Chapter 12

The Skin Senses

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The Skin Senses

As you sit in your chair reading this chapter, you feel the clothes against your skin, you might feel that the room is too hot or too cold, and you might even feel a certain about if discomfort from sitting too long. When you pick something up, say a drink cup, you both feel the pressure of the cup against your skin, and sense the shape of the cup that partly involves the activity of moving your hand around the cup to pick it up. Our skin is an important source of information important to us. Moreover, unlike audition and vision, the information arises both from the passive reception of the stimulus and the active interaction with the stimulus.

How Many Skin Senses

The sensations arising from your skin are varied. You feel pressure; you feel cold; you feel pain; you can sense where your limbs are; you even know if your limbs are moving or still. As a result, it is common to talk either about the skin senses (plural) or the **somatosensory system [to glossary]**. Somato- comes from the Greek word for body, so these collection of senses give us information about the body and what in the environment is impinging directly upon the body. Given the complex types of information needed from the body it is not surprising that many consider the somatosensory system to convey not one type of sensory information but several.

All of the skin senses are intertwined at the level of the physiology so we will depart from the usual organization of talking about senses. For both vision and audition a careful path was followed starting with the stimulus then following the physiology to the perception. For the skin sense, the common intertwined physiology will be discussed first and then the distinct types of sensations will be covered.

Anatomy of the Somatosensory System

The primary sensory surface for the detection of somatosensory information is the skin. The skin covers the surface of the body. There are different types of skin: **hairy skin [to glossary]**, **glabrous skin [to glossary]**, and **mucocutaneous skin [to glossary]**. Hairy skin has a rather obvious name and makes up most of the skin. If hair comes out of it, it is hairy skin. Glabrous skin is skin that had to put up with the most stress. It makes up the palms of hands and soles of feet. It does not have hair. Mucocutaneous skin is the skin that borders the entrances to our body such as the mouth and nose and border mucous membranes. The skin is made up of multiple layers; the layers can be grouped into two main divisions, the **dermis [to glossary]** and the **epidermis[to glossary]**. The dermis is the living portion of the skin where all of the skin senses receptors will be found. The epidermis is the layers of dead cells overlaying the dermis that seal the body from the outside elements (epi means on top of).

Receptors

Figure 12.x shows a cross-section of the skin highlighting some of the many types of receptors found there. It has been quite difficult to pair each of the receptor types with a particular sensory experience or even the fundamental way that they respond (Weisenberger, 2001). However, the receptors can be classified into three categories. **Mechanoreceptors [to glossary]** respond primarily to a deformation of the skin surface. Examples include Pacinian corpuscles, Meissner corpuscles, and Merkel disks. The response types of these mechanoreceptors can be categorized into two groups that resemble the magnocellular and parvocellular distinction seen in the retina. Mechanoreceptors can be either slow adapting or fast adapting. The slow adapting are similar to the response type seen in parvocellular cells of the retina. They start responding at the onset of the stimulus and then continue to respond as long as the stimulus is applied to the skin. The fast adapting cells are more like the magnocellular cells in their response. They respond when the stimulus is applied and then quickly return to their background firing rate. They might also show a burst of action potential firing when the stimulus is removed (Weisenberger, 2001). [DO I WANT A FIGURE ILLUSTRATING THIS DIFFERENCE?]

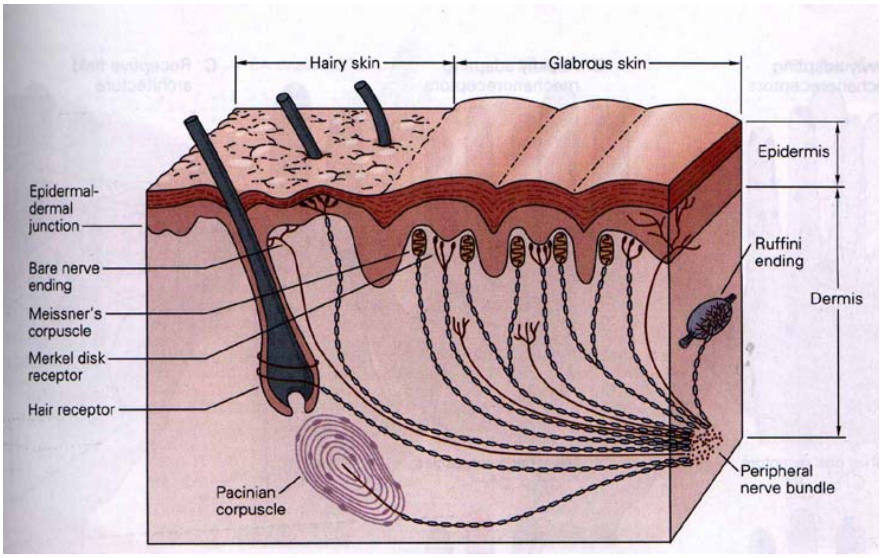

Figure 12.x. A cross section of skin showing several somatosensory receptors.

Thermoreceptors [to glossary] respond to temperature changes across the skin. From several types of experiments, it seems clear that there are two classes of thermorecetpors, warm receptors and cold receptors. The cold receptors respond to a temperature decrease and the warm receptors respond to a temperature increase across the skin. One way the difference between cold and warm receptors has been indicated has been with the warm and cold spots on the skin. In this type of experiment, a fine temperature probe stimulus is applied to the skin of an awake human. The temperature probe is applied and the person responds whether they feel the stimulus as either warm or cold. Often a grid is applied to the skin to indicate the places there the probe is to be touch to the skin. Then both warm and cold probes are applied to all of the points on the skin. The cold probe might be about 60 deg F and the warm probe might be about 115 deg F. What is found in such an experiment is that in many spots, probes feel neither warm nor cold. The participant does not experience any temperature experience at all. In other locations, the participant will respond to either the warm or the cold probe, but not either. In some cases, paradoxical responses result. Paradoxical cold occurs when the warm probe is applied to one spot the person says it feels cold. Paradoxical warm is the opposite, a cold stimulus is applied and the person responds that it feels warm (Dallenbach, 1927). A typical output from such an experiment is shown in Figure 12.x. The question then is what to make of these results. The fact that temperature sensations do not occur overall of the skin suggests that the person only responds when the stimulus is applied right above or near a receptor. So, it is not the entire skin surface but only where receptors are located that we can pick up thermal changes. The finding that different locations on the skin respond warm or cold suggest the difference between warm and cold receptors. That one location responds only to warm or to cold stimuli indicates that any particular thermoreceptor can only respond to either warm or cold. That is, there are warm receptors and cold receptors. The paradoxical responses amplify this conclusion. For paradoxical cold, a warm stimulus is applied above a cold receptor. However, it still, for some reason, makes the cold receptor fire. Since a cold receptor fires, our experience is that a cold stimulus was applied, thus, paradoxical cold. Paradoxical warm is simply the reverse situation. Physiological evidence supports the conclusions from this decidedly psychophysical experiment that you can try for your self (Somino & Dubner, 1981).

Despite the knowledge that we have about the existence of warm and cold receptors, it has been difficult to identify exactly what receptors in the skin do thermoreception. Several people have made different proposals, including that some of the mechanoreceptors also do thermoreception, but there is no widespread agreement in the field. Still current thinking is that some of the free nerve endings found in the skin are the warm and cold receptors (Weisenberger, 2001).

