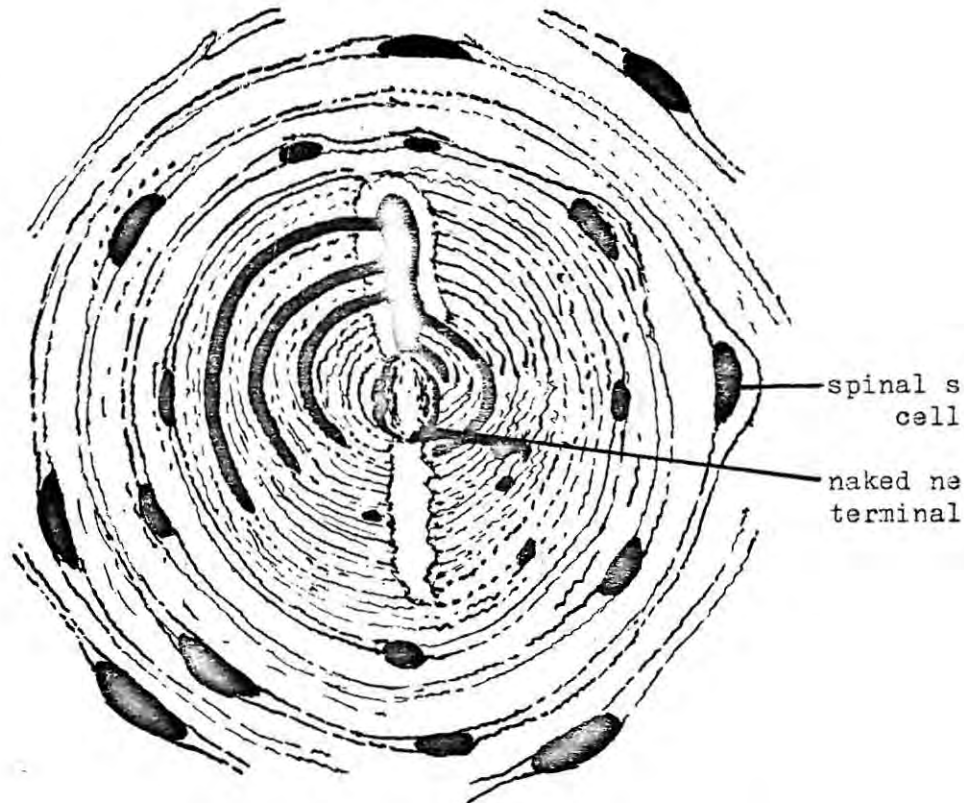
The corneal layer of the epidermis consists inter alia of keratin, and is the principle shield of the body. "In mammals the same tissue that produces the epidermis also differentiates into hair, spines, nails, claws, hooves, scales and horns" (Montagna 1965, p 56).

2 (ii). THE RECEPTORS.

The functioning of a Pacinian corpuscle is a good example of how a mechanoreceptor subserves touch or pressure perception. The actual stimulation of such a receptor depends on a deformation of the skin or the tissues due to pressure.

"The receptor element in the Pacinian corpuscle is the nerve terminal enclosed in a sheath made up of concentric layers like those of an onion, with some intervening fluid.

Pressure will compress the corpuscle with initial displacement of all its layers, including the nerve terminal.



(Taken from Wyburn G.M., Pickford R.W. and Hirst R.J. (1964)

"Human Senses and Perception" Oliver & Boyd, London, p17)

Displacement of the enclosed receptor is however, confined to the onset of compression and does not persist with sustained stimulation. Thus, the activation of the receptor will be limited to the initial stimulation and the characteristic

rapid adaptation of the Pacinian corpuscle is largely a mechanical attribute of the structure" (Wyburn, Pickford and Hirst p 17).

If only cutaneous touch is to be evoked, then only very light weights or weak hair stimulators must be used. Heavier weights or stronger stimuli will affect deep pressure receptors as well. The surface receptors seem to function in a "dead-beat" way (Jenkins 1951), whereas the deep pressure receptors have longer adaptation times. Some Pacinian corpuscles, for instance, such as those in deeper tissues round the joints, are slow adapting (Wyburn, Pickford and Hirst 1964).

By "dead-beat" is meant that the cells fire and return immediately to their former state. There is little or no reverberation or after-activity. Good evidence for saying that the surface receptors for touch are of this nature comes from work on vibration. Separate touches on the skin surface can be felt as discrete up to a frequency of about twenty a second (Jenkins 1951). When the rate gets above twenty a second, the touches melt into a smooth sense of vibration.

What is important in this perception of surface touch alone is either 1) the deflection of a hair or 2) the deformation of the skin. There is evidence (Jenkins 1951) that the direction of deformation is immaterial. "Thus if a small

stimulator is glued securely to the skin and lightly pulled and pressed, the average subject cannot distinguish the two directions (p II7I).

If a light weight is allowed to rest on the skin, it is soon not felt at all. This is because of the dead beat nature of the surface touch receptors and the fact that the weight no longer moves to give a rate of skin deformation. Jenkins (1951) illustrates this by quoting work by Nafé and Wagoner (1942), where it was found that when a light stimulator was allowed to sink into the skin, the touch sensation disappeared just when the rate of movement fell close to zero. The "deformation gradient" is also important. "If you put a finger in a bowl of mercury, there is contact all over the submerged finger, but touch is felt only at the surface of the liquid where there is a deformation gradient on the skin". (Jenkins 1951, p II77).

It is natural to ask whether there is a relationship between the various types of encapsulated end organs and the four somatic senses. But Jenkins (1951) holds that classification of the various encapsulated end organs according to function "is of dubious merit". Morgan (1965) quotes work by Gilmer (1942) in which he says "The verdict goes against any fixed relation between encapsulated end organs and the quality of sensation subserved". One will always find a nerve ending

of some sort at a sensitive spot, but there is no relationship between the type of encapsulated end organ and the type of sensation subserved (Morgan 1965).

Meissner corpuscles are found just below the epidermis of the hands, feet, forearm and other hairless regions (Wybarr 1960). Krause end bulbs are found only in a few areas such as the conjunctiva of the eye, while the Ruffini cylinders are even scarcer. This uneven distribution of various types of encapsulated end organs is further evidence against any fixed relationship between the receptors and the quality of sensation subserved.

Morgan quotes further work by Lele and Weddell (1956) to confirm this statement. These two investigators examined the cornea of the eye, which contains only free nerve endings and Krause end bulbs, and yet is sensitive to touch, pain, cold and warm. Furthermore, Weddell (1961) showed that encapsulated end organs are in a constant state of degeneration. Free nerve endings can turn into encapsulated end organs and the latter can simply disappear (quoted in Morgan p 246 - 247).

The conclusion is thus against any simple relationship between a particular type of somatic receptor and the four somatic sensations. Nevertheless, it is probable (Morgan p 247) that basket endings round the hair bulb serve

touch or pressure and the two deeper receptors, the pacinian corpuscle and the golgi tendon organ, serve "deep" touch or pressure. In addition, Morgan thinks it likely that free nerve endings subserve pain and may also subserve the other modalities.

2 (iii) INNERVATION.

The free nerve endings "finally lose their myelin sheaths and ramify in the epidermis of the skin" (Wyburn 1960). Meissner corpuscles occur in clusters of two or three and as many as ten of these groups (which probably correspond to touch spots) can be found in one square millimeter of sensitive human skin (Wyburn, Pickford and Hirst 1964).

Any one area of the skin is served by a great number of fibres. There is a great deal of interlocking of nerve terminals, and the overall effect is of a vast net spread out at the surface of the skin. Thus:- "Small groups of fibres leave the main nerve trunk in the subcutaneous adipose layer. In the dermis these small groups of fibres split up into individual nerve fibres" (Morgan p 253). Each nerve fibre then splits up into a number of branches. These branches interlock with one another to form a plexus or net. There are still smaller terminals which branch from the plexus, and these serve

the somatic receptors.

The branches and terminals from a single neuron can spread over an area of several hundred square millimeters. This area varies in different parts of the body so that Morgan (1965) reports that in the viscera of the frog for example, one neuron can serve six square centimeters at the surface. In some regions of the skin of man this area is more than one square centimeter. The area referred to is the receptive field of the neuron concerned. In sensitive areas of the body such as the thumb, these receptive fields are much smaller. Wyburn (1960) gives the receptive field as being "the area of skin surface innervated by a single afferent fibre" (p 36).

The branches of different fibres serve overlapping areas of the skin. Thus a compass or esthesiometer touched to the skin is likely to stimulate the branches of more than one neuron. Jenkins (1951 p II74) gives two examples to illustrate this point:-

(I) "A single hair bulb is found to have basket endings derived from two or more separate myelinated fibres. Other branches from these same fibres go to form basket endings around other hair bulbs. In addition, around each hair bulb is an accessory innervation of fine unmyelinated fibres, each a branch from a neuron supplying accessory innervation to other

hair bulbs". So the roots of hairs are encircled by a whole net-
of unmyelinated nerves. "As many as 300 groups of hair follicles
may be supplied by one nerve fibre, each group containing up to
ten hairs" (Wyburn 1960).

(2) "The free nerve endings in the Malpighian
layer of the epidermis are arranged in extensive nerve nets,
each covering an area of several hundred square millimeters and
overlapping repeatedly with other similar nets. Mapped spots
seem thus to be nothing more than points of functionally high
sensitivity".

The degree of overlap varies from region to region,
but the notion of overlapping receptive fields is established.
Thus Weber was not correct in drawing his "sensory circles" as
hexagons having no overlap.

THE C.N.S AND THE CUTANEOUS SENSES.

A dermatome is the area of the body served by a single spinal nerve. Fibres of the same nerves that serve the skin also serve the muscle joints and deep tissues. There are thirty one pairs of spinal somatic nerves, spaced at regular intervals along the spinal cord. However, the dermatomes served by each spinal nerve are not regularly spaced, and there is also considerable overlap.

The somesthetic fibres make up the dorsal root of the spinal cord. The cell bodies of the sensory fibres lie in the dorsal ganglia of the cord. Just before the cord itself, fibres for pain, temperature and touch from the skin, muscles and deep parts run together into one nerve.

In the spinal cord itself, fibres tend to remain separate according to the function they serve. Thus the dorsal columns contain the fibres for kinesthesia, and some of the fibres which mediate deep pressure and cutaneous touch. However, "Many of the fibres that represent pressure receptors of the skin do not remain in the dorsal columns but leave them at some point to run over to the ventral part of the cord. There they course up-

ward in a tract known as the central spinothalamic tract" (Morgan p262). Thus the spinothalamic tracts carry the balance of the deep pressure and cutaneous touch fibres in their ventral portion, and the neurons for pain, warm and cold in the lateral portion.

This central spinothalamic tract is the most important pathway for somesthesia from the skin of the body. The spinothalamic tracts run right up to the thalamus. In particular, they run to the posterovenral nucleus of the thalamus.

In the medulla and pons of the hindbrain, the spinothalamic tracts are joined by the bulbothalamic tracts from the face and the head. The bulbothalamic tract has four main contributors, the trigeminal, facial, glossopharyngeal and vagus nerves. Of these, the trigeminal is the most important (Morgan 1965). It divides into three roots which lead to three nuclei in the hindbrain and from which axons ascend to the thalamus itself. The pathway by which these axons ascend is the medial lemniscus.

In the posterovenral nucleus of the thalamus, division according to function disappears. Instead of a segregation such that different sensation impulses are kept separate in different tracts, a topographical representation is now found (Mountcastle and Henneman 1949, quoted in Morgan P 265).

As far as is known, the thalamus "shows no separate areas for pain, temperature or pressure". Instead, one part of the postero-ventral nucleus represents all somesthetic senses of the legs, another all the somesthetic senses of the arms, and still a third part (the arcuate nucleus) the face (Morgan p 265).

This topographical representation is also found at cortical level. Jenkins (1951) quotes early electrophysiological work by Marshall, Woolsey and Bard (1937) on the monkey, which showed a point for point projection for somesthesia analogous to that of the motor cortex. Jenkins (1951) could find no evidence for separate touch, pain, warm and cold areas in the cortex. These four senses all project to the same cortical area, and as yet we are not at all clear on the central mechanisms which distinguish them. It was hoped that work such as that of Penfield and Sem Jacobson on patients undergoing brain surgery under local anaesthetic would afford evidence on this point. But Penfield's (1958) reports do not really do so. Topographical representation in the cortex was clearly seen, so that stimulating one area of the cortex with an electrode led to the patient reporting a sensation in his leg, and stimulating another area of the cortex with an electrode led to the patient reporting a sensation in his arm. But "Sensations of pain, cold or warmth were seldom elicited from patients in this situation. The most common sensation re-

ported was one of tingling, movement or numbness" (Quoted Morgan 1965).

However, what is fairly well established is that each of the four modalities of the somatic senses is served by a definite size range of fibres.

"Touch fibres are in the A class, while slow pain impulses are carried by the small C fibres. Thus each modality will have its specific pattern of impulses in respect of timing, threshold stimulus and form of action potential" (Wyburn 1960 p 36).

Touch and pressure are just two varieties of the same modality. The nerve fibres serving them are from 1 μ to 20 μ in size, and conduction rates are fast (from 6 to over 100 meters per second). "The other cutaneous sense modalities have slower nerve fibre conduction rates and so you could get selective activation of central nervous systems" (Wyburn p 37). For pain, C fibres having conduction rates of two meters per second are involved.

Thus in spite of the fact that there is only topographical representation at the cortical level, we have at least this hint as to how signals from the four modalities are used selectively at the cortex. At the moment it seems little more than a hint, since electrophysiological work such as that of

Penfield has not isolated the corresponding central nervous systems.

The main cortical projection area from the thalamus is the postcentral gyrus of the parietal lobes. This area is usually referred to as either Brodmann 3, 1, 2, and 5, or as Somatic I.

Somatic area I is divided into four main parts, one for the legs, one for the arms, and one for the face, and a small area between the arm area and the face area for the trunk of the body. The leg area is right at the most dorsal part of Somatic I near the longitudinal fissure. Below it and more lateral to it is the arm area. Next to that is the trunk area and down towards the temporal lobe is the area for cutaneous sensation from the face including the teeth and cornea of the eye (Wyburn p42).

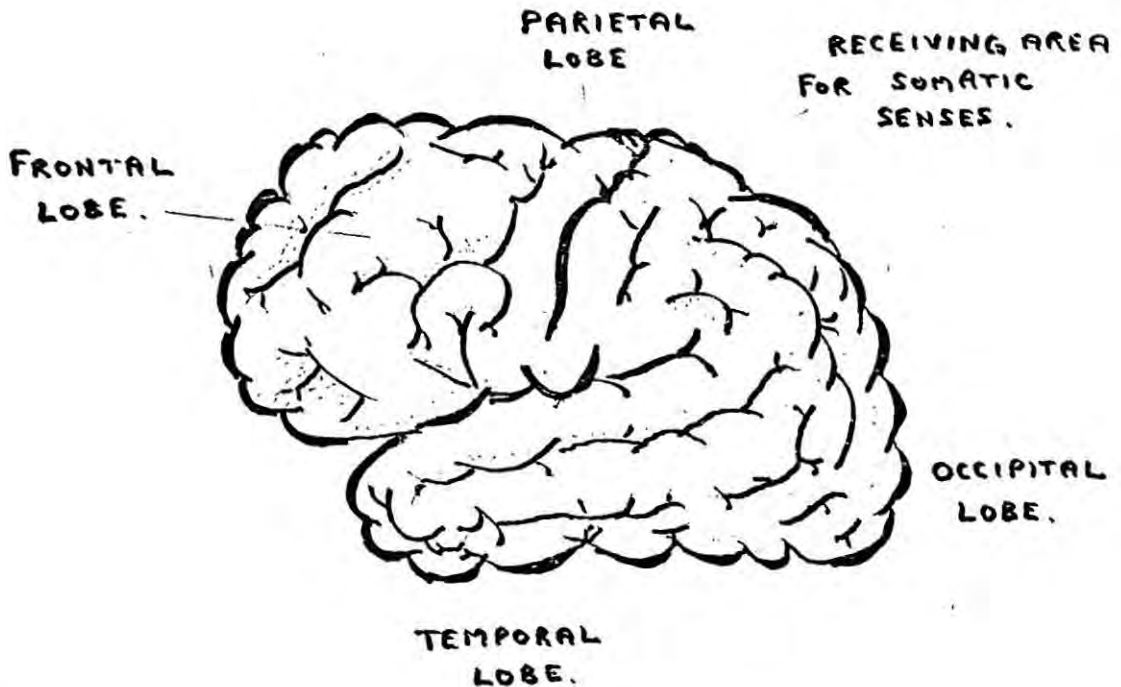
The main projection to Somatic area I is contralateral (Morgan 1965). However, no crossing of nerve fibres is ever complete, so there is some ipsilateral representation as well. Furthermore, there is ipsilateral representation of the face just in front of the main face area. Sensory input to the somatosensory projection areas seems to be well lateralised (Grossman 1967). Thus Stamm and Sperry (1957, quoted by Grossman) trained cats to perform roughness and form discriminations with one paw. Normal animals readily transferred this habit to the

contralateral forepaw, "but cats with complete collosal transections had to relearn all the problems and did not show any effects of the previous acquisition" (p 718).

