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SOMATOSENSORY SYSTEM; TOUCH

Physiology and Neuronal Correlates of Discriminative and Affective Touch

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Somatosensory System; Touch

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I hereby certify that all material in this final year project which is not my own work has been identified and that no work is included for which a degree has already been conferred on me.

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Abstract

This essay is about the somatosensory system, which is divided into different kinds of touch. Described briefly are the proprioceptive touch, which is transported to the brain via A-alfa fibers and transmits information about e. g. limb position and movement. The cutaneous touch is the main focus and it is divided into discriminative touch and affective touch. The first corresponds to stimuli such as vibration and pressure and is transported via A-beta axons. The second, affective touch, corresponds to e.g. painful and pleasant stimuli which are transported to the brain via A-delta and C-fibers. The aim of the essay is to give an overview of the sense of touch, by doing a literature search, including a discussion of relevant neuronal correlates focusing particularly on affective touch. Moreover, the physiological aspects of touch will be presented. The sources that are used are review and original articles taken from databases such as ScienceDirect, and some articles send by the author. Some books have also been used to find more general knowledge. The conclusion for the essay is that touch is important for humans to function in everyday life. Additional, a specific receptor called C-tactile (CT) is identified to correspond to gentle touch and is suggested to have a vital role for humans in maintaining and forming social bounds. Moreover, discriminative touch is associated with activation in the primary and secondary somatosensory cortex, whereas affective touch seems to be associated with activity in the orbitofrontal cortex, cingulate cortex and the insula cortex, as well as the prefrontal cortex, which is suggested to be activated during interpersonal touch. Further, the sense touch needs to be more researched in order to understand its functions and benefits deeper.

Keywords: somatosensory system, discriminative touch, affective touch, C-tactile afferents, somatosensory cortices, orbitofrontal cortex

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Introduction

In humans and other animals information about the world arises from the five sensory systems; vision, audition, taste, smell and touch (Field, 2001). The sense organ for touch is the skin, which is the oldest and largest sense organ and is the first to begin to develop within the fetus. Touch is also the sense that typically remains intact longest (if not damaged in e.g. an accident), while the other senses may begin to fail, because of e.g. increasing age. When one sensory system dysfunctions or is lost, other senses tend to show some plasticity. For example, increased sensitivity to touch may be found in blind people. However, regardless of its obvious importance touch is the sense least researched.

Without the sense of touch one would not be able to feel the body position in the environment. One would, feel neither pleasantness nor pain, which makes it difficult to live (Niell, 1991). Touch helps humans to discriminate the location of a stimulus on the skin surface and also helps one to explore, manipulate and identify objects in the external word (Serino & Haggard, 2010)

Thus touch can serve as a communication system helping the body to interact with the environment and can also be used as a form of communication between people, e.g. to encourage one another, as a greeting form, to enhance motivation and to share feelings with each other (Gallace & Spence, 2010). However, the feelings shared can be both positive and negative depending on the social context. Even the briefest touch of another person can elicit strong emotional responses within human bodies, both physical and psychological.

Touch is a component for cognitive and physical development in humans and touching others has a role in affiliative and social behavior (Guest et al., 2009). During the first years of life infants and young children explore the physical world through touch (Field, 2001). They learn about the world by putting things into their mouth, touching objects and persons, and learning how to avoid unpleasant, and seek pleasant surfaces (Field, 2001), since

the main part of the tactile sensations arise from contact with the external world (Klöcker, Wiertlewski, Théate, Hayward, & Thonnard, 2013).

The various sensations of touch arise from physical attributes of the surfaces being explored, such as temperature, softness, roughness, and hardness. These physical factors, together with force and velocity, combined with top-down factors (like expectations and previous experiences), and identity of the person touching contribute to the perception and interpretation of the touch (Ellingsen et al., 2014). The physical attributes also affect the degree of pleasantness the person experiences (Klöcker et al., 2013).

Touch can be divided into so-called discriminative touch and affective touch (McGlone, Vallbo, Olausson, Löken, & Wessberg, 2007). Discriminative touch is critical in providing sensory information about handled objects and is processed through low threshold mechanoreceptors within the skin. Affective, or emotional touch, refers to another system of receptors providing touch and has an essential role in providing and supporting emotional, behavioral and hormonal responses to skin-to-skin contact with con-specifics. Moreover, recent research suggests a specific system for the affective, gentle and pleasant, touch (Morrison, Löken, & Olausson, 2010). A receptor within the human glabrous skin has recently been identified and is suggested to respond to the pleasant aspect of touch, innoxious stimuli, and is called the C-tactile afferent (CT). In general it is suggested that affective touch produces activation within the orbitofrontal cortex, the anterior cingulate cortex and the insula cortex (Weiss et al., 2008), whereas discriminative touch is suggested to produce activation within the primary and secondary somatosensory cortices (Olausson, Wessberg, Morrison, McGlone, & Vallbo, 2010).