Finding the **noiciceptor [to glossary]**, the receptor for pain, has proved particularly difficult over the years. In fact at time it has been proposed that there are not particular receptors that respond to pain

(Schmidt, 1980). However, in recent years, it has become increasingly clear that the perception of pain particularly is the result of transduction of painful stimuli by receptors specialized for this purpose. Many of these receptors have both mechanoreceptor or thermoreceptor responses properties, but have very high response thresholds (Price, 1988; Weisenberger, 2001). It also seems that another subset of free nerve endings act as noiciceptors (Weisenberger, 2001).

Pathways to the Brain

The receptors, whether mechanoreceptors, thermoreceptors or noiciceptor, send their signals to the spinal chord [except for the somatosensory information from the face which enters the brain directly]. Once in the spinal chord, the somatosensory information follows two main pathways to the brain. Open **Interactive Figure 12.x, Somatosensory Pathways [link to media]**. Before exploring the primary pathways that somatosensory information follows from the skin to the brain, it is useful to have some general understanding of the anatomy being depicted. At the bottom of the screen, a cross section of the spinal chord is depicted. The outer light area of the spinal chord is what is known as white matter and is made up of myelinated axons that carry neural signals up and down the spinal chord. The inner darker area is called gray matter and is where neurons connect with each other at synapses. This organization is inside out from the way the brain is organized which has the gray matter on the outside on the cortex and white matter on the inside. At the sides of the spinal chord, peripheral nerves are created. If the peripheral nerve is created from the spinal chord it is surprisingly called a spinal nerve. Each spinal nerve has two roots into the spinal chord. The dorsal root of a spinal nerve is on the back side of the spinal chord, like the dorsal fin of a shark is on its back, and the ventral root is on the front side of the spinal chord. Very nicely, all of the sensory information traveling from the body all travels in via the dorsal root. All the motor pathways traveling from the central nervous system to the muscles of the body exit via the ventral root. The cross section of the spinal chord depicted in the figure is representative of many levels of the spinal chord. At the top of the spinal chord, the brain mushrooms over. At the very base of the brain is the medulla which is shown in the middle of the interactive illustration. At the top of the illustration, a cross section of the cerebrum is shown. It is a frontal section which is where the brain is cut to divide into a front and back section.

With that brief overview of the anatomy depicted in the interactive illustration, it will now be possible to describe how somatosensory information travels from the body to the brain. If the figure is still in the default condition, the pathways carrying somatosensory information from the right side of the body is shown. As mentioned above, there are two different pathways. These two pathways will be called the lemniscal and the spinothalamic pathways based on the names of some of the fiber tracts that the two sets of information follow to the brain (Geldard, 1972). It turns out that the lemniscal and spinothalamic pathways carry different types of information. The lemniscal pathway carries light touch that is very precise and also information about body position and movement (proprioception and kinesthetic sense). The spinothalamic pathways carry temperature, pain and deep pressure information. To understand these pathways and be able to interpret some of the implications of the pathways, it is useful to follow one pathway at a time. In the upper left corner of the screen are checkboxes. Click on these checkboxes so that only the **Right Lemniscal Path** is selected. This pathway is a saturated green. The receptors generate the sensory neurons which travel to the spinal chord. Since they are sensory information the will travel in the dorsal (back) root of the spinal never of which they were a part. One interesting feature of these neurons is that their have a rather unique structure. Their somas are not at the beginning of the neurons but actually are in the dorsal root where the dorsal root expands a bit (called the dorsal root ganglion). All of the sensory neurons have their somas in this dorsal root as shown by the small projection off of the side of the neuron. The sensory neuron enters the spinal chord and proceeds to the dorsal side of the spinal column and travels in a set of fiber pathways that are called the **dorsal columns [to glossary]**. Notice that the neuron has had a synapse yet. It is still the same neuron generated by the receptor. Moreover, the information is still on the same side of the body. The right lemniscal somatosensory information is traveling in the right dorsal columns. If you click on the **Left Lemniscal Path** checkbox to show the left pathways (in red), it shows even more clearly how the lemniscal fibers have not crossed while traveling in the spinal chord.

In the medulla, the dorsal lemniscal fibers finally synapse and new neurons take over carrying this information to the brain. After the synapse, the fibers finally decussate to the other side of the brain. In vision and audition, the decussation was partial with some of the information crossing while some information stayed on the same side of the brain. In the somatosensory system, the decussation is complete. All of the fibers cross to the other side of the brain. After the decussation, the lemniscal signals travel up the medial lemniscus, giving this pathway its name, to the ventral posterior nucleus of the thalamus. There is another synapse and then the lemniscal information travels to the bump of the surface of the brain that is farthest forward in the parietal lobe of the brain. A bump on the brain surface is called a gyrus and the somatosensory information travels to the postcentral gyrus also known as the primary somatosensory cortex (Figure 12.x). In the visual cortex the concept of the cortex being organized in columns was discussed. It is actually in the somatosensory cortex that columns were first discovered by Vernon Mountcastle (1957).

Now clear both the **Right Lemniscal Path** and the **Left Lemniscal Path** by clicking on their check boxes. Click on the **Right Spinothalamic Path** to show this pathway which will be a paler shade of green than the **Right Lemniscal Path**. In the periphery, the spinothalamic and lemniscal paths follow together, including the somas of nerves from both pathways being found in the dorsal root. However, the spinothalamic path diverges from the lemniscal path as soon as it enters the spinal chord. Follow the path. First, the spinothalamic information enters the grey matter region of the spinal chord and synapses. Then the fiber immediately decussates and travels to the brain in the lateral spinothalamic pathway of the spinal chord, giving this pathway of somatosensory information its name. From here, the spinothalamic information travels to the ventral posterior nucleus of the thalamus. While this is the same nucleus as the dorsal information, the two types of information actually synapse in separate regions of the nucleus. The spinothalamic information also travels to the primary somatosensory cortex of the brain. But the different types of sensory information, touch, temperature, pain, body position, and body movement are processed in different columns of the somatosensory cortex (Mountcastle, 1957).

The flow of somatosensory information in the spinal chord raises some interesting questions. Consider the following situation. Some unfortunate person is in a serious accident and has the right half of the spinal chord severed in the lower back. To simplify the situation just consider the legs. What somatosensory information will be lost from the right leg? What somatosensory information will be lost from the left leg? What somatosensory information will remain in each leg? Use the figure to figure out the answer.

Organization in the Somatosensory System

The anatomical organization of the nervous system has been crucial in our understanding of how the brain is able to make sense of the mass of sensory information being thrown at it. In the visual system, the separation of magnocellular and parvocellular provided insights into how the brain makes sense of the visual information. In the auditory system, the organization of sensory information implied by the Place theory and seen in the tonotopic organization of the brain helped illustrate how the brain can hear different frequencies of sound. Organization in the somatosensory information is going to be even more important. The huge area of the skin makes it imperative that the brain, among other pieces of information to track, must know where the sensory information is coming from. In this section, two levels of organization of somatosensory information in the nervous system will be discussed.

Dermatomes. The spinal chord is surrounded by the bony spinal columns. As such, it is not possible for nerves, called spinal nerves, to leave the spinal chord at every possible location along the spinal chord. There is one spinal nerve for each vertebra of the spinal column. The spinal nerves are then numbered along with the vertebrae of the spinal column. The top vertebrae of the spinal column are called the cervical. There are eight cervical vertebrae and they are numbered from the top. So the very top vertebra of the spinal column is called c1. The next group of vertebrae are called the thoracic vertebrae of which there are 12. Below that are the lumbar (5) and the sacral (5) that generate spinal nerves. This brief deviation into the anatomy of the spinal chord was taken because it relates to how the information from the somatosensory system is organized as it enters the spinal chord. Each spinal nerve collects information from a specific region of skin called a **dermatome [to glossary]**. The root of dermatome (derm-) comes from the same work that means the layers of skin where the somatosensory receptors are found (dermis). Figure 12.x shows the layouts of the dermatomes for the human body.