Grossman quotes further work by Glickstein and Sperry (1960), which purports to show that there are nevertheless subcortical pathways which can by-pass even corpus callosal transections. These workers trained monkeys on somesthetic discriminations with one paw. This ability was transferred to the other paw in normal monkeys, but no transfer took place on cutting corpus callosum. However, if "the somesthetic projection area corresponding to the first paw was destroyed, the somesthetic discrimination would transfer quite readily". This suggests that the other hemisphere can take over in the event of a loss of the relevant hemisphere. "There must thus exist some subcortical pathway which is normally inhibited by the presence of both somatosensory projection areas" (Grossman, p 718).

There is also a cortical projection area for somesthesia called Somatic Area II. It is served by a second thalamic relay through the lateral nucleus of the thalamus. Anatomically this area seems to be the back part of the postcentral gyrus, the posterior parietal lobule, the parietal lobe other than the postcentral area. But electrophysiologically, it is given as the lateral surface of the cortex between somatic I and the

temporal auditory area. This seems to be one of those cases when the brain has proved too complex for investigators - it is not clear why the results of anatomical and electrophysiological mapping should be inconsistent to this extent. Wyburn places Somatic II as the "base of the post central sulcus" (p 47). Electrophysiology indicates a face, arm and leg area for Somatic II as well. The face area of Somatic II adjoins the face area of Somatic I, but not so with the other parts. The main difference between the two projection areas is in the matter of lateralisation. Somatic II receives impulses both ipsilaterally and contralaterally, with a preference for contralateral projection (Morgan 1965). Further, Somatic II seems to have motor functions in addition (Morgan p 269).



This brief outline of the cutaneous senses and their central nervous system pathways and projection areas will be referred to later. Any model which attempts to link up discrimination abilities with receptive field organisation must do justice to this outline at least.

In summary then, the 31 spinal nerves serve dermatomes on the body. Prolific branching of neurons serving the spinal nerves results in a vast net of innervation at the receptor surface. The four sensations of the cutaneous senses are kept segregated in the tracts and nuclei of the spinal cord and hindbrain. Kinesthetic impulses travel mostly via the gracilis and cuneatus tracts to the nucleus gracilis and nucleus cuneatus of the hindbrain and thence via the medial lemniscus. Touch impulses run mostly via the ventral spinothalamic tract and the trigeminal nerve. Pain, warm and cold impulses run mostly via the lateral spinothalamic tract and the trigeminal nerve.

In the posteroventral nucleus and lateral nucleus of the thalamus, separation of this sort no longer applies. And a fortiori at the cortex, "all the primary receiving (sensory) areas of the brain have an orderly representation of peripheral receptive fields, ie they show a precise topography in respect of receptor surface " (Wyburn, Pickford and Hirst, page 30).

THE TWO POINT THRESHOLD.

There is a threshold separation of two points applied to the skin. Below this threshold the subject is not able to discriminate an application of one point from one of two points.

Sir Henry Head used the two point threshold as a clinical test of sensation, measuring cortical defect. To a limited degree it was used in clinical neurology (Ruch 1951), especially to diagnose pathological conditions of the spinal cord (Whipple 1924).

There are no specific sensory systems that serve the two point threshold. In fact, each of the four cutaneous senses would have its own two point threshold. The sense of touch happens to be served by a system capable of making finer discriminations than those made by the other three cutaneous senses (Ruch 1951), and so it is the one usually studied. But there is no reason why others should not also be studied (Ruch 1951).

Sherrington (1900) listed the following properties for the two point threshold:-

- (I). It varies in size from region to region on the skin.

- (2). It is inversely proportional to the mobility of the surface on which it is measured.
- (3). It is longer in the long axis of the limbs.
- (4). It is increased by stretching the skin. It is increased on the skin of the throat, for example, by bending the head backwards.
- (5). Passing a subliminal current between two needles at just discriminable difference produces a report of fusion.
- (6). The two point threshold is reduced by practice.
- (7). This practice effect transfers to the surrounding area of the skin.
- (8). The practice effect transfers to the symmetrical part of the other side of the body.

In drawing up this list of properties for the two point threshold, Sherrington seems to have followed in part earlier work by A.W. Volkmann (1858). Volkmann was G.T. Fechner's brother in law (Woodworth and Schlosberg), and "Fechner appended a discussion of these properties to Volkmann's longer work.

Volkmann had noted:-

- (1). A marked increase in sensitivity or decrease in the two point threshold in the practised skin area.
- (2). An almost equal improvement in the corresponding area of the other hand or arm.

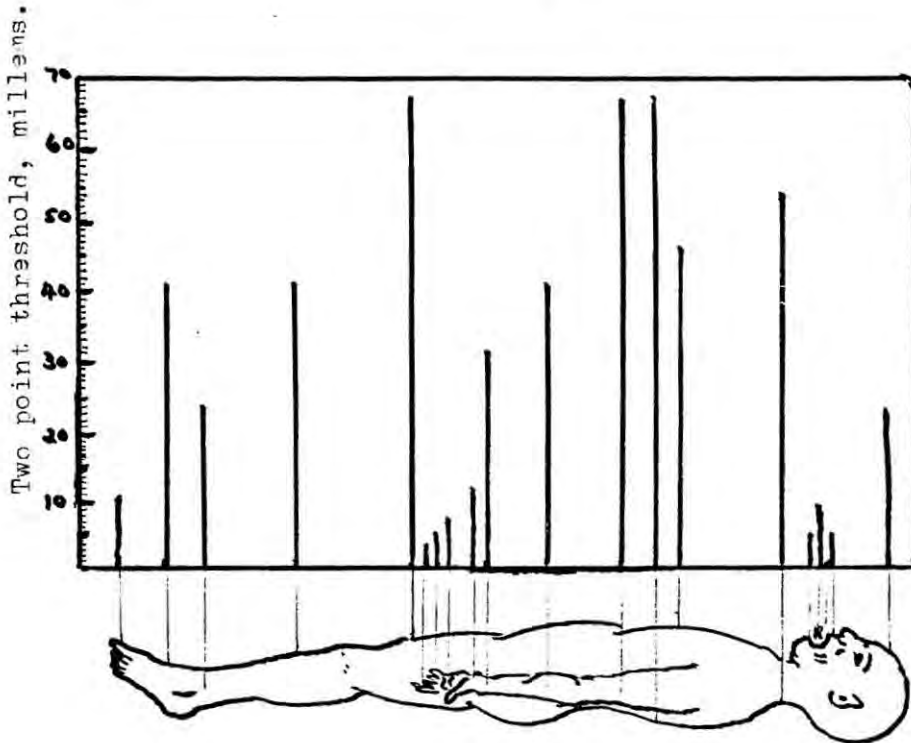
- (3). A rapid disappearance of this acquired sensitivity in a few days of disuse.
- (4). The transfer of the practice effect was not general, but was confined to areas adjacent or symmetrical to the area receiving practice.
- (5). A good transfer of the practice effect from the tip to the base of the same finger on the volar side, and from one finger to another, but not from the finger to the forearm" (Woodworth & Schlosberg page 738).

Dresslar (1894) "obtained the same sort of results when the practised area was on the forearm. The two point threshold went down enormously on the practised area and on the bilaterally symmetrical area, but not in other areas" (p 738). Dresslar's two adult observers reported that the points "felt very different after practice".

Any analysis which relates the two point threshold to receptive field organisation in the cutaneous senses will have to include at least these listed properties.

Ruch (1946) gave a mnemonic diagram showing the magnitude of the two point threshold in various regions of the body. The length of the vertical line closely approximates the actual separation of compass points just perceptible as "two"

when applied to the point from which the line is erected.



The size of the two point threshold in various regions of the body. (Adapted from Ruch 1946 and Ruch 1951 in S.S. Stevens, "Handbook of Experimental Psychology", Page 148)

When these measurements are compared with those of Weber, they are seen to be the same.

Weber's (1834) findings were:-

| | |
|-------------------------|----------|
| tip of tongue | 1.1 mm. |
| tip of fingers | 2.2 mm. |
| mucous membrane of lips | 4.5 mm. |
| end of nose | 6.7 mm. |
| cheek | 11.2 mm. |

| | |
|--------------|----------|
| forehead | 22.5 mm. |
| back of hand | 31.5 mm. |
| forearm | 40.5 mm. |
| back | 54.1 mm. |
| thigh | 67.6 mm. |

Ruch's diagram and Weber's measurements illustrate two of the properties listed by Sherrington (1900), namely, that the two point threshold varies from region to region on the skin and is inversely proportional to the mobility of the surface on which it is measured. This latter fact is documented to the extent of having a name - Vierordt's Law (1870), quoted Whipple page 251. Vierordt's Law states that "the delicacy of discrimination of two regions on the skin of a portion of the body that is moved as a whole is proportional to the average distance of these regions from their common axis of rotation".

The measurements given are those of Weber (1834 and 1846, quoted by Ladd and Woodworth 1911). Subsequent writers have tended to accept these measurements without question (Ladd and Woodworth 1911, T.C. Ruch 1946, Ruch 1951, Woodworth and Schlosberg 1961, Boring 1921, and Whipple 1924). However, Von Skramlik (1937, quoted by Jenkins p 1190) gave measurements which differed markedly from these. In fact, the determination of the two point threshold is no easy task. Tawney (1895) was so pessimistic about achieving a stable measurement that he wrote

that the two point threshold "undergoes such irregular fluctuations that it is impossible to find a measurement that is constant for half an hour at a time". Some investigators have thought that the two point threshold varies with the diurnal rhythm (Whipple page 252), but Mukherjee (1933) found no difference between morning and evening measurements of the threshold on two subjects over a month.

Some German investigators (Whipple p 253) argued that the two point threshold gives a good measure of fatigue in children doing school work. Others were equally adamant that it does not.

"Conflicting results in the two point threshold are often referable to differences in the instructions given to the subjects. Perceptually the transition from one point to two points is not at all clear cut, but passes through a series of intermediate stages before it comes out as two clearly separate points" (Jenkins 1951 p 1187). The exact perception derived from each application of the stimulus varies from "one point" to "line", "circle", "oval-shaped", and "dumb-bell-shaped" before becoming two separate points (Boring 1921). "There is really no abrupt transition between the clear perception of two points and the clear perception of one point. A real illusion of two points may even arise when one point is applied " (Whipple 1924).

If a subject calls "two" as soon as he suspects that there is "duality" of stimulation, his two point threshold will be very low indeed. "If he waits until there is a clear perception of duality before he calls "two", his threshold will be much higher" (Jenkins 1951). The true two point threshold is usually taken where there is a clear perception of two points (Rivers 1905, Burt 1909, Mukherjee 1933, Jenkins 1951).

The first three properties of the two point threshold as listed by Sherrington, namely that the two point threshold varies from region to region on the skin, that it is inversely proportional to the mobility of the surface on which it is measured, and that it is longer on the long axis of the limbs, appears to be consistent with physiological findings:-

"The areas most sensitive to touch are those with the richest nerve supply and the greatest number of touch endings. There are said to be over 600,000 touch spots scattered over the surface of the body, but the density varies in different regions and is lowest in the skin of the back" (Wyburn 1960 p 37). By "touch endings" here Wyburn refers to the free nerve endings proliferating round hair follicles, Meissner corpuscles in the hairless parts, and probably Pacinian corpuscles and golgi tendon organs for deep pressure. "The regions of maxi-

imum sensitivity in man are the finger tips, the lips, the palms of the hands and the tongue" (Wyburn, Pickford and Hirst p18).

These three properties may be explained by the geometry of the receptive fields of the primary afferents. What follows is a schematic model which is capable of explaining these three properties. The model has the advantage of being able to handle other properties of the two point threshold as well.

A SUGGESTED MODEL.

The model consists of three related schemata,

- (1) The Array (2) The Counter (3) The Rescaler.

(1) The Array. Although this is represented schematically, it should do justice to what is known of the physiology of the skin (chapters 2 and 3 above).

The receptor surface of the array consists in the simplest case of overlapping circular receptive fields, uniform in radius and spaced at equal distances T in the x and y coordinates. They are equal in sensitivity across their surfaces. A point applied to the skin will have either greater or lesser physical spread. The primary afferents are either on or off.

A point applied to such a receptor surface will excite all those receptive fields whose borders fall within a circle of radius " r " centered at that point. This circle will include the area affected by the physical spread of effect from the point.

Thus if we know the receptive field spacing " T ", the density of receptive fields per unit area of skin surface may be stated. This will be inversely proportional to " T ", and will be given as a number per square centimetre. For example,

the receptive fields on the skin of the finger are closely packed, so that T is small and the density great.

Let the density of receptive fields per area of skin be M per square centimeter. The number of primary afferent fibres activated by a point can then be stated:-

$$\text{The area containing active fields} = \pi r^2$$

The number of receptive fields activated (N) is then given by the formula $N = \pi r^2 \cdot M$

A single point or two coincident points will thus activate N primary afferent fibres, but two non-interacting points will activate twice that number.