There are a few interesting feature to note about the dermatomes. First, they are very neatly organized. The dermatome for the top thoracic spinal nerve, t1, is mostly between the dermatomes for the spinal nerves for c8 and t2. Secondly, these dermatomes have some historically interesting patterns. Examine the dermatomes that overlay the hand, c6, c7, and c8. Notice how the dermatomes that receive the information from the hand also run up the arm and across the back. In the 19th century, some people complained of not feeling anything from their hand. The arm was ok; only the hand was involved. This symptom is called glove anesthesia. From the knowledge of the dermatomes, the physicians of the day knew that the problem had to be psychological in origin. Given the dermatome organization, if these nerves were damaged, then part of the arm and back would also loose feeling. If only one of the nerves was damaged, more likely, then only part of the hand would loose feeling and also part of the arm and the back. Later in this chapter we will see other ways that the organization of the dermatomes are relevant to our experience.

Somatotopic Organization in the Brain. When the somatosensory information reaches the brain it is processed in the cortex, as indicated above, in the gyrus right behind the major central dividing indentation that runs left to right. This region is called the somatosensory cortex. In the visual system, it was found that the retina was laid out on the visual cortex according the retinotopic organization. The retinotopic organization referred to the ability to map, point by point, the retina on the cortex. Two adjacent points on the retina are found on two adjacent points on the cortex. That does not mean that the map in the brain is an exact match to the retina. The takes up much more of the cortex than it does of the retina. This discussion is all a preamble to the **somatotopic map [to glossary]**. Figure 12.x shows the somatotopic map for the layout of the skin and some internal regions along the somatosensory cortex. Starting on the inside of the brain, the body is laid out across the somatosensory cortex starting with the feet. Just as in the retinotopic map, the size of the brain area responding to each part of the body is not of the same proportion as the actual body part is. The hands, lips and tongue take us a much larger percentage of the somatosensory cortex than they do of the actual body. Figure 12.x shows the shape of four organisms if their body proportions matched the proportions of the body parts on the somatosensory cortex. These representations are sometimes called the **somatosensory homunculus** [to glossary] for that organism. The animals depicted are a rabbit, a cat, a monkey, and a human. By looking at the differences in the relative sizes of comparable body parts, some sense of how that organism works in the environment can be discerned. Examining the difference between the monkey and the human is instructive in this regard. Notice the relatively small thumb on the monkey and their relatively large feet and toes when compared against the human. We require the use of our thumb to grasp objects via the important movement called opposition. To move well, it is important to have accurate sensory information from the skin and muscles. Monkeys cannot make the same sort of oppositional movement and as a result do not need the same sort of information from their thumbs. Conversely, monkeys use their feet a great deal more for climbing, swinging and even manipulation. Since we do not use our feet for the same sort of movements it is clear that we do not need the same degree of information from the feet. Examine the homunculi from each of the organisms and see if you can deduce any further ways that these homunculi reflect the differences in each of the organism's needs.

Touch

Touch usually refers to the sensation that occurs when our skin comes in contact with some object. The contact can be either active or passive. That is the object can press against the skin or the person can move to put the skin, often the hands, against the object.

Stimulus

The primary stimulus for touch is pressure applied to the skin. The pressure is best detected when there is a change in pressure between one area and another that causes a change in the shape of the skin, a deformation (Geldard, 1972). A vibrating stimulus, where the pressure changes in a regular and rapid fashion is also an effective stimulus. The observation that a deformation in the skin is an important element of the touch stimulus can be related to observations from the visual system. In the visual system a completely white or grey stimulus is not an effective way to stimulate the eye. The eye likes contrast. This finding was explained as being the result of the fact that receptive fields had both excitatory and inhibitory regions. While the somatosensory receptive fields seem to be very differently organized than those in the visual field, it does seem that receptive fields with both excitatory and inhibitory features can be found (Johansson, 1978).

Thresholds

Pressure. Pressure sensitivity has proved to be difficult to measure as many ways of creating and measuring pressure on the skin varied more than just the pressure applied to the skin. For example, when the skin is pressed in at one location, as the pressure is increased a larger and larger area of the skin is being indented, even though the stimulus is not really bigger. In recent times, many of the factors have been better controlled with newer methods of applying the stimulus.

One clear finding is that our sensitivity to pressure varies across the surface of the skin. Figure 12.x shows how pressure varies across the surface of the skin for passively applied pressure (Weinstein, 1968). Humans are most sensitive to pressure on the face and least sensitive to pressure on the feet. See what you can conclude about why the feet might be least sensitive to pressure. What might be the consequence of having feet that are very sensitive to pressure? One finding that could be considered a bit surprising is the relatively low sensitivity to pressure by the hands. Hands are very important to us for exploring the environment and it might be expected that they would be more sensitive to pressure.

Discrimination. Another way to examine the sensitivity of the skin to pressure stimuli is to examine what is called the **two-point threshold [to glossary]**. Two-point thresholds are similar to acuity in vision. In a two-point threshold experiment, two fine pressure stimuli are placed on the skin gently and simultaneously. The participants' task is to report whether the stimuli feel as two points or only one stimulus. The two-point threshold, therefore, represents the smallest distance between two stimuli on the skin that can actually be felt as two stimuli. It is in this sense that two-point thresholds are like acuity. Figure 12.x summarizes results for two-point threshold experiments over the human body (Weinstein, 1968). The hand has the finest ability to discriminate the presence of two stimuli. Here the fine sensitivity expected of hands shows forth. The face is the next in discrimination ability (Stevens & Choo, 1996; Weinstein, 1968). The calf, thigh and upper arm show very poor two-point thresholds. The thresholds on the calf are about 2" in distance.

Lateral Inhibition. When vision was discussed, the concept of lateral inhibition was introduced. Lateral inhibition was the term given to the observation that stimulating one region of the retina actually makes neighboring areas less able to respond to light. The concept was used to explain explain such illusions as Mach Bands. Open **Interactive Experiment 12.x, Mach Band Review** and run the experiment to remind yourself about this illusion. It is the same experiment as in Chapter 5. Or if you wish, just look at the screen. At the two vertical edges of the large white bar in the center of the screen are narrow even brighter white bars. Also at the edges where the white bar finishes blurring into the gray background you see dark vertical narrow bars. As you recall from Chapter 5, these bars do not exist and are created by lateral inhibition. Lateral inhibition operates to enhance edges and this function was discussed to be important in our perceptions of form. It turns out that the skin also shows evidence of lateral inhibition. Von Bekesy (1959) has demonstrated that it is possible to elicit Mach Bands on the Skin (Figure 12.x). What von Bekesy did was very similar to the stimulus in **Interactive Experiment 12.x, Mach Band Review**. Von Bekesy applied a s high pressure at on part of the skin and gradually reduced the pressure till it reached a low pressure value. The participants experienced an extra push on the skin next to the high pressure area and an area of extra light pressure next to the low pressure area.

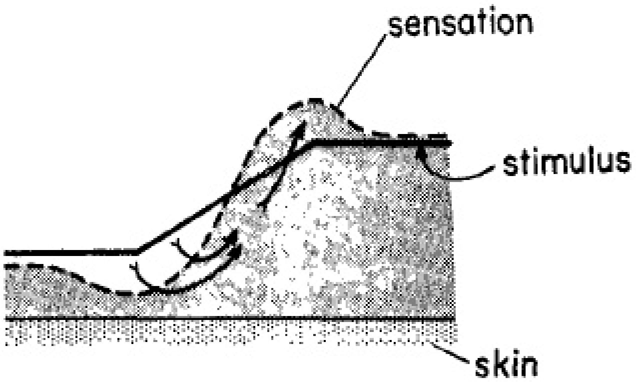

Figure 12.x: Illustration of eliciting Mach Bands on the skin (Bekesy, 1960).