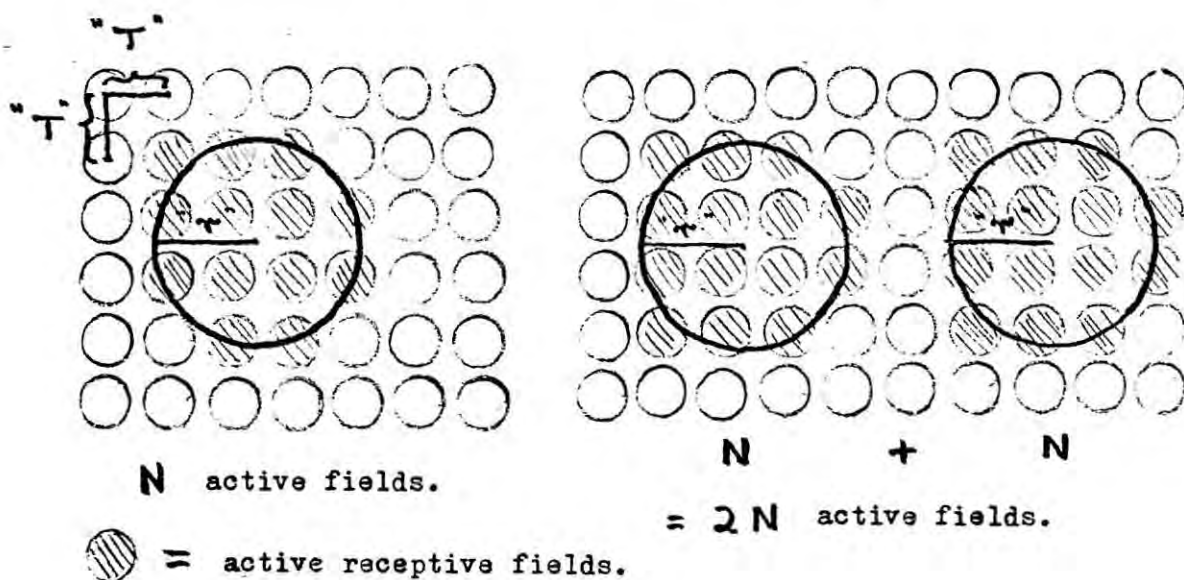
The overlapping receptive fields which make up the array could be elliptical. A point applied to the array will again excite those receptive fields whose borders fall within the spread of effect from the point. To specify the number of primary afferent fibres activated would now be more complicated, but quite possible. It will be given by area of ellipse $\times M$.

$$N = \text{AREA OF ELLIPSE} \cdot M.$$

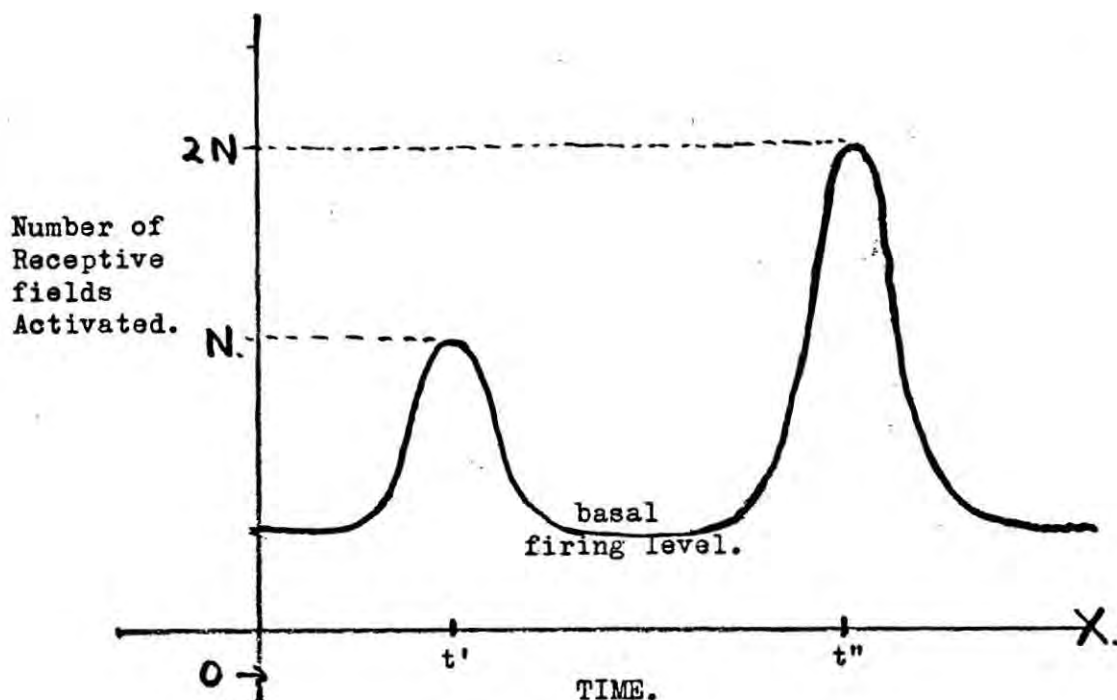
A point would again excite N afferent fibres, while two non-interacting points would activate $2N$ fibres.

The Counter. The number of primary afferent fibres activated by one point and by two independent points has thus been derived for receptor surfaces organised into circular and elliptical fields.

It is suggested that the mechanism involved in the two point threshold counts the number of primary afferent fibres active in any given situation. The threshold emerges as the count passes from that corresponding to one stimulus to that corresponding to two independent stimuli. This is a notion familiar in, for example, signal detection models (Tanner, Swets and Birdsall 1965, Treisman 1964), where decision processes are related to a decision axis E , a distribution of "central effects". The simplest case, where the receptive fields are circular, uniformly sensitive, either on or off and spaced at equal distances T in the x and y coordinates, may be represented diagrammatically as follows:- The left hand diagram represents one point (or two coincident points) activating N receptive fields. The right hand diagram represents two non-interacting points activating $2N$ receptive fields.



At the counter level, there is a counter axis X , and the central effect of an application of one point at time t' and of two points at time t'' would be thus:-



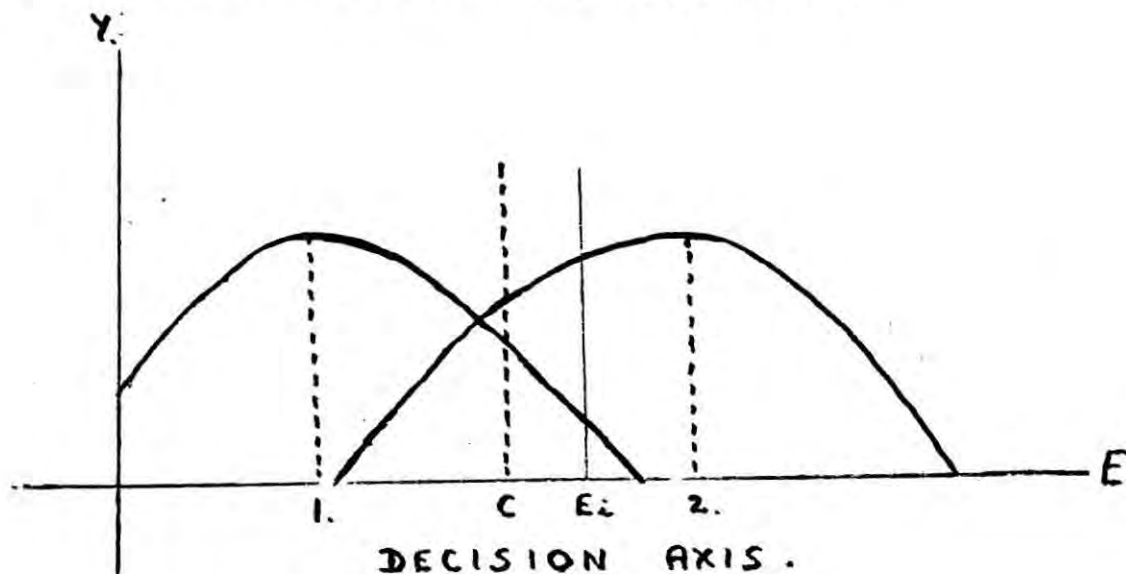
This is the very simplest way in which a signal detection model for the two point threshold would function. The counter is situated somewhere in the C.N.S., and is fed with a basal firing rate from the receptors in question. At time t' one point or two coincident points applied to the skin would cause a count of N to be recorded. Only where two non-coincident points touch the skin will a count of $2N$ be made.

The Rescaler. The array and counter as they stand would be very easy to confuse. By applying a cylinder instead of a point to the skin, many more afferent fibres would be activated. The counter would then produce a score of "two" and be wrong. The simplest way to overcome this would be for a Rescaling mechanism to divide the count for a stimulus by N. This would rescale all single stimuli, whether points, cylinders or whole areas, to an output of one. All independent pairs of stimuli would be rescaled to an output of two.

The rescaler is, in affect, a mechanism to perform size transfers, that is, to make the two point discrimination regardless of size of the stimulus probes. However, there is a further complication for the model. With an increase of stimulus intensity, there is not only an increase in impulse frequency of cortical neurons, but in addition, a greater number of cortical neurons become involved. "So the response at the cortex in terms of the total impulse discharge in a unit of time increases with an increase in the strength of the stimulus" (Wyburn, Pickford and Hirst p 31). The importance of uniform application of the two points of the esthesiometer has often been mentioned in the literature. As far as the model is concerned, it is assumed that such uniform stimulus intensities are obtainable, in which case this complication falls away. It would be a complication if for some reason the single point was applied with greater intensity than the two points.

It is envisaged that the output of the rescaler is fed to a decision axis E , following Tanner and Swets (1954). This decision axis will display readings with means at 1 and 2, each with variance. This variance will result from several sources, such as transmission error in the afferent pathway, from computational error in counting N and from the rescaling process. The brain is thus faced with a decision problem in order to characterise a reading on the E axis.

A criterion value C might be selected on the E axis equal to the upper limit of the variance of the distribution of effects due to one applied stimulus. Following Tanner and Swets (1954), a call of "two" is given when the central effect E_i exceeds the criterion C . The criterion position on the E axis is a function of the number of false positives permitted and the "cost" to the subject of missing a signal of two applied points.



The variance of the distributions having means at 1 and 2 could be considerable. As far back as 1860, G.T. Fechner recognised the importance of "spontaneous" activity in a sensory system in the absence of a stimulus. More recently, Kuffler, Fitzhugh and Barlow (1957) have observed maintained discharges in the retinal ganglion cells of a cat in complete darkness. These may arise from a number of sources, for example, the spontaneous breakup of visual pigments, "or the excitation of fine dendritic terminals in the visual system by random electrical noise" (Treisman, 1964).

Treisman (1964) mentions a second important source of noise in the irreducible physical variability of a stimulus of constant nominal intensity. He was thinking particularly of the variability in the number of quanta of light emitted by a light source of nominal intensity. But the difficulties of applying the points of the esthesimeters evenly have already been mentioned, and are clearly as important.

Thirdly, a source of noise by no means specific to vision or to any other modality is so called "neural noise". This results from variability in the responsiveness of afferent pathways to sensory inputs. This is of course affected by such things as latency factors and conduction speeds.

These sources of variability in the primary afferent

pathways of the somesthetic senses are very important in subsequent discussions of practice effects on the two point threshold.

In many ways the neural bases of the two point discrimination are suggestive of the sort of mechanism that underlies sensory discrimination in the other sense modalities. For example, there is great overlap of receptive fields in the visual system. Fine detail is appreciated from the pattern of visual fibres excited (Ruch 1951). This is also how the somatic receptors work, for example, "The first sensory neuron (in the cutaneous senses) plus its receptive field constitute a sensory unit" (Wyburn page 41). There are many more first order neurons than there are second order neurons, "which means that the impulses from a number of fibres converge on each second order neuron, implying a form of selection and crispening of sensory information, so that certain essentials are abstracted for further transmission" (Wyburn p 45).

The model proposed here accommodates this variability in the primary afferents in that it is part of the distribution of central effects on decision axis E. The model is of sufficient simplicity to specify what the central effect of applied stimuli is. It gives, for example, some minimal ways in which the central effect must be treated by the brain if observed behavioural data are to be explained.

PRACTICE EFFECTS.

Marked practice effects are found in relatively complicated tasks such as cigar making. The improvement made in such tasks is a function of a number of things, one of which is the number of times the task is repeated. After a certain number of trials, asymptotic values for time taken and quality of product are reached (De Jong's Law).

Part of the improvement made with practice in such complicated tasks may be related directly to increased perceptual skills. Perception certainly can be educated (Gibson, 1953). Thus when a customer asks for a pound of tomatoes, the greengrocer is able to pick fruit from a box, and judge a pound in weight with almost no error. Tea tasters and wine tasters differ from the norm in respect of highly developed perceptual skills of a specific sort, while the extraordinary auditory and olfactory skills of blind people are well known eg. Jastrow 1894 on Helen Keller.

It is recognised in psychophysics that allowance for practice must be made in obtaining a threshold measurement. Thus Guilford (1936) in discussing the method of measuring the lower threshold for pitch in the auditory modality suggested

that the difference between the results from the first and the last trial was "almost significant enough to suggest a lowering of the limen as if by a practice effect during the course of the experiment" (quoted by Gibson).

Gibson (1953) took it as evident that improvement in perceptual judgement occurs with practice. However, she pointed out that psychologists want to see, in addition, the learning curves involved. Yet only a few experiments "have measured the effects of practice at enough points along a baseline to describe a function" (p 413).

Woodworth (1938, quoted by Gibson 1952) plotted learning curves for Volkman's (1858) data for the effect of practice on the two point threshold. Woodworth's work shows that the curve of errors made falls very gradually, "with a negative acceleration" (cited by Gibson).

Taylor (1964) in discussing practice effects in sensory psychophysics experiments came to a similar conclusion. He pointed out that "experimentally naive subjects typically show an initial improvement in performance, the magnitude and duration of which will vary with the nature of the experimental task and the method used".

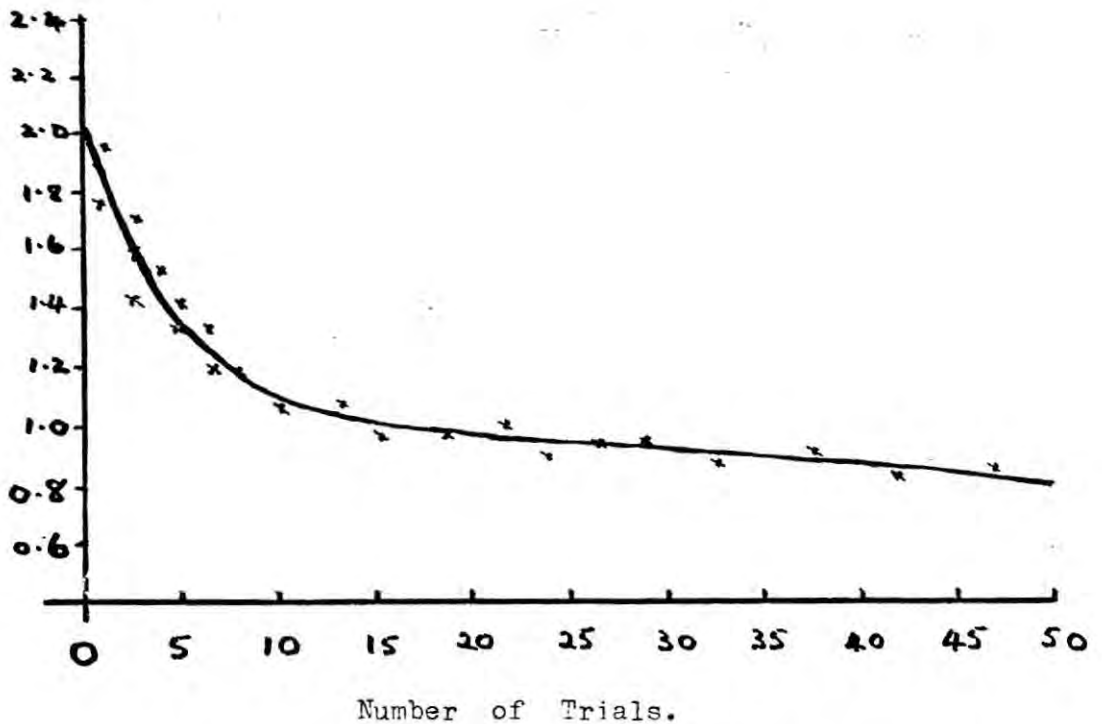
Taylor goes on to point out that in most experiments, only the short term effects of practice on a sensory task have been measured. It is thus very difficult to estimate when a subject

becomes fully "trained" in the sense that continued practice will not result in a further improvement in performance.

The criterion of improvement in perceptual skill is usually defined in terms of veridical judgement (Gibson 1953). Veridical judgement refers to getting the answer right when the experimenter can measure the subject's performance against standards known to him. If a subject is trained to estimate distance, such distance may be checked. "Improvement is then arbitrarily defined as closer, more precise, more immediate approximation of O's judgement to the appropriate physical standard or measure" (Gibson 1953). In a two point discrimination task, improvement would be defined in terms of a lowering of the threshold.

To offset the lack of experimentation on long term practice effects, Taylor tried to measure practice effects in a simple visual detection task over a period of four months. The task set to four College students was that of detecting a circular uniformly bright target which appeared brighter for one third of a second on a background of ten foot lamberts illumination, using a temporal forced choice method. Taylor analysed the results of 50,000 presentations of the stimulus over the four month period for the four students, all of whom had different absolute visual thresholds. By calculating the mean end threshold over the last 45 trials for each subject, he converted all earlier threshold

readings into proportions of this near end threshold. From these results Taylor was able to demonstrate "a large initial improvement in performance during the first experimental sessions, followed by a more gradual drop in the threshold", right up to the end of the last session.