The implications are pretty important from this observation. First and simplest, the skin seems to have lateral inhibition. Second, the existence of lateral inhibition implies that the skin has receptive fields. Well, that has been discussed above, but these receptive fields must have both excitatory and inhibitory areas. Without both excitatory and inhibitory areas, lateral inhibition cannot occur. Open **Interactive Illustration 12.x, Mach Bands and Center-Surround Receptive Fields** for a review of how the existence of both excitatory and inhibitory regions play a role in causing Mach Bands. This illustration is a reprise of the illustration on the same topic from chapter five. Think of the light levels as pressure. The brighter the light the greater the pressure. To keep the analogy the strongest, turn on the stimulus and make it blurred by using the check boxes at the bottom of the screen. As you can see the responses at the bright edge and the dark edge are the most different from the background firing rate. Reviewing how center surround receptive fields work will help you see how the presence of both inhibitory and excitatory regions of a receptive field causes Mach Bands. It is not beyond the reach of speculation to think that it might be possible that the receptive fields in the skin could also be center-surround.

Finally,these findings are suggestive about the role of pressure as a sense. Lateral inhibition in vision was shown to be important in our form perception. Finding edges, places of change, are important in demarcating objects and parts of objects. If the brain is using lateral inhibition in processing pressure, then the brain is probably also trying to figure out about the objects causing the pressure. The brain is processing both vision and pressure in some way that is similar. This similarity implies, potentially, some similarity in purpose. Since lateral inhibition plays a role in detecting objects it seems reasonable to conclude that the brain wants to know about objects against the skin. In other words, the brain is not simply content with knowing that the skin is being touched, it wants to know about the object that is doing the pressing.

Localization?

Adaptation.

Like the visual and auditory system, the human somatosensory system tends to adapt to pressure stimuli that are applied constantly to the skin. The time that it takes to adaptation tends to vary depending upon a number of factors such as the pressure and size of the stimulus. Generally the greater the pressure the and the smaller the size of the stimulus the longer the adaptation (Zigler, 1932). While it is not possible to get an exact value for adaptation, generally it is a rather short period of time, much shorter than, for example, the time it takes for the visual system to dark adapt. One way that adaptation in the skin is different for pressure than vision is how the sensitivity can be restored. All it takes to restore sensitivity to a tactile stimulus is merely to move the stimulus or change it in any small manner (Shiffman, 1982). Try pulling up your socks.

Complex Touch Phenomena

Temperature

Temperature sensitivity is a sense that is tied into our need to maintain our internal temperature at a nearly constant value. In other words, one main reason for temperature sensitivity is to help or body to maintain its homeostatic balance. If the outside air is too cold the body will act to keep heat in the body. Such actions include reducing blood flow to the skin surface, shivering, and even behaviors such as putting on a coat. Conversely, if the outside air is warm, the body will work to release heat from the body such as dilating blood vessels near the skin and slowing down behaviors. Temperature sensitivity is really the sensitivity of temperature at the dermis of the skin where the thermoreceptors are found. So, when it is cold and less blood flows near the skin surface it can even make us feel cooler. When a fever breaks, there is a lot of blood near the skin an we can break out in a sweat at this time because we feel hottest at this point in time while we might shiver when the fever really has a hold of us.

Stimulus and Thresholds

The stimulus for thermal sensations is a bit of a complicated topic. In most cases, the stimulus is determined to be a change temperature of a part of the skin. It is also important to use a stimulus that radiates the heat or cold instead of a stimulus that has to be put into direct contact with the skin. If the stimulus source has to touch the skin it is possible to have an interaction between thermal sensation and pressure sensation that can confuse the issue under study. Under optimal or near optical conditions, threshold for a temperature increase of as small as 0.003 deg C have been observed with a similar value for cooling (Hardy and Oppel, 1937). Just as different body parts show different sensitivities to pressure and two-point thresholds, different body parts show different sensitivities to temperature. From the thresholds to pressure, it is not surprising that the face (forehead and cheek) is the most sensitive region and the least sensitive is the calf and thigh (Stevens et al., 1974). In all cases, thresholds for temperature stimuli get smaller as the stimulus gets larger, spatial summation, and last longer, temporal summation (Stevens et al., 1974).

It has also been discovered that lateral inhibition occurs for temperature stimuli (von Bekesy, 1962). von Bekesy (1962) applied temperatures to the skin using light bulbs. By varying the distance of the bulbs from the skin, he was able to generate more warmth on on part of the skin and then a gradual reduction of warms to another part of the skin. It took a bit of time, but at the edge of the warm area, an extra warm band developed and next to the cooler area an even cooler area was experienced.

The Perception of Hot

The discussion to this point of thermal responses of the body has been in terms of cold and warm, not cold and hot. In the stimulation of discussion of stimulating the skin with fine thermal stimuli, cold and warm spots were discovered (Dallenbach, 1927). But most of us have acute experiences of hot. Still, all of the physiology to still finds two types of sensory fibers responding to temperature and they seem to correspond to cold and warm, well mostly. Zotterman (1959) found that cold fibers respond strongly to both cold stimuli and at hot stimuli. Warm fibers respond most around body temperature but still seem to respond to the higher temperatures. This leads to a hypothesis about how the experience of hot might be generated. Perhaps, hot is experienced when both the cold and warm receptors fire at the same time. A simple apparatus, called the heat grill, supports this contention about how a hot experience happens, Figure 12.x. In the heat grill a cold stimulus is placed right next to a warm stimulus. Neither stimulus along generate the perception of heat or hot. In fact, the cold stimulus alone generates a cold experience and the warm stimulus feels pleasantly warm. However, together the person feels heat and many will jerk their arm away as if it were being burnt. Others report a stinging burning sensation but can still keep the arm on the heat grill.

Localization

So far in all of the senses discussed, the ability to localize the stimuli have been very important. However, the ability to localize a thermal stimulus is not precise at all. It has even been reported that thermal stimuli presented on the front side of the body can be confused with stimuli presented on the back (Cain, 1973). This poor localization may in part explain a curious observation that results from the finding of temperature spots mentioned above. It would seem from the finding of temperature spots that when a cold or warm room is entered it might be experienced as a collection of unconnected cold or warm stimuli. But since temperature stimuli are not well localized, it is easy to see why the cold or warm air is experience as one continuous stimulus.

Adaptation and Physiological Zero

Prolonged exposure to a thermal stimulus, either cold or warm, will cause adaptation to that stimulus, i.e., we will perceive the stimulus to become less intense over time. To demonstrate thermal adaptation, try the following demonstration obtained from Shiffmann (1982). Place one hand in a bucket of water at about 40 deg C (104 deg F) and the other hand into a bucket of water at about 20 deg C (68 deg F). After leaving the hands in each bucket for a few minutes, shift both hands to a bucket with water at about 33 deg C (91.4 deg F). The hand that had been in the 40 deg bucket will feel cold and the hand that had been in the 20 deg bucket will feel warm. In a narrow temperature range it is possible to completely adapt to the stimulus, that is, to feel that the stimulus will be neither warm nor cold. When neither warm nor cold is experienced, then it is said that the person is at **physiological zero [to glossary]**. The range depends upon several factors including even the area of the body stimulated (Kenshalo & Scott, 1966). However, it is still a narrow range. Outside of the temperature range of complete adaptation, there is adaptation but it is partial. Think of going outside on a cold winter day. Yes, you adjust, but you always still feel cold. It is just a less intense cold. Tests that have lasted as long as 30 minutes have found that outside the temperature range where physiological zero is possible, complete adaptation is not seen (Schmidt, 1982). To compare this situation to vision, it is possible to have complete adaptation over a very large range of light levels, several factors of 10. In about 30 minutes it is possible to change from being adapted to the brightest light to reaching the visual systems maximal sensitivity. Recall that it takes a far less time to adapt to brighter situations than to darker. Adaptation in the thermal sense is much less than in the other senses that have been described.

Pain

The Experience of Pain

Pain is distinctly different from the other sensory modalities that are discussed in this book. While we like to see, hear, smell, etc most stimuli that we experience and would feel the loss of each of these senses keenly, there is a whole industry built up around the elimination of pain perception and much of the time we do not want to feel pain. Pain, to put it briefly, is unpleasant. But, as most of use would admit, pain is just as vital, if not more so, to survival than any other sensory system. Some people are born with a congenital insensitivity to pain. These people often fail to survive childhood. They simply have trouble avoiding situation that cause injury and illness (Nagasako et al., 2003). Pain informs us about injury but also about situations that can lead to injury. We learn from pain. So despite unpleasantness of pain, it is necessary.

In addition to the congenital insensitivity to pain, which seems to be the results of a loss of peripheral pain neurons (Dyck, et. al., 1983), there is also congenital pain indifference. These people have normal pain sensations and now peripheral nerve loss but seem to just do not seem to respond to the pain (Jewesbury, 1970). These people suffer from many of the same dangers as those with congenital pain insensitivity but for a very different reason. In one case, the person does not perceive the pain; in the other case, the person does not seem to care about the pain. This observation leads to the important distinction the sensory and the psychological aspects of pain (Melzack & Casey, 1968). While this distinction is present in all of our sensory experiences, the importance of this distinction in pain is critical. Given the importance of pain to our survival, it might seem odd that we can psychologically choose not to respond to pain, but that ability is important as will be discussed below.

There is also more than one type of pain experience. While, it does not seem that there is any one common means to categorize pain, Figure 12.x gives one way of organizing pain experiences (Schmidt, 1982). Pain does not arise just from the skin and muscles, where most of the other somatosensory sensation arise, but also arise in the viscera such as experienced in appendicitis. Even when the pain arises from the skin and muscles, there seems to be some variation as to whether it is the skin (superficial) or deep (muscles and joints). Even for pain on the skin there is the distinction between the sharp initial pain and the duller delayed pain. This experience is sometimes called double pain. The complexity and importance of pain experience suggests that the operation of the system will be subtle and complex. This expectation will be born out.

Stimulus

The determination of the pain stimulus is probably the most difficult to measure and determine. The difficulty starts with the definition of pain. Rollman (1991) asks "Is pain a sensation, a perception, an emotion or a thought?" (p. 91). The question is asking how to think of pain and the question arises because of the some of the complexities in the neural processing that is unique to pain. More specifically, the stimulus for pain has been under debate. Some of this debate was discussed above in whether there was a distinct receptor for pain. To highlight the difficulty try to think of as many painful stimuli as possible. Can you determine any commonalities among them?

In many cases pain is an extreme experience of any other somatosensory experience. A high level of pressure from a base ball hitting your arm will hurt, so will extremes of heat and cold. This finding fits with the relatively high level of thresholds for pain receptors mentioned above. Now think of a paper cut. It often happens that the person does not even feel the original stimulus that caused the damage. Obviously this is not caused by an extreme level of stimulation, but it still is painful.

Generally, in an experimental situation, painful stimuli have included intense pressure, chemical irritants, and electrical shock (Weisenberger, 2001) and even cold water (Kahneman et al, 1993). However, as implied by the quotation above, pain experience can have both a sensory and an emotional (affective) component. For research purposes, it seems useful to try and separate these two components. Different techniques have been tried and scaled developed with some success (Melzack, 1975; Rollman, 1979; Weisenberger, 2001);

Localization and Referred Pain

Pain receptive fields, like temperature receptive fields, are quite large and cover large areas of the skin (REF). As such localization of pain often require the use of other somatosensory sensations to aid in localizing the source of the pain. The problem is even more acute when the pain arises from an internal source, particularly from internal organs such as the heart. It does not seem that there are nay internal receptors for pressure and temperature and other sources of somatosensory information (REF). As has been seen in many examples throughout the book, the brain looks to try to organize the information into a meaningful pattern. Refer back to the Gestalt laws. Still, the brain needs to find a way to know where the source of a pain is. Using the Gestalt laws as a pattern, one way to approach the problem of trying to figure out how the brain might organize and, as a result, localize pain stimuli, particularly internal pain stimuli. The dermatomes (Figure 12.x) might serve as an organizing principle. The pain information has to enter the spinal chord just as other somatosensory information. For a second, speculate, consider the brain having connections that register that some internal pain sensation enters at the same level of the spinal chord as some pressure information. The brain then uses this correlation to localize the pain stimuli along the dermatome associate with the pressure information. But as you may have heard elsewhere, correlation does not mean causation. Just because two events occur together does not mean that one causes the other. So the pain, in this case would be misperceived in the incorrect location.

That leads to the concept of **referred pain [to glossary]**. With referred pain, pain from the internal organs are perceived along the skin, often following the associated dermatomes. Physicians are aware of the patterns of pain reference and use it in diagnosis. For example, a classic symptom of heart attack is a shooting pain down the inside of the arm (REF). There are many other symptoms, but this symptom is relevant to the present discussion. The shooting pain is caused by the damage to the heart itself but it is not experienced at the heart. Looking at the figure of the dermatomes, you can see the one labeled T1. It runs down the inside of the arms and it just so happens that the pain information from the hear travels in the first thoracic vertebrae (T1).

Adaptation to and Modulation of Pain Signals

Pain is a spinothalamic sense just as temperature. Since they share a common physiology, it might be expected that pain might also not adapt as fully as the other senses. There are other good reasons to suppose that pain stimuli would not adapt. The need to continue to experience pain while the body is still being threatened or damaged is a powerful argument for the continued experience of pain. Pain might also aid in recovery by indicating the need to use injured body parts more gently to allow recovery. However, there are times when pain might prevent necessary actions. If the injury is sustained in an emergency situation, it might be better to block the pain perception until the emergency is over.

[discuss pain adaptation]

[discuss evidence that pain experiences are modulated – get some anedotes if possible]

The most comprehensive theory to date that attempts to explain pain perception is the gate control theory of Melzack and Wall (1965). While the theory is old, it still stands as the most comprehensive theory of pain experience that exists to date (Dickerson, 2002). While both authors have supplemented their initial theory, the gate control theory remains at the core of both authors thinking (Loesor & Melzack, 1999; Wall, 1978). Open **Interactive Illustration 12.x, Melzack and Wall's Cate Control Theory** to explore how their theory works. The version depicted is an update of their first model (Dickerson, 2002) but has very few differences from the original model.

When the illustration first appears, you will see a schematic layout of how pain is thought to be transmitted to the brain. On the left hand side are the neurons that carry pain information from the body to the central nervous system. These are the peripheral sensory nerves that enter the body through the dorsal root. The neurons are not two neurons but two types of neurons, a large diameter neuron (**Large Diam Fiber**) and a small diameter neuron (**Small Diam Fiber**). In the real nervous system there would be many of each type of neuron. The fact that they have a different diameter is a good clue that they will play a different role in our perception of pain.