(Adapted from Taylor (1964) Nature vol. 201 p691)

These results show that the short term practice effects, which are probably caused by the subject becoming

familiar with the experimental environment and the mode of response, are definitely followed by long term practice effects of a gradual reduction in the threshold. After 50 trials and over four months, this admittedly small slope was still continuing.

Taylor suggests that this reduction of the threshold value over the long term has long remained undetected "because of trial by trial variability".

When dealing with long term practice effects of this nature, the possibility of changes in the environment of the subject became very important. For example, in Taylor's work the experimental months ran from December to March. Thus the amount of daylight impinging on the subjects was increasing over most of the experimental run. Taylor specifically tested for changing thresholds due to increased outside illumination, but was able to rule this factor out. In any case, the changes should have been in the opposite direction, that is, in the direction of increased thresholds, so that Taylor's case is actually strengthened by this factor.

Gibson (1953) pointed out that practice effects in perceptual tasks do pass away with time. She found that she could not, as yet, make any statement as to whether this happened

because of sheer disuse or because of some more positive cause such as interference. She noted that the degree of retention seems to be different depending on the nature of the practised perceptual performance. For example, "Dresslar (1894) and Mukherjee (1933) found a rapid loss with disuse of improvement in the two point threshold on the skin" (Gibson p 421). Mukherjee (1933) reports that "after a week's interval it was found that the sensitivity was greatly lost". The practice effect on the two point threshold does seem to be lost very quickly. "Within 8 days it is reduced very definitely and is completely lost within a month" (Whipple, 1924). On the other hand, improved visual acuity was said to be retained for as long as two years in a study by Mc Fadden (1941 quoted by Gibson p 421). Whipple considers the low two point threshold of blind people to be a special example of practice, and says that it does not imply necessarily the presence of any other factor. These statements would be consistent with Taylor's work on the visual system in that Taylor showed not only a retention of practice over a four month period, but an actual improvement in the perceptual performance throughout that time.

PRACTICE EFFECTS AND THE TWO POINT THRESHOLD.

Practice effects on the two point threshold have been well documented. As early as 1855, Czermak studied the effect of practice on the two point threshold in his investigation into the touch sensitivity of the blind (Helen Keller). Volkman (1858) studied the phenomenon more carefully and found that the distance at which two points could be perceived as two points could be halved with practice on certain parts of the skin. Whipple (1924) reports that "the practice effect is visible within two hours and may be pushed to unexpected lengths by continued work" (p 255). Dresslar (1894), showed marked practice effects in the case of one subject who started with a two point threshold in a particular part of the body measuring 29 mm. After one week of practice this was reduced to 21 mm. After two weeks it was reduced to 10 mm, after three weeks to 5.5 mm. and after four weeks to 2.8 mm. Solomons (1897) and Tawney (1897) both showed practice effects on the two point threshold, and Luciane (1917) (quoted by Gibson 1953) in his textbook on Human Physiology commented on the effectiveness of practice in lowering the two point threshold.

A very relevant more recent study is that of Mukherjee (1933). He used two subjects and tested them morning and evening over four weeks, and demonstrated a very large practice effect on a small area of skin on the left forearm, about 50 mm. from the wrist on the palmary side. For the one subject (female) the two point threshold dropped from 20.5 mm. (average) to 3.1 mm. over 28 days, and for the other subject (male) from 14.1 mm. to 5.3 mm. over 28 days. With a certain amount of variability, the threshold went down every day, but there was a very great drop in the third and fourth weeks of the experiment.

Hoisington (1917) did not find practice effects on the two point threshold, and says (p 589) "There is (in the regular sense of the term) no practice effect". However, Gibson (1953) suggests several reasons which could account for this negative finding. She gives the high level of practice which Hoisington's subjects had already had on the two point discrimination on the forehead as the most important reason for the lack of obvious practice effects. Hoisington did seem to be measuring the two point threshold on a highly practised area. But Taylor's (1964) work would suggest that small improvements may still have been possible. Hoisington used two subjects both of whom had to leave for military service half way through the experiment, and says himself (p 596) that "the situation which finally resulted

in P's departure from the University for military service appears to have unfitted him for observation". For these reasons, reviewers such as Gibson have tended to discount Hoisington's negative findings.

Solomons (1897) found that the two point threshold was lowered more effectively when the experimenter gave "correction". This finding is in accordance with findings in the field of learning in other areas of psychology, namely, that knowledge of results speeds the learning process. Rivers (1905) worked on uncultured subjects (the Todas) and told them whether they were right or wrong after each application of the esthesiometers. Gibson (p 413) has made an important observation in this connection, namely, that the psychophysiological method of limits employed in experiments such as those on the two point threshold actually provides the subject with a clear example both of what two points feel like and of what one point feels like. Whipple (p 247) gives the "Method of Contrast" as an acceptable alternative method of finding the "esthesiometric index", the two point threshold. Gibson's suggestion is that even if no deliberate reinforcement or correction is given by the experimenter, "the subject may still be able to predict and check for himself his concept of the range of stimuli to be handled by virtue of his experience with these stimuli". The possibility of a "reward" effect through knowing that he is right should not, therefore, be

ruled out, even in the case where the subject has no reinforcement from knowledge of the results.

Gibson (1953) noted that the receptor surface of the skin is spread out like the retina, and therefore "the techniques of investigating cutaneous sensitivity are analogous to methods of determining visual acuity" (p 404). Mention has already been made in this paper of the neural bases of the two point discrimination and how they are suggestive of the sort of mechanism that underlies sensory discrimination in other sensory modalities such as vision.

Illustrative of this are the findings on the transfer of a practice effect on the two point threshold from one side of the body to the other (Sherrington 1900), and the transfer of a practice effect to neighbouring parts of the body which are reported for a number of sense modalities. Volkman (1858) reported the transfer of a practised two point threshold to the symmetrical part of the sensory surface. So did Dresslar (1894) and Mukherjee (1933).

Mukherjee measured the two point threshold on each of three different points on both forearms on the palmary side. The six points were named a, b, c, d, b" and e. Of these only b on the left forearm received practice. b" was the symmetrical part of the right forearm, and a, c, d, and e were the non-symmetrical parts on them. The following table is taken from Mukherjee's

results and gives good examples of the transfer of a practised two point threshold both to the symmetrical part of the body and to neighbouring areas of the skin.

| Subject 1. | left fore-arm. | | | right fore-arm. | | |
|------------------|----------------|-----|----|-----------------|-----|-----|
| | a | b | c | d | b'' | e |
| Before Practice. | 19 | 20 | 22 | 21 | 22 | 18 |
| After Practice | 4 | 3.2 | 5 | 4 | 4 | 5.3 |
| Subject 2. | left fore-arm. | | | right fore-arm. | | |
| | a | b | c | d | b'' | e |
| Before Practice | 16 | 14 | 12 | 16 | 15 | 15 |
| After Practice | 7 | 5.2 | 8 | 9 | 7 | 6 |

(Reprinted from Mukherjee K.C., Dacca University, "The Duration of Cutaneous Sensation and the Improvement of its Sensible Discrimination by Practice", Journ. Exp. Psy. 1933 13 p339).

The practice effect is greatest at b, the practised area. But the practice effect has transferred both to the symmetrical part b'', and the surrounding areas on both sides.

In the visual system, Franz et alia (1933 quoted Gibson 1953) showed that a practice effect transferred from one peripheral retinal area to the corresponding area of the opposite eye. The test set was the accuracy of recognition of forms presented peripherally at the retina. Franz found transfer of the

practice effect to untrained areas of the retina neighbouring on the trained area as well, but to a lesser degree. The untrained area chosen to test transfer was actually more peripheral than the trained area.

Czarmak (1855 quoted Whipple p 255) gives the two point threshold on the tip of the left forefinger for Helen Keller as being 1.5 mm. Hall (1855 quoted by Whipple p 255) gives a two point threshold on the tip of the right forefinger for Laura Bridgman of 0.7 mm. "Her general sensitivity of touch was from 2 to 3 times as great as that of an ordinary person" (Whipple p 255)

The transfer of practice effects on the two point threshold and these findings on increased "general sensitivity" in the blind are suggestive of some central process underlying the phenomenon. Thus Mukherjee (1933) sets himself the task of answering the question, "Is this improvement central or peripheral?" Wundt had written, he says, that "the difference in the structure of the sense organ is the chief cause of the different quality of sensation. So that Wundt definitely opts for a peripheral explanation. So does Dresslar (1897), "but he admitted that he had not tested any alternative hypothesis" (Mukherjee 1933).

Mukherjee, on the other hand, argues that "if the improvement is central, it will be an improvement in cutaneous sensitivity in general, and so other parts of the skin will be practised as well". He takes his results to show that such a

central effect is in fact what happens.

This conclusion is supported by Boring (1920) in his paper on the control of attitudes in psychophysical experiments. He thought that the reduction of the two point threshold on the skin with practice was a case of the subject learning to "use a finer criterion for identification - a better acquaintance with the difference in feel between two points and one".

This explanation is not inconsistent with the explanation of the practice effects on the two point threshold which could be given from the model proposed earlier in this paper. Gibson found the fact that there may be a transfer of practice effects from one area to another suggestive of "some process of abstraction". "At least, O seems to abstract the quality common to the scales, that is, he gets a concept of the dimension of stimulation being varied. He might next, under some conditions of training, conceptualise the scale unit, the ends of the scale, and perhaps proportional intervals". (p 423)

She finds an experiment by Werner (1940) on "Micro-melodies" in the auditory modality suggestive here. Werner's subjects learned a whole new "microscale" which had twelve distinguishable notes, in a pitch range so narrow that before training the discrimination of them was impossible for the subject. She suggested that this is an example of a subject gaining "a concept of the dimension of stimulation to be varied".

The subject then worked inside that dimension and was able to improve his discrimination ability within the new range, with practice. Gibson's suggestion was made before the publication of the Tanner and Swets (1954) paper. But again, her suggestion is consistent with the explanation provided by the model suggested earlier. Her "dimension of stimulation" can be seen in terms of the decision axis E , while the placing of the criterion C on that decision axis is analagous to her process of "conceptualising critical intervals along that scale".

PRACTICE EFFECTS ON THE TWO POINT THRESHOLD.

There are at least three other factors which affect the size of the two point threshold apart from the ones such as fatigue and practice, which have already been mentioned. Firstly, the age of the subject:- Czermak (1855, quoted by Whipple, p 250) found that children have a greater sensitivity, ie, lower two point threshold, than adults. This has been confirmed by Wissler (1901 quoted by Whipple). Whipple suggests two explanations for this, firstly, that a child has a greater number of nerve endings per unit area of skin and secondly, that "the skin of a child is thinner and tenderer, so that a given impact produces a sharper sensory experience".

Secondly, some investigators have found clear differences in the size of the two point threshold between the two sexes, eg. Thompson (1903, quoted by Whipple). Burt and Moore (1912) support this finding by saying "that the curves for the two sexes scarcely overlap" (Whipple, p 250). However, Wissler (1901) found no differences and Mukherjee (1933) tends to support him. Mukherjee's two subjects did have different thresholds, but he does not consider this noteworthy (p 341). At the same time, what Whipple says about the skin being tenderer may apply here

as well.

Thirdly, it was repeatedly noticed in the experimental work reported here that if the skin gets too cold, the sensitivity goes down i.e. the two point threshold goes up. This is perhaps significant in the light of what Whipple says about the two point threshold depending on circulation of the blood (p255)

Tawney (1895) thought that he could influence a subject's responses a great deal by suggestion i.e. he could get a subject to call "two" when only one point was given, and vice versa. So the experimenter should be careful not to say or do anything which may let in this criticism of two point threshold measurements.

Mukherjee (1933) used a small area of the left forearm about 50 mm. from the wrist on the palmary side. Experimental runs were twice a day for 28 continuous days. At each session, 30 observations were made with the arm resting on a felt table top. Fatigue was off set by dividing the series of observations into three parts and having a pause of ten minutes between parts. The esthesiometers were applied every three seconds and the subject was instructed not to call "two" unless he felt two distinct points.

Mukherjee obtained the results set out in the table below. The results are the average for seven days' applications each week:-

| WEEK. | Subject 1. (woman) | | Subject 2. (man) | |
|--|-----------------------|----------|---------------------|----------|
| | Morning. | Evening. | Morning. | Evening. |
| First Day. | 20 mm. | 21 mm. | 14 mm. | 15 mm. |
| Average 2 Pt. Thres. for First Week. | 13.7 mm. | 14.0 mm. | 14 mm. | 14.2 mm. |
| Average Two Point Threshold for the Second Week. | 8.7 mm. | 8.4 mm. | 10.7 mm. | 10.2 mm. |
| Average Two Point Threshold for the Third Week. | 3.5 mm. | 3.7 mm. | 5.5 mm. | 6.2 mm. |
| Average Two Point Threshold for the Fourth Week. | 3.0 mm. | 3.2 mm. | 5.2 mm. | 5.4 mm. |

Reprinted from Mukherjee K.C. (Dacca University) "The Duration of Cutaneous Sensation (i) and the Improvement of its Sensible Discrimination by Practice (ii)". Journal of Experimental Psychology 1933 Vol. 13 p 339.

A large reduction in the threshold value is apparent from Mukherjee's work.

The part of the body chosen by Mukherjee for work on the two point threshold is a very convenient one. The initial

threshold is large enough to allow of considerable reduction with practice. At the same time, the area is sensitive enough for the practice effect to take place.

In a short pilot study preceeding this experiment, the volar side of the first joint of the index finger of the left hand was chosen for testing. But the threshold is already so small on this part of the body that the reduction with practice was in terms of tenths of a millimeter over two or three days. And when an insensitive area in the small of the back was tried, little or no practice effect was noted. It was thus decided to follow Mukherjee in his choice of the region of the body to be tested. Throughout this experiment, then, the palmary side of the left forearm, 50mm from the wrist, was used.

Section II. Experimental Section.

9. EXPERIMENTATION.

The immediate aim of this experiment was to demonstrate a practice effect on the two point threshold on the forearm on the palmary side, 50mm from the wrist, and to test for a transference of this effect to the surrounding areas of skin and to the symmetrical part of the body.

While this had been done by various workers in the past (Mukherjee 1933, Dresslar 1894 etc.), the workers often used only one subject, or at most two subjects. Quite often these two subjects consisted of the experimenter and his wife or an assistant.

Because the practice effect and the transference played such a crucial part in the development and structure of the physiological model explaining the two point threshold which is proposed here, it seemed vital that it should be established that such a practice effect is demonstrable fairly readily in a number of subjects.

(1) Subjects.

The aim of the experiment required only that the practice effect be demonstrated adequately in a number of subjects. As soon as testing started, it became apparent that the number of

avenues for further research was very large. For example, a difference between the sexes both in absolute size of the two point threshold or in susceptibility to practice has not really been demonstrated in the literature (Mukherjee 1933). The age and health of the subject, the time of day, and the state of fatigue of the subject are further variables which have already been mentioned.

Then C. Burt (1909) considered research work done by Rivers (1905) on the Todas, by McDougall on Papuans and Dayaks and by Burt and McDougall on various social classes in England. On the basis of this work he came to the conclusion that there was an inverse relationship between cultural development and the size of the two point threshold, which he used as a measure of tactile sensitivity. "The least intellectual group tend in average tactile discrimination to be the more acute" (quoted Whipple, 1924). To establish the validity of such a statement would, however, require a separate study.

Although the variations due to the sex, age, health, and level of acculturation of the subject, and to the climate etc. are beyond the scope of this investigation, they were kept in mind while choosing the subjects. It seemed that if the practice effect could be demonstrated in as wide a variety of subjects as possible, then the danger of incorporating a false finding into

the model would be reduced.

Ideally, a number of subjects should be chosen from all the categories mentioned, but the sheer time involved in testing just one subject precludes the testing of large numbers of subjects. To test one subject during one session involved the application of the esthesiometers some 100 times, with 100 judgements being made and recorded. Such a session took half an hour. Each subject did two sessions per day, morning and evening for twenty-eight consecutive days. This meant that each subject ended by giving $2 \times 100 \times 28 = 5,600$ judgements all told. Using fifteen subjects, this meant that some 84,000 judgements were made and recorded.