The gray rectangle contains the gate of the gate control theory and exists in the spinal chord. Pain, as you recall, is a spinothalamic sense. The sensory neurons synapse right after entering the spinal chord. According the theory, these sensory neurons synapse both on interneurons and on what the theory call T cells for transmission cell. It is signals that travel up the **T Cell** that indicate pain to the brain. The interneurons then are the gates. Look particularly to the upper interneuron. It has an inhibitory connection between it at the **T Cell**.

First, adjust the small fiber strength of firing using the **Small Fiber** slider on the lower left side of the screen. As you increase the firing on the small fiber, it stimulates both its interneuron and the **T Cell**. In addition its interneuron stimulates the **T Cell**. The combined firing of the small fiber and its interneuron on the **T Cell** leads to a strong firing of the **T Cell** which is indicated by a red firing on all neurons involved. In this illustration red means pain.

Reset the **Small Fiber** slider to 0 and start increasing the firing strength of the large diameter fiber using its slider. The large diameter fiber, which can be considered to be coming from the lemniscal sense of light pressure, both directly stimulates the **T Cell** and its interneuron. But, the interneuron for the large diameter fiber inhibits the **T Cell**. This is a very different outcome from the small diameter fiber. As a result wen only the large diameter fiber is operating, no pain is transmitted to the brain as seen by the tranquil green **T Cell**. The function of this pattern of connection can be seen by restoring the large diameter fiber to 0 and setting the small diameter fiber to its maximum (100). Then increase the activity of the large diameter fiber and observe what happens. As you increase the firing strength of the large diameter fiber, the firing rate of the **T Cell** goes down. This feature of the model explains how sometimes rubbing a hurt area can reduce the perception of pain. Say you bruise yourself. Well, we often rub the bruise to bring some mild relief. Rubbing stimulates our lemniscal light pressure pathways which travels up large diameter fibers. Since rubbing reduces our perception of pain, there must be some place in the nervous system were such sensations can help reduce the transmission of pain. Melzack and Wall place this function right in the spinal chord.

On final feature of this model to be discussed. At the top of the screen is a slider labeled **CNS Input**. Move that slider to the right to increase the input into the gate from the central nervous system. There is a neuron drawn from below the slider to the large fiber interneuron and it stimulates or excites this interneuron. Since the large fiber interneuron inhibits the **T Cell**, the central nervous system acts to inhibit pain transmission. It is well known that activities that distract can lead to the reduction in the perception of pain. [REFERENCE AND EXAMPLE] There is also evidence of other central factors that lead to the reduction of pain right at the spinal chord[SPELL OUT?]. This feature of the model accounts for these observations.

Is There a Spinothalamic Sense?

Summary

Key Terms

Figure 12.x. A typical result on an experiment using cold and warm probe stimuli on the skin. EXPLAIN SYMBOLS WHEN I KNOW WHAT THEY WILL BE.

Figure 12.x. Location of the somatosensory cortex in the human brain.

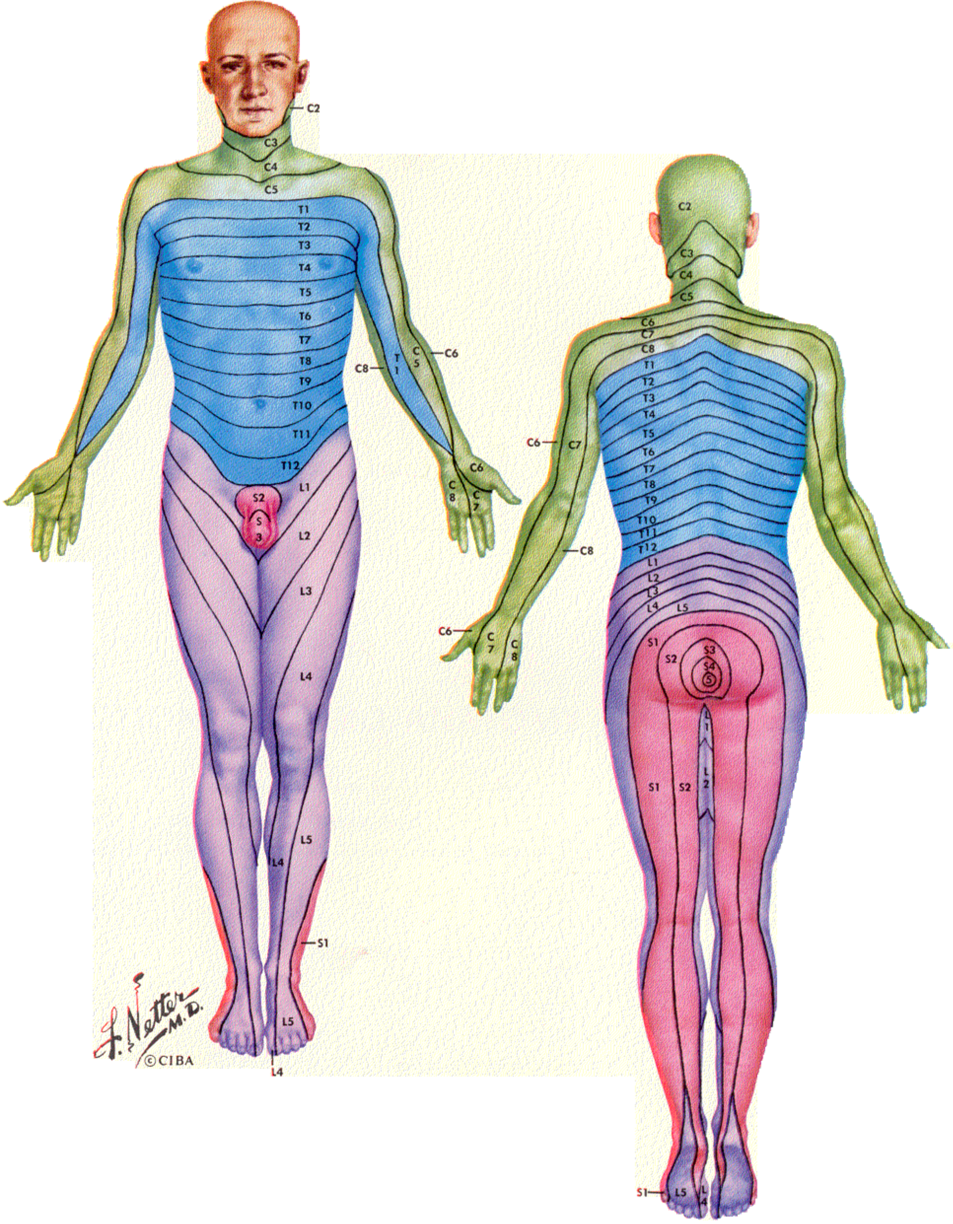

Figure 12.x. Dermatomes on the Body [Can I turn this into an interactive figure?]