In the end fifteen subjects were tested. Of these eight were European, and seven were African, eight male and seven female. Of the Europeans, four were British and four were South African, while of the Africans, six were Rural Africans and one an Urban African.

The mean age of the subjects was 29.8 years (taking each subject's age to the nearest year), with a range of 17 years to 63 years and the median age at 27 years. For the Europeans, the average age was 28.0 with a range of 20 to 63, and the median at 22, while for the Africans the average was 32.29 years, range 17 to 50 and median at 33.

During the course of testing, one male African's results had to be discarded, as he suffered an assault while on his way home and had to be hospitalised for a week. Although this took place during the third week of his testing, he was not tested further on his discharge from hospital. Complete results are thus available for only five Rural Africans.

(ii) Apparatus Used.

In a list of eight factors which will affect the two point threshold, Whipple (1924) gives "The Instrument Used". "In general, the development of the esthesiometer since Weber's time has been in the direction of greater complexity and delicacy, giving better control over the separation of the points, over the simultaneity of their application and the degree of pressure exerted". He mentions that improved esthesiometers have been made by Jastrow, Blazek, Binet, Washburn, Ebbinghaus, Von Frey, Spearman and Hill. He suggests the use of either Jastrow's improved esthesiometer or a set of Hill's needles. Mukherjee (1933) used Spearman's esthesiometers. Good quality dividers can be used. Weber used what he called "compass points".

For this experiment, ten pairs of good quality esthesiometers of the "divider" type were used. They could be

preset at any separation between the points from nought millimeters upwards, using an accurate ruler. The esthesiometers were such that once set they were not easily thrown out during use. At intervals during testing, the point separations of all the esthesiometers were checked. But not once was it found that they had shifted. In addition, there were available some twelve esthesiometers which were made in the Departmental workshops. These were adapted from Hill's needles, and were found to be satisfactory as well. However, because of the possibility that their points might not be the same as those of the factory made esthesiometers, they were never used interchangeably with them.

The rest of the apparatus consisted of a hardboard screen, draped with black cloth, made in the workshops and designed so that the subject could sit comfortably at a table with his arm through an opening in the cloth. It was not possible for the subject to see round, over or under the screen, so that the Experimenter was able to test the subject on the forearm without the subject seeing either the site of application or any of the esthesiometers, or, indeed, the experimenter himself.

The subject leant his arm on a folded cloth (Whipple 1924), and the esthesiometers were laid out on a cloth as well, so that no auditory cues were available to the subject either. This was to eliminate the possibility of a sophisticated subject learning where the esthesiometers were put down and taken up by

localising the "click" as the metal instrument touched or scraped the table.

Results were recorded by the experimenter using pencil and a standard scoring pad.

(iii) Experimental Procedure.

The investigator applied the points of the esthesiometers as evenly as possible to the area of the subject's skin to be tested. Contact with hairs, projecting veins or tendons (Whipple 1924 p 246) was avoided. The investigator attempted to maintain a constant pressure on the two points by letting them rest lightly on the skin for a second or two. The subject was then required to report whether he felt one point or two points. He was instructed not to call "two" unless he definitely felt two points. If he was not sure, a call of "one" was preferable. In this, Rivers (1905), Burt (1909) and Mukherjee (1933) were followed. The area of skin to be tested was always marked with an ink line, so that the esthesiometers were always applied to the same area of skin.

This experimental procedure has two important aspects to it which were noticed throughout the course of experimentation.

- (i) It is difficult for the experimenter to ensure that

he rests the two points evenly on the skin. Should he apply more pressure to the one point than to the other, the results could be affected. Even more important is the requirement that the two points be applied simultaneously. Any asynchrony of application of the two points is readily perceptible and leads to spurious results in the direction of lower thresholds; it is far easier to perceive two points under these conditions than when the two points are applied simultaneously. "It is imperative that both points be applied simultaneously because the limen for successive stimuli is only one third to one quarter of that for simultaneous stimuli" (Whipple p 246).

(ii) In the threshold region in particular, the subject often found it very difficult to decide on a call of "one" or "two". He would often request a further application of the stimulus. This was granted, but after that further application he was asked to give his decision.

As Gibson (1953) pointed out, an ordinary psychophysical method of limits is not really satisfactory in dealing with the two point threshold. The subject soon gets a clear idea of what to expect, and even perhaps when to expect it. To obviate this difficulty, the following method was used:-

A rough estimate of the two point threshold for the relevant area was made for each subject in a preliminary testing

session, using the ordinary psychophysical method of limits and using extreme values. Then the ten pairs of esthesiometers were preset at different point separations on either side of this threshold value. These separations were then entered on the results sheets, on which were drawn ten columns.

The experimenter then applied each of the esthesiometers ten times, but he did so in a random order. The order used was obtained from a list of random numbers generated by a computer, using the digit 0 as the tenth esthesiometer. This method, coupled with the fact that the subject could hear and see nothing of what went on otherside the screen, was designed to ensure that the subject reported only what he felt, without interference from expectancies or other cues.

(iv). False Positives.

Whipple (1924) noted that a real illusion of two points could and does occur even when only one point is applied. It has already been mentioned that Tawney was very pessimistic about being able to obtain a two point threshold reading at all.

To attempt to overcome this problem, the following method was adopted. In the initial sessions of testing each subject, at least twenty percent of all the applications were made

using one point only. If the subject called "two" when only one point had been applied, a "false positive" was scored, following signal detection theories (Tanner and Swets (1954)).

A limit of five percent of false positives was set as the "criterion" (Tanner and Swets), and results giving a false positive rate higher than five percent were disregarded and the session started again. Especially in the initial stages of testing, and especially in the Rural African subjects, such high false positive rates were common. Invariably, this was found to be the result of inadequate understanding of the experimental task, leading to guessing or a perseveratory response of "two" for every application. However, once the subject grew accustomed to the experimental task, such high false positive rates were not often found.

(v). Scoring.

The experimenter recorded the subject's response of "one" or "two" by writing "1" or "2" under the appropriate point separation. As there were ten point separations, and each point separation was applied ten times in a random order, the block was completed when there had been one hundred "one's" or "two's" called.

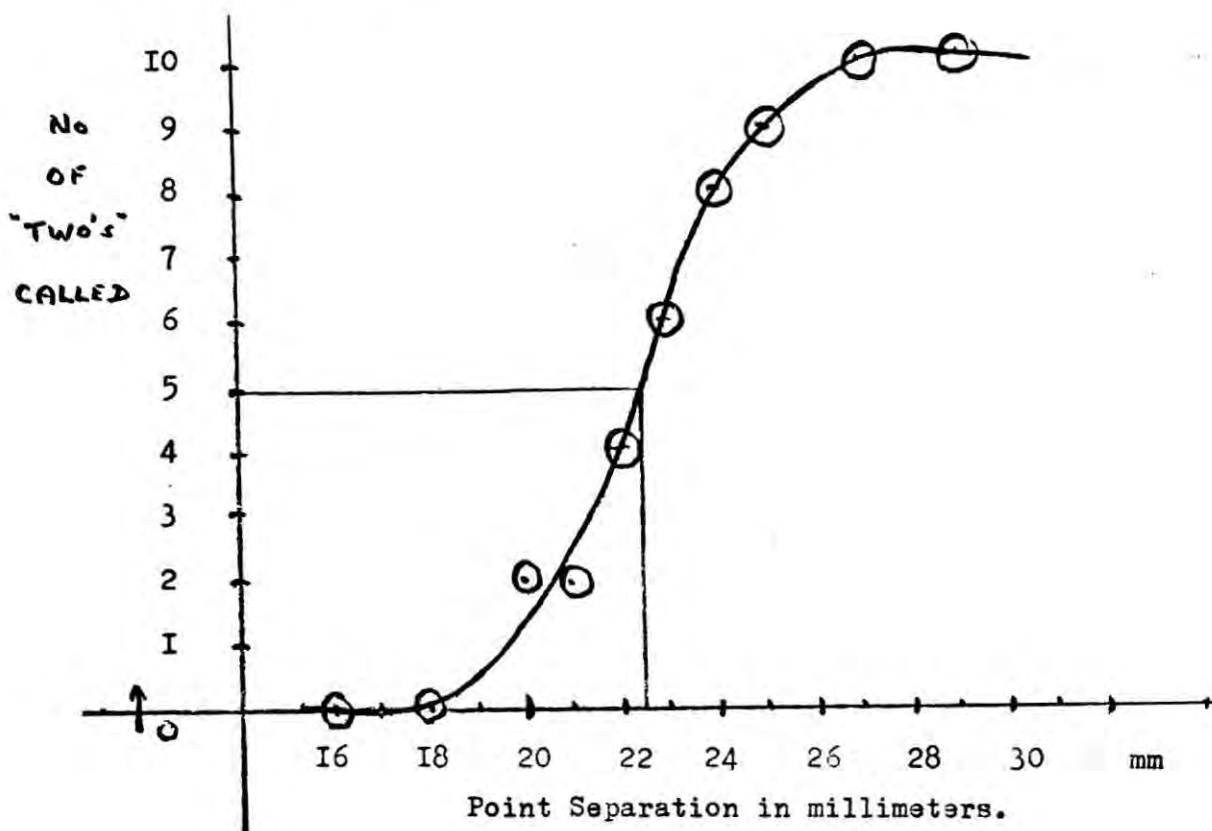
When an application of a single point was made, the result was recorded in the usual way. However, a practised subject seldom made a false positive call of "two" here.

When a subject has completed his testing sessions, there are 56 completed blocks, with various point separations down the left hand side and "1's" and "2's" opposite them. Then for each point separation, the number of "Two's" called out of ten applications are written down on the right hand side. Typically for the small point separations, there will be no "Two's" called, while for the large separations there will be ten "Two's" called.

What follows could be such a typical block:-

| Point Separation | Subject :- N.N. Date :- 10/11/1970 A.M. Call. | No. of "2's" Called |
|------------------|--|---------------------|
| 29mm | 2 2 2 2 2 2 2 2 2 2 | 10 |
| 27mm | 2 2 2 2 2 2 2 2 2 2 | 10 |
| 25mm | 2 2 2 1 2 2 2 2 2 2 | 9 |
| 24mm | 2 2 2 2 1 2 1 2 2 2 | 8 |
| 23mm | 2 2 1 2 1 2 2 1 1 2 | 6 |
| 22mm | 2 1 1 1 2 2 1 1 1 2 | 4 |
| 21mm | 1 1 1 2 1 1 1 2 1 1 | 2 |
| 20mm | 2 1 1 1 1 2 1 1 1 1 | 2 |
| 18mm | 1 1 1 1 1 1 1 1 1 1 | 0 |
| 16mm | 1 1 1 1 1 1 1 1 1 1 | 0 |
| False Positives. | 1 1 1 1 2 1 1 1 1 1 1 | One False Positive. |

The next step was to compute the two point threshold for that particular experimental session. Underwood (1966) uses a graphical determination of thresholds (page 136), and this method was followed. The number of "two's" called for each point separation was plotted against the appropriate point separation, and that point separation which gave 50% of "two" responses (ie 5 out of 10) was taken as the two point threshold. This is illustrated in the diagram below:-



Graphical determination of the two point threshold. The threshold value in this example is 22.5mm.

This is the ideal curve, and in the actual experimental runs the curves were not always smooth (although as a matter of fact, they were smooth on a surprising number of experimental sessions). It was usually possible to draw the line of best fit through the points on the graph.

(vi) Results.

After 28 days of testing there were thus 56 two point threshold readings for each subject found after 100 applications of the esthesiometers, morning and evening, each day.

Following Mukherjee (1933), it was decided to present these results in the form of a table, giving the two point threshold on the first day and the MEAN two point threshold for the first, second, third and fourth weeks of the experimental run.

It should be noted that apart from the first day's readings, the results given are mean readings for 14 experimental sessions (7 morning and 7 evening sessions). Further, the results are given correct to only two decimal places. The threshold measurements originally taken were correct to two decimal places. But in the statistical treatment of results, because mean readings were involved, calculation was always to four decimal places. The raw scores from which these means were calculated, are given in Appendix I.

| SUBJECT No. | SEX. | SUBJECT. | FIRST DAY. | MEAN FOR 1 ST WEEK. | MEAN FOR 2 ND WEEK | MEAN FOR 3 RD WEEK | MEAN FOR 4 TH WEEK | TRANS-FER. TO RIGHT. |
|-------------|--------|------------|------------|--------------------------------|-------------------------------|-------------------------------|-------------------------------|----------------------|
| I | Male | African | 25.00 | 21.06 | 17.51 | 13.86 | 10.34 | 9.12 |
| 2 | Male | African | 21.50 | 20.49 | 18.12 | 15.94 | 13.67 | 13.59 |
| 3 | Female | African | 25.00 | 18.16 | 15.29 | 14.74 | 10.41 | 8.60 |
| 4 | Female | African | 23.33 | 19.79 | 15.64 | 15.24 | 13.61 | 14.10 |
| 5 | Female | African | 21.00 | 17.57 | 15.33 | 16.19 | 15.06 | 15.34 |
| 6 | Female | African | 25.00 | 19.59 | 16.11 | 15.71 | 15.47 | 16.16 |
| 7 | Male | British | 21.11 | 21.91 | 18.69 | 15.52 | 13.27 | 12.71 |
| 8 | Male | British | 23.33 | 21.72 | 19.93 | 14.89 | 11.77 | 11.75 |
| 9 | Female | British | 19.10 | 18.17 | 15.65 | 12.69 | 11.19 | 11.21 |
| 10 | Male | British | 20.83 | 18.58 | 16.01 | 13.43 | 9.85 | 8.50 |
| 11 | Female | White S.A. | 17.11 | 18.63 | 16.71 | 15.84 | 12.97 | 11.03 |
| 12 | Male | White S.A. | 21.50 | 19.64 | 15.82 | 14.06 | 9.72 | 9.00 |
| 13 | Female | White S.A. | 21.20 | 17.87 | 15.54 | 13.22 | 9.71 | 8.37 |
| 14 | Male | White S.A. | 22.67 | 18.27 | 15.33 | 11.32 | 10.29 | 11.10 |
| 15 | Male | African | 26.00 | 23.89 | - | - | - | - |

Results Table I. Showing the two point threshold on the first day, the mean threshold week by week, and the mean of a morning and evening session to test transfer of the practice effect to the symmetrical part of the body on the right hand side.

(vii) Analysis of Results.

The aim of the experiment requires that a practice effect be demonstrated on the two point threshold for the 14 subjects chosen.

The one way analysis of variance (fixed effects) is, unfortunately, not appropriate here. Taking the mean scores for $N = 14$ on week one and week four, the null hypothesis would be set up that:- $\mu_1 = \mu_2$

Stated formally:- $H_0 : \mu_1 = \mu_2$

As against this, the hypothesis that a treatment difference exists because of practice:- $H_1 : \text{not } H_0$

Then choose an alpha level of .01 and test the null hypothesis.

But for this statistical treatment of results to be acceptable, there has to be "statistical independence among the error components" (Hays 1963, p 379). What this means in effect is that the one way analysis of variance, fixed effects, requires independent observations both within and across groups.

In this experiment, such a requirement is not met. There is "good reason" to think that the treatment given to the subject during the first week has a "systematic effect on his subsequent performance" (Hays, op. cit.) during the fourth week of the experiment. In which case, it cannot be assumed that there is

statistical independence among errors. Indeed, the study is concerned to show just this thing, that the treatment in week one does have an effect on week two, week three and so on.

For the same reason, the t - test for the significance of a difference between the means of two small uncorrelated samples cannot be used (Milton Smith, 1965).

To meet the aim of this experiment, then, the difference between the means of two small correlated samples has to be shown to be significant. The performance of a group of subjects was measured before and after an experimental factor had been introduced, and now it must be determined whether any differences between the mean scores which resulted could have been due to chance variations in sampling alone.