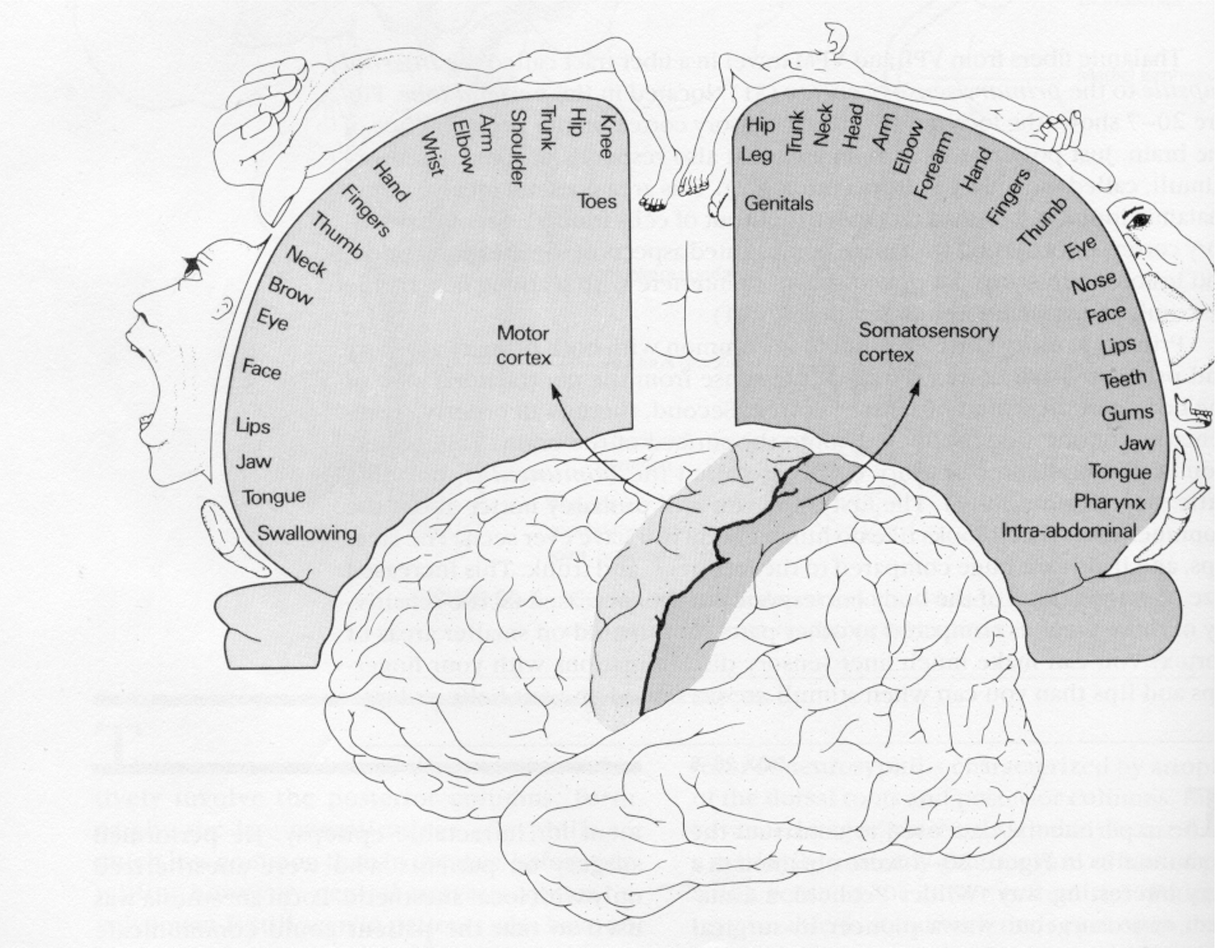

Figure 12.x. The somatosensory homunculus.

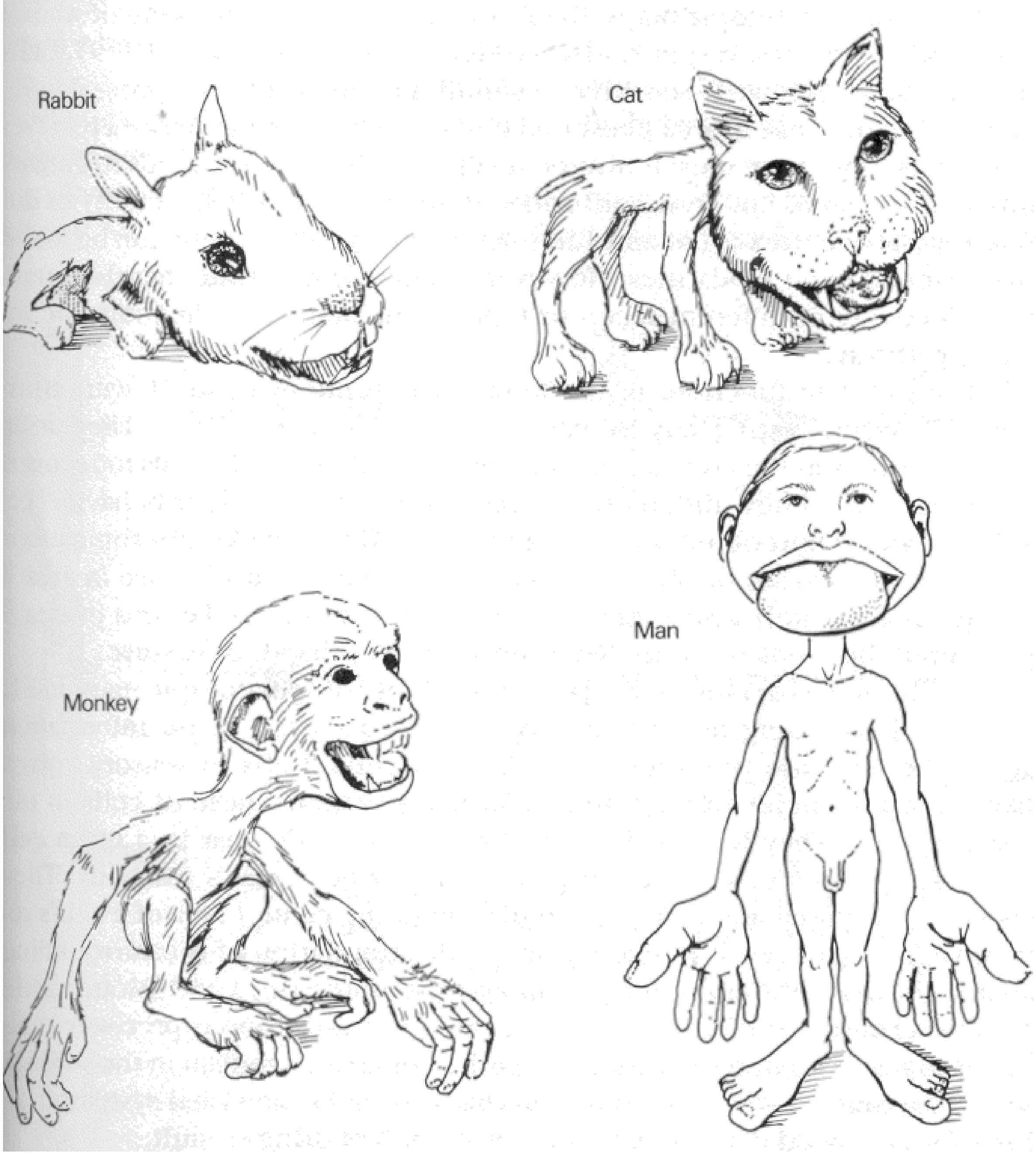

Figure 12.x. Somatosensory homunculi, drawn out, for different animals.

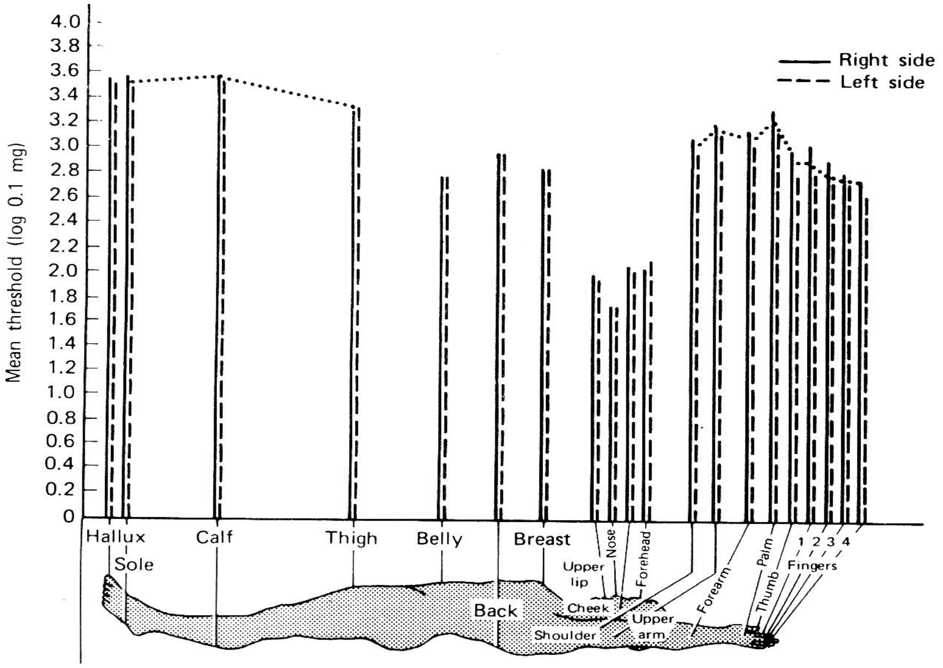

Figure 12.x Pressure sensitivity of different body parts for males. The data is similar for females. Data from Weinstein (1968).

Fig. 7.8 *Two-point thresholds for males. (The corresponding thresholds for females are very similar.) The ordinate represents the minimum distance between two stimuli necessary for the perception of two distinct stimuli. (Source: Weinstein, 1968, p. 202. Reprinted by permission of the author and publisher.)*

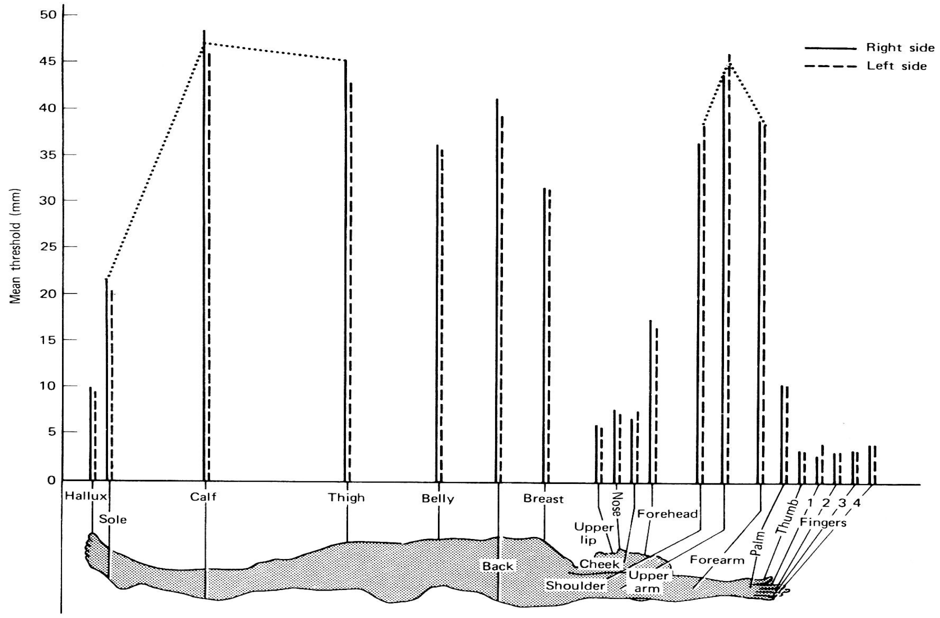

Figure 12.x. Two-point thresholds for different regions of the body. Data for females are similar. Data from Weinstein (1968).

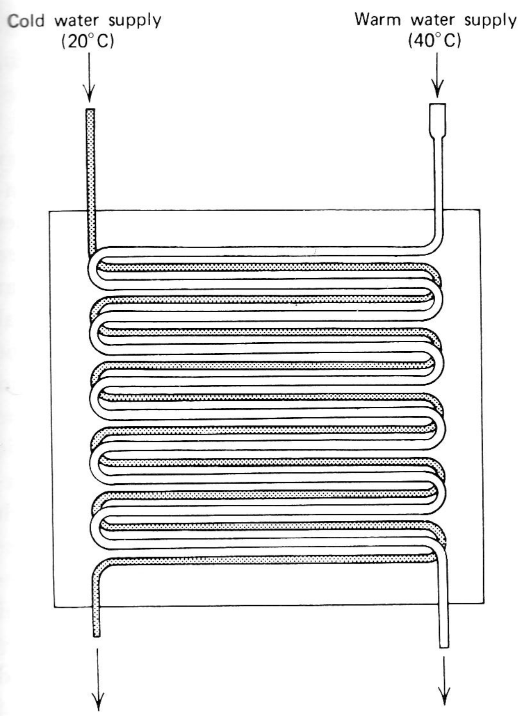

Figure 12.x. The layout of a heat grill.

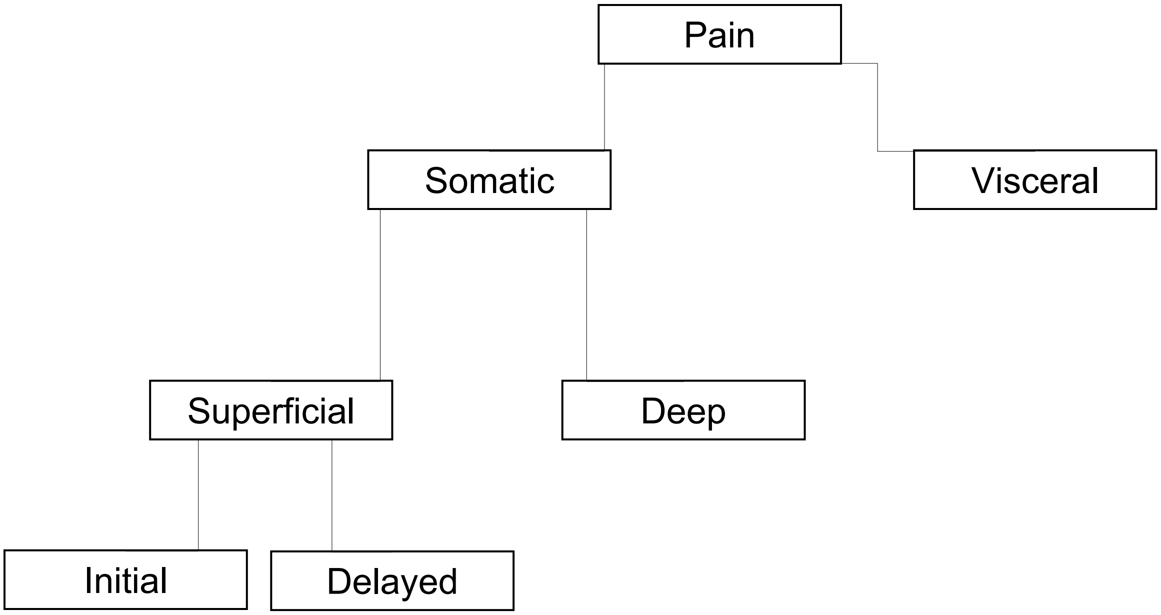

Figure 12.x. A categorization of pain experiences after Schmidt (1982).