Following Milton - Smith (1965), the most convenient way to do this is to set up the null hypothesis that the mean of the differences between the two scores on week one and week four for all the subjects is zero. Then the alternative hypothesis would be that the mean of the differences is not zero.

The calculation of t will then give an answer to the null hypothesis (either to accept it or to reject it) at the stipulated level of confidence. The value t will be referred to Fisher's Table of t at a value of $2P = .01$ (two tailed), and the degrees of freedom (d.f.) = 13.

The actual calculation of t is shown in appendix II,

and is found to be $t = 12.176$.

Referring to Fisher's Table of t , for $P = .005$ ($2P = .01$) and $df = 13$, then $t = 3.012$.

Therefore the null hypothesis is rejected.

Had the stipulated value for P been $.001$ or even $.0005$, the null hypothesis would still have been rejected.

Therefore the alternative hypothesis that the mean of the differences is not zero, is accepted.

Since such a result could only have been due to chance variations in sampling something much less than once in a hundred times, it is concluded that practice made a significant difference to the two point threshold of these subjects under the conditions of the experiment.

Although it was not strictly necessary for the aim of the experiment, further statistical analysis was carried out in the same way on all the week by week scores.

Week one was tested against week two and then against week three. Then week two was tested against week three and week four, and lastly, week three was tested against week four.

Setting up the null hypothesis in each case that the means of the differences between the two scores on the two weeks is zero, a value for t was calculated in each case. The value t was referred to Fisher's table ($2P = .01$) and $df = 13$.

In each case it was possible to reject the null hypothesis at the .01 level.

Because these results could only have occurred by chance less than once in a hundred times for each week by week test, it is concluded that practice took place each week in that the mean two point threshold was significantly different each time.

The overall conclusion for the analysis of results is thus that a practice effect on the two point threshold has been demonstrated for 14 subjects over 28 days.

Although no analysis was done to show this, it seemed as if the largest drops in threshold occurred during weeks three and four. This is in the same direction as the result of Mukherjee (1933).

The final thing which should be demonstrated from the results is the transfer of the practice effect to the symmetrical part of the body (a spot 50 mm from the wrist on the palmary side of the right forearm). This presents something of a problem as far as the design of the experiment is concerned. It is not possible to get a mean reading on the transfer side over a number of experimental sessions, since that area would then itself be subject to a practice effect. So that the reading must be taken just once (or at most twice) on

the specified spot. But then the reading is liable to error, since any one measurement of the two point threshold, as already mentioned a number of times, is subject to great variation (Tawney, 1897).

It is also something of a design problem to decide on what to measure the transfer reading against. The mean threshold for the fourth week is one possibility. But we know that practice is going on all the time within the 14 readings of the last week, so that the mean reading for this week is not really the most appropriate reading.

To overcome these difficulties, it was decided to average the readings for the morning and evening sessions on the first day of the experimental run and to compare these results with the average of the readings for a morning and evening session on the transfer spot. This design should reduce the error component to a certain extent in that the mean readings for the day are taken. Since only one day's readings for the transfer spot are taken, the amount of extra practice involved should not be too great.

This is something of a compromise, and the experimenter would not like to place too much weight on this aspect of the experiment. Nevertheless, the readings for the transfer spot after practice are obviously much smaller than the readings for the

practice spot on the left wrist on the first day. This means that it is possible to set up a null hypothesis to make a test for transfer.

The null hypothesis is set up that the difference between the means of the readings on day 1 and the readings on the transfer spot is zero.

The calculations necessary for this are shown in Appendix III. Referring to Fisher's table of t , df 13 and $P = .01$, it is seen that the hypothesis can be rejected. However, as has already been mentioned, not much weight is set by this result. The statistics look impressive, but this aspect of the experimental design is too weak to support strong conclusions. All that the experimenter would like to conclude here is that as far as he could see, the practice effect transferred to the symmetrical part of the body, as Sherrington (1900) said it would.

Section III. Conclusions.

IO.

TWO TYPES OF PRACTICE EFFECT.

It seemed from this study that there are two distinct types of practice effect. These may conveniently be named Type 1 or "Reduction of Variability" practice effects and Type 2 or "Increase in Sensitivity" practice effects. A clear pattern emerged when a naive subject was tested on the two point discrimination. At the outset, the subject appeared to have no clear "strategy" with which to deal with the task. His responses were therefore randomly scattered and typified by the presence of false positives. But after just a few experimental runs, the subject was able to reduce the variability of his responses and limit the number of false positives made. He had then shown a Type 1 or "Reduction in Variability" practice effect. A clear two point threshold emerged at this stage.

This first type of practice effect can be accommodated on the model by calling it a "distribution effect", following signal detection theory. This would mean that the variability of the distribution of central effects on E is reduced by practice. Obviously part of the improvement in two point discrimination with practice consists in becoming more familiar with the experimental set up and procedure. Such a "central effect" is expected to be associated with a decrease in display variance,

which will carry the criterion down with it and result in a decrease of the two point threshold.

In this case there will be no increase in the number of false positives made, and there will be a decrease in the range over which the threshold occurs. The overall effect of Type 1 or "Reduction of Variability" practice is one of "sharpening" or clarifying central effects along decision axis E.

To simplify the presentation, it was stated in the model that the receptive fields of the primary afferents were either "on" or "off". In practice, primary afferents do not behave in that simple a way. One could thus expect that activity would not be identical in each of the driven units. Some units would fire spikes at a higher rate than others, and there would be a randomness in the activity of the population as a whole. The concept of a unit usually refers to a first order neuron plus its receptive field, following Wyburn (1960 p 41). Unfortunately, "very little information is available with regard to the comparative sizes of receptive fields activating the second, third (or thalamic) and fourth (or cortical) order of neurons" (Wyburn, Pickford and Hirst, 1964 p 31). As far as the model is concerned, a unit would be a cortical neuron plus its receptive field.

The model allows for the counting of the number of active units in the following way. All the spikes arriving at a

counting station are summed in one observation interval, and this sum is divided by the mean firing frequency of the units sampled. This action of the rescaler, as mentioned earlier, specifically allows for size transfer.

The smaller the variance in the firing pattern, the closer will the answer come to either a clear "one" or a clear "two". But even with a considerable degree of variance, the answer will not be greatly wrong, since those units firing below the mean frequency will tend to lower the count for example, to 0.8 or 1.8, while those firing above the mean frequency will tend to raise it, for example, to 1.2 or 2.2. In this way, the distribution of central effects along E produced by the rescaler can form a ready basis for decision making.

There is physiological evidence which supports the notion of a Type I or Reduction in Variability Practice Effect. "The peripheral receptive field for any cortical neuron is surrounded by skin, the stimulation of which will inhibit the cortical neuron. This means that any stimulus produces a group of activated cells and a surrounding zone of inhibited cells, a mechanism which will obviously help tactile discrimination" (Wyburn, Pickford and Hirst, 1964). Afferent inhibition of this sort has the effect of crispening or sharpening sensory input. Such afferent inhibition is well known in the visual system (Hubel and Wiesel 1962, Dodwell 1966).

There is of course also descending cortical control over sensory input. "The C.N.S. can influence its own sensory input at every level from peripheral receptors to cortical receiving neurons. It has been determined that there are relays of centrifugal fibres running down from the higher cortical areas to connect up with each level of any sensory pathway, and that stimulation of these fibres diminishes or abolishes responses in the sensory pathways" (Wyburn, Pickford and Hirst 1964 p 33).

The effects of both afferent inhibition and descending cortical control are to stabilise the firing frequencies of units in the class for which they operate. This has been shown for the sensitive hair cells in the nucleus gracilis of the cat (Gordon and Paine 1960, Gordon and Jukes 1964). The benefits of afferent inhibition for stable firing frequencies in the somatosensory cortex of the cat have been shown by Mountcastle (1957).

So at least a part of Type 1 or Reduction of Variability practice effects could be the result of inhibition of this sort. Another part could be the result of afferent facilitation. "Activation of cortical cells would appear to induce facilitation, whereby they become more responsive to a succeeding stimulus and in this way they are better able to deal with natural stimulation" (Wyburn, Pickford and Hirst p 31). Afferent facilitation will of course raise the driven frequencies of the afferent units. It

will also underlie Type 2 or Increase in Sensitivity Practice Effects and will be mentioned later. Afferent facilitation has been shown in the nucleus gracilis of the cat for the sensitive hair cells by Gordon and Paine (1960).

Descending cortical control over the units will further preserve the afferent effect. Gordon and Jukes (1962) showed this clearly for sensitive hair cells and touch pressure cells in the nucleus gracilis of the cat. If the touch pressure units are excited, the sensitive hair cells are inhibited. This finding was confirmed by Gordon and Jukes (1964). This mechanism is certainly relevant to Type 1 practice effects and probably to Type 2 practice effects as well. If these afferent and descending mechanisms are active they will tend to control the variance in the driven population. This particular physiological evidence thus supports the idea of Type 1 practice effect as envisaged on the model.

Type 2 practice effects could be due to a lowering of the criterion C in the face of an unchanged display variance. This increase in sensitivity could be bought at the cost of a higher false positive rate. But there is a fixed maximum false positive rate, and so an increase in sensitivity leading to a lower two point threshold is the alternative way in which the criterion can go down. As the experimental run continued, the subject was able to lower his two point threshold without

incurring further false positives. In doing this he was showing a type 2 practice effect.

As far as the physiological mechanisms underlying this type of practice effect are concerned, a few possibilities have already been mentioned. Afferent facilitation (Gordon and Pain 1960) could certainly be involved. So could more "central effects" of the type discussed by Gibson (1953), in terms of "getting a concept of the dimension of stimulation being varied, and of conceptualising the scale unit, the ends of the scale and perhaps proportional intervals" (p 423 quoted earlier).

The term "Increase in Sensitivity" for Type 2 practice effects was suggested to the investigator during the course of experimentation. A subject just happened to mention after one series of applications that the area of skin involved had become very tender and painful to the touch. It seemed almost as if there was mild hyperalgesia in the area stimulated (Jenkins 1951, p 1181). The physiological condition of hyperalgesia is a very complex one, and it is not suggested that enhanced tactile sensitivity is necessarily connected with it at all. The pain and tenderness need not be at all related to the increased skin sensitivity leading to a threshold fall. On the contrary, practice effects were obtained on subjects without accompanying pain and tenderness in the skin area involved.

Hyperalgesia suggests the release of some chemical

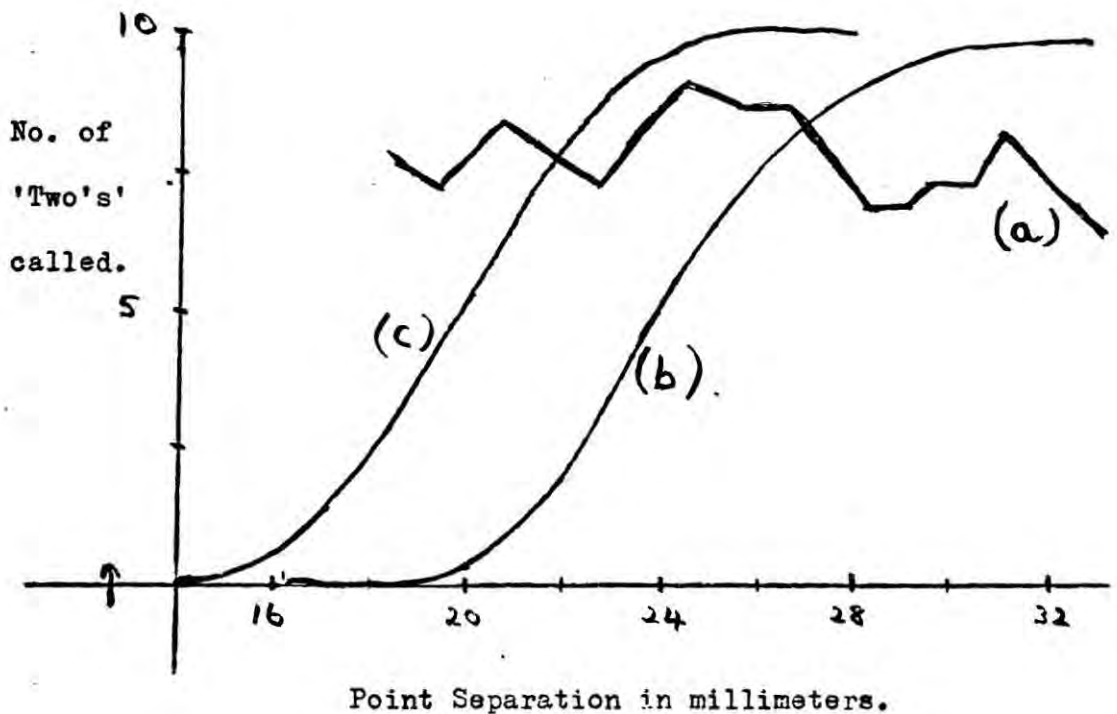
by damaged tissue. Histamine is released by painful stimulation (Rosenthal and Muard 1939, cited by Jenkins 1951). And it causes pain when injected into tissue. But so do many other chemicals. If it could be shown that repeated applications of the esthesiometer points to the skin caused a build up of one of the nerve facilitators such as acetylcholine, then the type 2 practice effect could be explained in terms of increased peripheral sensitivity just as Wundt said it could be. Then "central" explanations would be superfluous. This study does not aim to distinguish between these two possibilities other than to point out with Mukherjee (1933), that transfer effects suggest a central rather than a peripheral mechanism. As far as the model is concerned, it is not necessary to choose between the two. An increased sensitivity at the periphery is accommodated by saying that the whole distribution of central effects moves down, pulling the criterion and thus the two point threshold down with it.

Jenkins (1951) states that "there is no clear-cut evidence of touch enhancement as there is of temperature enhancement" in the cutaneous senses. Temperature enhancement refers to the positive enhancement by which dipping an arm into cold water makes a stimulus at 30 degrees C feel warm although this is below normal skin temperature. However, Jenkins was writing before the work of Gordon and Jukes (1962, 1964) Mountcastle

(1957) and others. Wyburn, Pickford and Hirst (1964) agree that afferent facilitation is an established fact in sensory systems, so that Jenkins is perhaps wrong in his statement here.

Theoretically, the two types of Practice Effect discussed here can be represented as follows:-

In type I or "Reduction of Variability" practice effects, there is a change in the form and slope of the curve eg from curve (a) to curve (b). But in type 2 or "Increase in Sensitivity" practice effects, the slope of the curve stays the same. All that happens is that the curve moves down the scale, taking the threshold with it, ie, moving from curve (b) to curve (c).



SOME SUGGESTED EXPLANATIONS.

The model which has been suggested in this paper is little more than an application of the general signal detection model (Tanner and Swets 1954) to the specific case of one of the four cutaneous senses. However, a number of useful properties of the model have already been mentioned. It was pointed out that the model should violate no established physiological findings, and it should account specifically for the known properties of the two point threshold.

Although he wrote before the signal detection models were formalised, Ruch (1946, quoted in Ruch 1951) anticipated some of the structures proposed here. For example, he gives a "theoretical diagram of the neural factors involved in the discrimination of two points applied to the skin" (Ruch 1951 p 149), which has the same sort of "array" as the one proposed in the model given above. Ruch's diagram has "levels", namely, the receptor surface, the spinal cord, the thalamus and the cortical levels. His "modal excitation curves" of neural activity at the cortex are rather like the central decision axes of later signal detection models. However, Ruch's diagram is limited. It would be confused, for instance, in the matter of size transfer.

The model accounts for the first five properties of the two point threshold (Sherrington 1900) simply by the geometry of the receptive fields of the array, as was mentioned earlier. The two point threshold varies in size from region to region on the skin because the spacing T between receptive fields on the array varies from region to region on the skin. This accords with histological findings on cell densities on various regions of the body, and the size of the receptive fields (Wyburn 1960). Sherrington expressed this further by saying that the two point threshold varies inversely with the mobility of the surface on which it is measured. Roughly, this is so, especially as one moves from shoulder to finger tip and from hip to toe.

So that the size of the two point threshold is determined by a) the display variance in N , the number of primary afferents firing b) by the size of the receptive field radius and c) by the spacing T between receptive fields. The model thus predicts a systematic relation between receptive field size and spacing and the two point threshold, and is simply making explicit the idea that receptive field properties and the density of innervation are related to some purpose (cf. Mountcastle and Powell 1959).

The fact that the two point threshold is longer in the long axis of the limbs is accommodated by the elliptical nature of some of the receptive fields of the array. Stretching

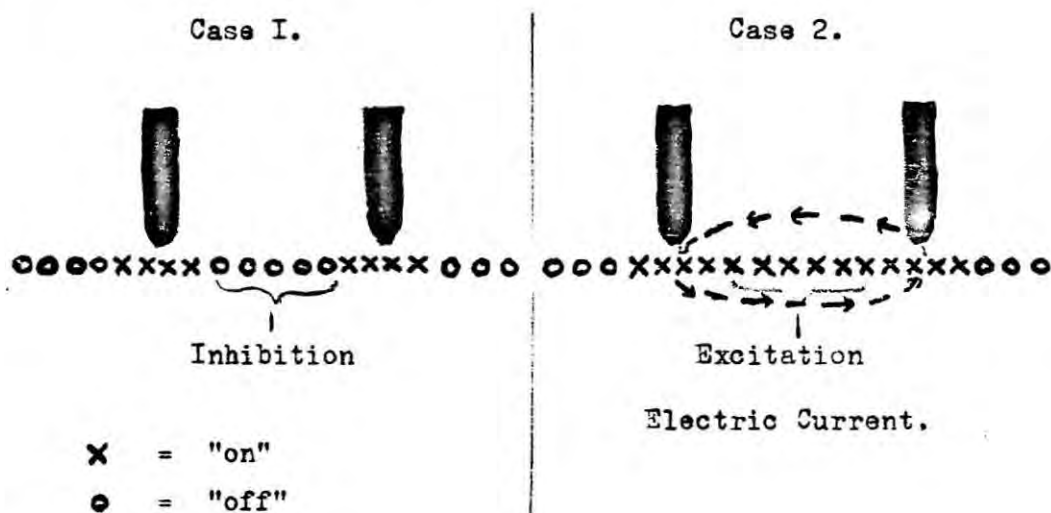
the skin in any one direction could be expected to displace receptive fields along an axis pointing in that direction, and thus cause them to take on an elliptical shape as well.

In the human forearm, the two point threshold is longer in the long axis of the arm. This would lead one to suspect that the receptive fields are elongated in this axis too. This is in fact the case for primary afferent units in the cat and for cortical units in the monkey (Hunt and McIntyre 1960), (Mountcastle and Powell 1959).

The passing of a subliminal current through the two points of the esthesiometer presents something of an anomaly for the model. Sherrington (1900) noted that this produces a report of "fusion". On Weber's formulation of "sensory circles", each having a separate pathway to the cortex, this was easy to explain. The electrical stimulus fired "artificially" the inactive sensory circle which lay between the two active ones and which made the two point discrimination possible. As soon as this "spacer" circle was fired, the organism had to respond with a call of "one".

On this model, however, such an explanation is not available. Any "artificial" firing of the cells whose receptive fields come under the electrical field below the two points of the esthesiometer should actually raise the count taken by the counter and so affect the distributions along the decision axis E.

However, descending inhibition from higher centers to the array and afferent inhibition from the surround were both mentioned in the last chapter. Both of these were seen to be important in "crispening" sensory messages, and they could be expected to play a vital role in the action of the Rescaler. What the subliminal electric current passed between the two points could do, is to interfere with this important crispening process. For example, it may fire those cells whose receptive fields should be inactive due to descending inhibition and afferent inhibition in the area surrounding the stimulus points. In this way, the whole crispening effect of the two types of inhibition could be lost, since the effect is now akin to that of applying a whole area to the skin. Instead of having a situation which could be diagrammatically represented as in 1), one now has an effect which can be represented as in 2).



In other words, the suggestion is that the electric current is so strong that its effects override the normal excitation/inhibition receptor arrangements and cause a signal effect equivalent to that obtained from an application of an elliptical area stimulus to the skin.

The Rescaler once again divides the sum of the spikes arriving at the counter in a given interval by the mean firing frequency of the units sampled. But of course, the big difference now is that the number of units sampled has gone up. It now includes all the units marked as "excitatory" in diagram 2. And the answer to this division sum, with variance, is "one" and not "two".

Even the original formulation of the model in its simplified presentation, may have predicted this effect, since the Rescaler was specifically designed to allow for size transfer, i.e. to make the two point discrimination irrespective of the size of the stimulus probes.

The way in which the model accomodates practice effects on the two point threshold was outlined in the last chapter. The model went further in that it seemed to be able to account for both types of practice effect observed in this study.

The model deals with the transfer of practice effects in terms of a "clarifying" of central effects along the

decision axis E. The spread of afferent facilitation could form a part of the transfer of practice effects to the surrounding skin, but it would do so in terms of a central decrease in display variance or a shifting of this display downwards.

Transfer to the symmetrical part of the body is more difficult. More evidence on the exact patterning of bilateral interaction at cortical level may suggest a clearer picture of what would be involved. It was noted earlier that most cutaneous projection was to the contralateral cortical area. There were, however, ipsilateral projections as well, particularly in Somatic area II. Gibson's (1953) suggestion about obtaining a concept of the "dimension of stimulation to be varied" should be noted once more. Actually, there are bound to be cross-hemisphere influences across the corpus callosum, but on the model all this could be doing is setting the position of the criterion C. At the same time, if the central effects of practicing an area of skin on the left forearm are being carried to both hemispheres through contralateral and ipsilateral projections, then there is no reason why some record of this should not be available in the left hemisphere. Any record made there is very relevant to the two point threshold on the right forearm. Thus on the model, this transfer is accommodated by saying that decision axis E is the result of cortical effects in both hemispheres, and therefore what happens to the display variance will

apply to both sides of the body.

Woodworth and Schlosberg much earlier wrote "Slight cues of 1 and 2 points must differ greatly in differently structured regions of the skin, but they could be almost identical in bilaterally symmetrical regions".

The model is thus able to deal with the transfer of practice effects to the symmetrically opposite part of the body as well.

The properties of the two point threshold listed by Sherrington have thus been related to the model proposed in this paper, and the model is able to accomodate them.

CONCLUSIONS.

This paper has suggested certain areas to which a study of the two point threshold is important. The signal detection models of the last fifteen years have replaced classical statements about absolute thresholds with a formulation in terms of the probabilities of detecting a signal under specified conditions. These specified conditions are all important, since they are what determine any one particular decision outcome.

As has been mentioned earlier, the fact that there is a two point threshold at all presents a problem. What is it about the physiology of the organism that sets a limit to its perceptual ability in this way? The model proposed in this paper was designed to consider just this problem.

The fact that practice can serve to lower this limit in perceptual ability has been demonstrated experimentally in this study. Using a number of subjects of differing ages, sex, and level of westernisation confirmed what earlier experimenters using only one or at most two subjects had found.

The model of the neural mechanisms underlying the two point threshold proposed here will have to be discarded when its predictions no longer accord with the experimental findings

on the two point threshold.

For example, cortical perception may be found in time to be something other than a quantitative analysis of active neurons. Such a finding from the physiology laboratory would mean that models such as the one proposed here would have to be replaced by others more in touch with the new findings and more able to yield experimentally testable hypotheses.

APPENDIX I.

RAW SCORES FOR 15 SUBJECTS.

Two point threshold a.m. and p.m. for 28 days.

| SESSION No. | Subject | Subject | Subject | Subject | Subject | Subject | Subject | |
|----------------|---------|---------|---------|---------|---------|---------|---------|-------|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | |
| | Male | Male | Female | Female | Female | Female | Male | |
| | African | African | African | African | African | African | British | |
| | | | | | | | Male | |
| | | | | | | | British | |
| 1. | 25.00 | 21.50 | 25.00 | 23.33 | 21.00 | 25.00 | 21.11 | 23.00 |
| 2. | 21.11 | 22.22 | 20.00 | 21.71 | 20.00 | 22.22 | 23.20 | 21.50 |
| 3. | 21.33 | 23.20 | 19.20 | 22.22 | 22.00 | 21.33 | 21.40 | 23.33 |
| 4. | 23.20 | 22.00 | 20.57 | 23.00 | 17.67 | 22.14 | 22.50 | 21.80 |
| 5. | 21.29 | 21.00 | 18.67 | 21.80 | 17.78 | 24.00 | 23.00 | 22.22 |
| 6. | 20.00 | 20.50 | 20.00 | 20.00 | 17.20 | 20.86 | 22.00 | 21.20 |
| 7. | 22.40 | 23.50 | 17.33 | 19.83 | 16.40 | 18.40 | 23.50 | 21.67 |
| 8. | 18.86 | 18.80 | 16.67 | 19.67 | 15.40 | 15.83 | 22.80 | 22.67 |
| 9. | 20.00 | 18.00 | 15.50 | 18.50 | 16.20 | 17.00 | 21.11 | 21.50 |
| 10. | 23.00 | 20.00 | 15.50 | 18.00 | 15.50 | 18.00 | 21.50 | 20.50 |
| 11. | 21.00 | 19.00 | 18.87 | 16.80 | 18.00 | 16.00 | 20.75 | 20.67 |
| 12. | 21.20 | 21.20 | 16.80 | 19.50 | 14.50 | 17.50 | 21.40 | 21.71 |
| 13. | 16.50 | 20.00 | 14.50 | 16.67 | 18.00 | 18.60 | 23.00 | 21.80 |
| 14. | 20.00 | 16.00 | 16.40 | 16.00 | 16.40 | 16.33 | 19.50 | 20.57 |
| 15. | 21.88 | 16.00 | 16.40 | 17.60 | 15.50 | 16.00 | 20.25 | 19.70 |
| 16. | 21.12 | 18.00 | 14.80 | 18.40 | 17.00 | 16.00 | 20.80 | 20.70 |
| 17. | 19.00 | 18.00 | 15.17 | 16.00 | 15.00 | 17.00 | 19.70 | 21.50 |
| 18. | 19.20 | 20.00 | 14.83 | 15.00 | 15.33 | 16.00 | 18.50 | 20.83 |
| 19. | 20.00 | 20.00 | 14.33 | 15.20 | 15.00 | 16.11 | 19.75 | 21.80 |
| 20. | 20.00 | 20.00 | 15.50 | 16.67 | 15.80 | 15.55 | 18.60 | 19.70 |
| 21. | 20.86 | 20.00 | 16.00 | 14.00 | 15.50 | 15.50 | 19.00 | 18.67 |
| 22. | 18.75 | 20.00 | 16.00 | 14.00 | 14.00 | 15.52 | 18.50 | 18.70 |
| 23. | 16.00 | 16.50 | 15.25 | 16.33 | 14.00 | 16.20 | 18.00 | 20.83 |
| 24. | 15.00 | 16.00 | 15.50 | 13.20 | 14.50 | 16.12 | 19.00 | 20.70 |
| 25. | 14.50 | 15.67 | 15.60 | 14.00 | 15.75 | 16.00 | 17.80 | 19.50 |
| 26. | 12.00 | 20.00 | 14.83 | 17.50 | 15.17 | 17.00 | 17.75 | 19.00 |
| 27. | 13.33 | 16.86 | 15.00 | 16.00 | 15.00 | 16.21 | 17.50 | 19.22 |
| 28. | 13.50 | 16.67 | 14.75 | 15.00 | 17.00 | 16.33 | 16.50 | 18.22 |
| 29. | 13.33 | 18.00 | 17.00 | 15.28 | 17.40 | 12.00 | 16.00 | 18.67 |
| 30. | 15.33 | 16.50 | 15.00 | 16.00 | 16.00 | 16.00 | 15.33 | 16.50 |
| 31. | 18.00 | 16.67 | 16.17 | 16.86 | 16.40 | 15.33 | 16.60 | 17.00 |
| 32. | 13.12 | 18.00 | 16.00 | 16.20 | 16.20 | 16.67 | 16.33 | 16.50 |
| 33. | 15.44 | 19.00 | 16.00 | 16.00 | 15.50 | 18.00 | 16.00 | 15.80 |
| 34. | 14.00 | 15.71 | 14.50 | 16.00 | 16.00 | 15.53 | 15.50 | 15.33 |
| 35. | 15.50 | 16.17 | 15.20 | 16.00 | 15.50 | 15.13 | 15.33 | 14.37 |

(continued)

| Session No. | Subject 1 | Subject 2 | Subject 3 | Subject 4 | Subject 5 | Subject 6 | Subject 7 | Subject 8 |
|----------------|-----------------|-----------------|-------------------|-------------------|-------------------|-------------------|-----------------|-----------------|
| | Male African | Male African | Female African | Female African | Female African | Female African | Male British | Male British |
| 36. | 15.50 | 15.67 | 14.67 | 14.00 | 15.67 | 14.00 | 15.00 | 13.86 |
| 37. | 12.67 | 15.57 | 14.28 | 13.50 | 16.00 | 15.40 | 16.00 | 13.43 |
| 38. | 13.89 | 15.00 | 14.50 | 15.00 | 16.75 | 15.67 | 15.67 | 13.50 |
| 39. | 12.17 | 15.75 | 15.00 | 15.67 | 15.33 | 15.67 | 15.50 | 13.00 |
| 40. | 12.00 | 14.60 | 13.00 | 15.50 | 16.00 | 16.33 | 14.50 | 13.50 |
| 41. | 11.67 | 13.17 | 13.00 | 14.00 | 17.20 | 17.00 | 15.00 | 14.50 |
| 42. | 11.43 | 13.50 | 12.00 | 14.33 | 16.75 | 17.20 | 14.50 | 12.50 |
| 43. | 10.00 | 15.00 | 13.00 | 13.57 | 16.75 | 15.00 | 14.33 | 11.33 |
| 44. | 11.17 | 18.00 | 12.25 | 13.80 | 17.00 | 16.67 | 14.80 | 11.67 |
| 45. | 9.25 | 15.57 | 13.33 | 14.00 | 16.00 | 16.00 | 14.00 | 12.00 |
| 46. | 11.00 | 13.75 | 13.67 | 14.00 | 15.50 | 17.20 | 13.50 | 12.00 |
| 47. | 10.50 | 13.00 | 12.50 | 13.80 | 15.40 | 15.67 | 13.80 | 12.00 |
| 48. | 11.67 | 13.50 | 12.00 | 15.50 | 15.00 | 15.33 | 13.33 | 11.67 |
| 49. | 11.00 | 13.57 | 10.25 | 14.25 | 13.67 | 16.33 | 13.80 | 12.50 |
| 50. | 10.50 | 13.17 | 9.20 | 13.50 | 14.00 | 16.33 | 12.33 | 13.00 |
| 51. | 11.00 | 12.75 | 8.00 | 14.00 | 13.75 | 14.00 | 13.00 | 11.67 |
| 52. | 10.00 | 12.50 | 8.25 | 13.60 | 14.00 | 14.67 | 12.50 | 11.33 |
| 53. | 9.75 | 12.17 | 8.00 | 15.20 | 15.33 | 14.50 | 13.25 | 11.33 |
| 54. | 10.50 | 12.50 | 8.25 | 11.40 | 14.50 | 15.33 | 12.33 | 12.00 |
| 55. | 9.25 | 13.17 | 8.75 | 12.25 | 14.00 | 15.00 | 12.33 | 11.00 |
| 56. | 9.17 | 12.75 | 8.25 | 11.67 | 16.00 | 14.50 | 12.50 | 11.33 |
| TRANSFER :- | | | | | | | | |
| A.M. | 9.25 | 13.18 | 8.00 | 15.20 | 15.00 | 16.33 | 12.75 | 11.00 |
| P.M. | 9.00 | 14.00 | 9.20 | 13.00 | 15.67 | 16.00 | 12.67 | 12.50 |

| SESSION No | Subject | Subject | Subject | Subject | Subject | Subject | Subject |
|---------------|-------------------|-----------------|-------------------|-----------------|-------------------|-----------------|-----------------|
| | 9 | 10 | 11 | 12 | 13 | 14 | 15 |
| | Female British | Male British | Female Wht.S.A | Male Wht.S.A | Female Wht.S.A | Male Wht.S.A | Male African |
| 1. | 19.00 | 20.83 | 17.00 | 21.50 | 21.20 | 22.67 | 26.00 |
| 2. | 18.75 | 22.50 | 19.00 | 20.83 | 18.75 | 21.67 | 27.50 |
| 3. | 18.75 | 18.00 | 19.70 | 21.80 | 19.25 | 21.50 | 25.50 |
| 4. | 18.80 | 19.50 | 18.00 | 22.50 | 18.25 | 17.71 | 25.33 |
| 5. | 18.50 | 18.50 | 18.67 | 21.00 | 17.33 | 18.00 | 26.00 |
| 6. | 18.80 | 19.67 | 17.00 | 18.00 | 17.17 | 21.00 | 25.33 |
| 7. | 18.33 | 18.75 | 19.00 | 18.80 | 17.20 | 17.20 | 25.00 |
| 8. | 18.33 | 19.25 | 19.75 | 16.75 | 18.00 | 16.00 | 22.00 |
| 9. | 18.75 | 18.25 | 18.00 | 19.50 | 16.00 | 16.00 | 22.50 |
| 10. | 17.50 | 17.23 | 20.00 | 18.50 | 17.00 | 18.80 | 22.80 |
| 11. | 17.33 | 17.17 | 20.40 | 19.67 | 17.00 | 16.00 | 22.67 |
| 12. | 18.00 | 17.17 | 18.00 | 19.33 | 18.00 | 16.80 | 21.50 |
| 13. | 17.00 | 18.00 | 18.00 | 18.50 | 17.50 | 18.00 | 20.67 |
| 14. | 16.50 | 18.25 | 18.40 | 18.33 | 17.50 | 15.50 | 20.67 |
| 15. | 16.75 | 20.83 | 17.20 | 19.00 | 16.40 | 18.00 | 21.00 |
| 16. | 17.33 | 17.33 | 18.20 | 18.00 | 17.00 | 15.50 | 20.50 |
| 17. | 16.33 | 16.40 | 17.00 | 18.00 | 17.00 | 15.33 | 21.67 |
| 18. | 16.25 | 18.00 | 17.67 | 17.50 | 16.00 | 15.60 | 23.00 |
| 19. | 17.00 | 15.57 | 17.00 | 15.90 | 17.60 | 15.80 | 22.67 |
| 20. | 16.50 | 16.50 | 16.00 | 17.40 | 15.57 | 15.00 | 20.50 |
| 21. | 15.80 | 16.67 | 16.20 | 15.50 | 15.33 | 16.00 | |
| 22. | 15.33 | 17.17 | 15.42 | 15.00 | 15.57 | 16.00 | |
| 23. | 14.50 | 15.50 | 16.60 | 15.00 | 14.50 | 15.33 | |
| 24. | 15.00 | 14.75 | 16.75 | 15.00 | 14.67 | 13.87 | |
| 25. | 12.75 | 14.40 | 15.50 | 13.83 | 15.20 | 14.37 | |
| 26. | 15.33 | 16.30 | 16.80 | 15.00 | 13.33 | 18.00 | |
| 27. | 15.50 | 15.60 | 17.00 | 13.50 | 14.00 | 12.86 | |
| 28. | 14.80 | 15.73 | 16.57 | 14.80 | 15.33 | 13.00 | ASSAULTED. |
| 29. | 13.50 | 15.40 | 18.00 | 15.40 | 16.00 | 13.43 | |
| 30. | 14.75 | 15.80 | 18.00 | 13.00 | 14.00 | 12.50 | |
| 31. | 13.75 | 13.67 | 16.43 | 14.60 | 13.00 | 12.00 | |
| 32. | 13.00 | 13.67 | 19.00 | 14.40 | 14.00 | 11.33 | |
| 33. | 13.25 | 12.80 | 17.43 | 16.30 | 14.43 | 10.00 | |
| 34. | 12.33 | 13.83 | 15.67 | 14.75 | 13.00 | 12.00 | |
| 35. | 12.67 | 13.50 | 17.00 | 14.40 | 14.00 | 11.00 | |
| 36. | 13.00 | 14.17 | 15.44 | 15.00 | 12.60 | 10.00 | |
| 37. | 12.33 | 13.50 | 15.60 | 14.00 | 13.00 | 11.00 | |
| 38. | 12.00 | 13.00 | 14.50 | 13.00 | 12.00 | 10.00 | |
| 39. | 11.67 | 14.00 | 13.33 | 13.50 | 12.00 | 11.67 | |
| 40. | 11.50 | 12.40 | 13.50 | 13.20 | 12.00 | 11.25 | |
| 41. | 12.67 | 13.33 | 13.33 | 13.20 | 12.00 | 11.25 | |
| 42. | 11.33 | 11.00 | 14.50 | 12.53 | 13.00 | 11.00 | |

| SESSION No. | Subject | Subject | Subject | Subject | Subject | Subject | Subject |
|--------------------|-------------------|-----------------|-------------------|-----------------|-------------------|-----------------|-----------------|
| | 9 | 10 | 11 | 12 | 13 | 14 | 15 |
| | Female British | Male British | Female Wht.S.A | Male Wht.S.A | Female Wht.S.A | Male Wht.S.A | Male African |
| 43. | 12.50 | 12.00 | 15.00 | 10.40 | 11.33 | 10.75 | |
| 44. | 12.00 | 11.17 | 12.75 | 11.60 | 11.00 | 11.25 | |
| 45. | 11.20 | 11.67 | 15.00 | 13.33 | 11.33 | 10.00 | |
| 46. | 11.33 | 11.33 | 15.00 | 12.40 | 10.00 | 10.00 | |
| 47. | 11.75 | 10.00 | 14.71 | 12.83 | 10.50 | 11.67 | |
| 48. | 11.00 | 10.50 | 14.25 | 11.33 | 10.00 | 9.75 | |
| 49. | 11.17 | 9.20 | 12.83 | 10.20 | 9.00 | 9.87 | |
| 50. | 11.33 | 9.40 | 12.33 | 9.00 | 9.67 | 9.50 | |
| 51. | 10.50 | 9.50 | 12.60 | 10.00 | 9.00 | 10.00 | |
| 52. | 10.80 | 9.17 | 12.33 | 9.17 | 8.75 | 12.20 | |
| 53. | 11.25 | 9.00 | 11.33 | 9.50 | 10.00 | 10.20 | |
| 54. | 11.00 | 8.33 | 12.33 | 8.50 | 8.50 | 9.50 | |
| 55. | 10.33 | 8.25 | 10.83 | 8.40 | 8.50 | 9.50 | |
| 56. | 10.50 | 8.50 | 10.27 | 9.40 | 8.43 | 9.87 | |
| TRANSFER :- | | | | | | | |
| A.M. | 10.20 | 8.33 | 10.32 | 9.00 | 8.00 | 10.20 | |
| P.M. | 12.22 | 8.67 | 11.75 | 9.00 | 8.75 | 12.00 | |

APPENDIX II.

Calculation of t , mean scores for the first week
against mean scores for the fourth week.

| Subject number | Mean for first week | Mean for fourth wk. | Difference D | Difference ² D ² |
|-------------------|------------------------|------------------------|-----------------|---|
| 1. | 21.0635 | 10.3400 | 10.7235 | 114.99345 |
| 2. | 20.4942 | 13.6714 | 6.8228 | 46.55059 |
| 3. | 18.1650 | 10.4071 | 7.7579 | 60.18501 |
| 4. | 19.7878 | 13.6100 | 6.1778 | 38.16521 |
| 5. | 17.5750 | 15.0642 | 2.5108 | 6.30411 |
| 6. | 19.5864 | 15.4664 | 4.1200 | 16.97440 |
| 7. | 21.9121 | 13.2714 | 8.6407 | 74.66159 |
| 8. | 21.7242 | 11.7735 | 9.9507 | 99.01643 |
| 9. | 18.1671 | 11.1900 | 6.9771 | 48.67992 |
| 10. | 18.5835 | 9.8585 | 8.7250 | 76.12562 |
| 11. | 18.6321 | 12.9685 | 5.6636 | 32.07636 |
| 12. | 19.5435 | 9.7185 | 9.9250 | 98.50562 |
| 13. | 17.8678 | 9.7150 | 8.1528 | 66.46814 |
| 14. | 18.2750 | 10.2900 | 7.9850 | 63.76022 |
| Totals: | 271.4772 | 167.3445 | 104.1327 | 842.46277 |
| N = 14. | | | = ΣD . | = ΣD^2 . |

$$\text{Step 1.} \quad \bar{D} = \frac{\sum D}{n} = \frac{104.1327}{14} = 7.43805$$

$$\begin{aligned} \text{Step 2.} \quad s^2 &= \frac{\sum D^2}{n} - \bar{D}^2 = \frac{842.46277}{14} - (7.43805)^2 \\ &= 60.17591 - 55.32458 \\ &= 4.85133 \\ \therefore s &= \sqrt{4.85133} = 2.20257 \end{aligned}$$

$$\text{Step 3.} \quad s_{\bar{D}} = \frac{s}{\sqrt{n-1}} = \frac{2.20257}{\sqrt{13}} = \frac{2.20257}{3.60555}$$

$$\begin{aligned} \text{Step 4.} \quad t &= \frac{\bar{D}}{s_{\bar{D}}} = \frac{7.43805}{1} \times \frac{3.60555}{2.20257} \\ &= \underline{12.17589} \end{aligned}$$

APPENDIX III.

Calculation of t , mean scores for the first day
against mean scores for the transfer spot.

| Subject number | Mean for first day | Mean transfer spot. | Difference D | Difference ² D ² |
|-------------------|--------------------|---------------------|----------------------|--|
| 1. | 23.055 | 9.12 | 13.935 | 194.1842 |
| 2. | 21.86 | 13.59 | 8.27 | 68.3929 |
| 3. | 22.50 | 8.60 | 13.90 | 193.2100 |
| 4. | 22.52 | 14.10 | 8.42 | 70.8964 |
| 5. | 20.50 | 15.34 | 5.16 | 26.6256 |
| 6. | 23.61 | 16.16 | 7.45 | 55.5025 |
| 7. | 22.155 | 12.71 | 9.445 | 89.2080 |
| 8. | 22.25 | 11.75 | 10.50 | 110.2500 |
| 9. | 18.875 | 11.21 | 7.665 | 58.7522 |
| 10. | 21.665 | 8.50 | 13.165 | 173.3172 |
| 11. | 18.00 | 11.03 | 6.97 | 48.5809 |
| 12. | 21.165 | 9.00 | 12.165 | 147.9872 |
| 13. | 19.975 | 8.37 | 11.605 | 134.6760 |
| 14. | 22.17 | 11.10 | 11.07 | 122.5449 |
| Totals: N = 14 | 300.300 | 160.58 | 139.72 = $\sum D$ | 1494.128 = $\sum D^2$ |

Step 1. $\bar{D} = \frac{\sum D}{n} = \frac{139.72}{14} = 9.98$

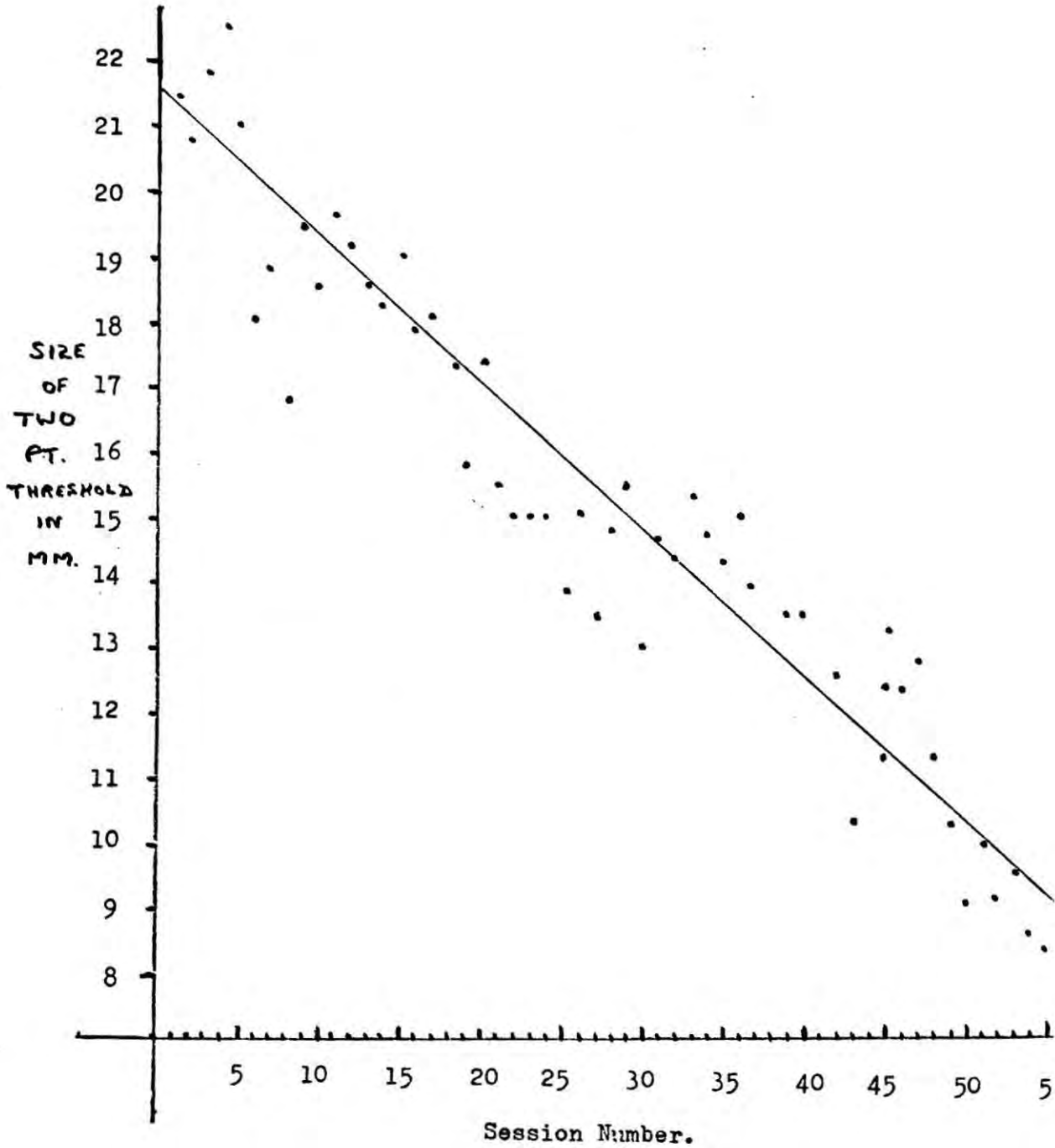
$$\begin{aligned}
 \text{Step 2.} \quad s^2 &= \frac{\sum D^2}{n} - \bar{D}^2 = \frac{1494.128}{14} - (9.98)^2 \\
 &= 106.7234 - 99.6004 \\
 &= 7.1230 \\
 \therefore s &= \sqrt{7.1230} = 2.6689
 \end{aligned}$$

$$\text{Step 3.} \quad s_{\bar{D}} = \frac{s}{\sqrt{n-1}} = \frac{2.6689}{\sqrt{13}} = \frac{2.6689}{3.60555}$$

$$\begin{aligned}
 \text{Step 4.} \quad t &= \frac{\bar{D}}{s_{\bar{D}}} = \frac{9.98}{1} \times \frac{3.60555}{2.6689} \\
 &= \underline{13.4825}
 \end{aligned}$$

APPENDIX IV.

A graph showing the improvement with practice for subject number 12 (male, white, S.A.) over 56 sessions.



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