The overall aim of this essay is to give an overview of the sense of touch, including discussion of the relevant neuronal correlates, focusing particularly on affective touch, which is the specific aim of this essay. The different kinds of touch and their definition

will be presented. Physiology factors relating to touch will be described briefly, types of receptors and axons responding to various types of touch. Evidence for neural correlates will be presented and discussed.

Specifically, the somatosensory system with its different kinds of touch and receptors will be defined first. Secondly, the physiology – different kinds of axons and receptors responding to touch stimulation over the skin – will be described. Thirdly, neuronal correlates activated within the brain when different kinds of touch are applied to the skin surface of both healthy and non-healthy subjects will be provided. Fourthly, there will be a discussion about further directions of the research and why touch may be important.

Definition of Touch

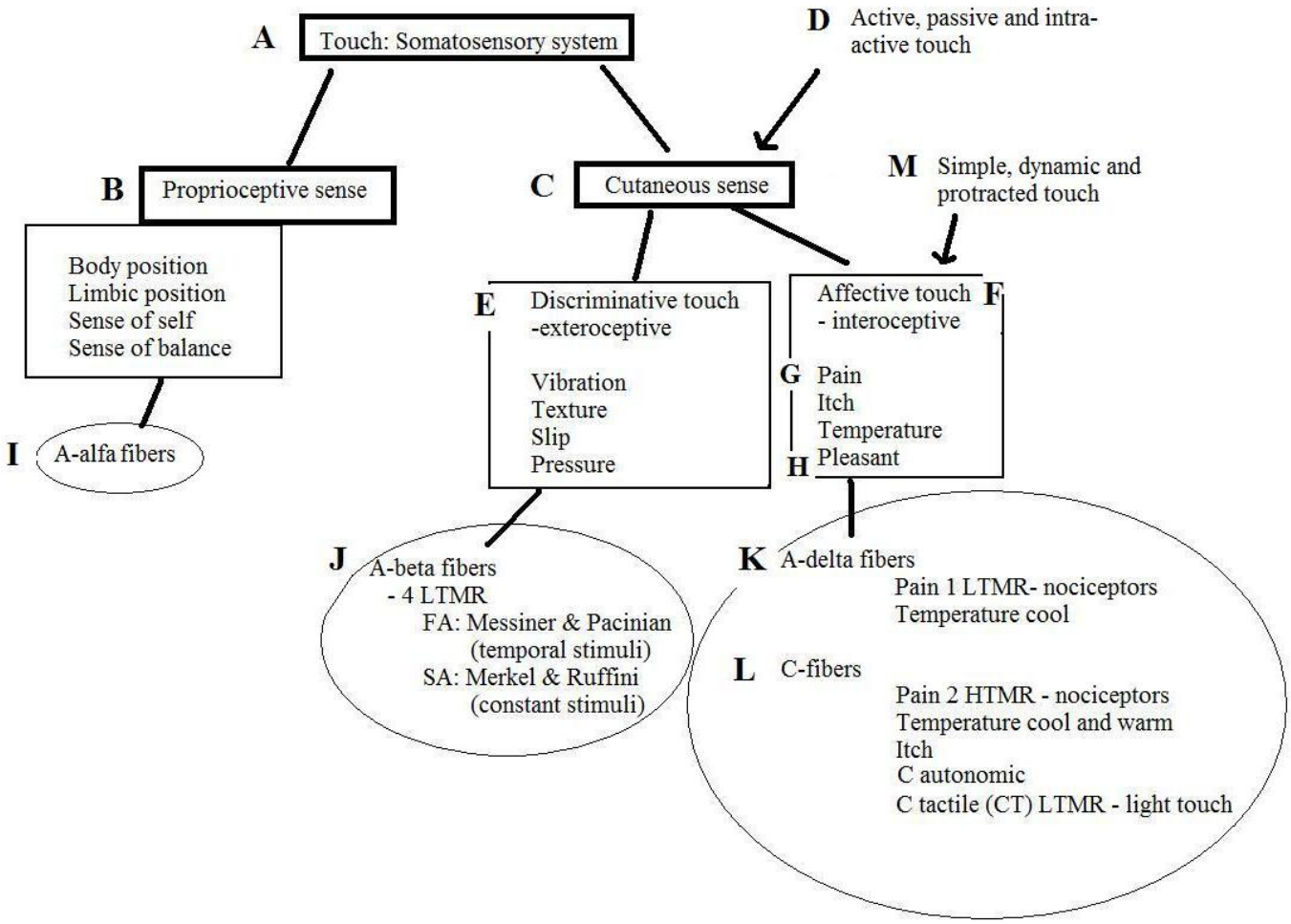
The sense of touch (see figure 1: A) is also called the somatosensory system and contains both peripheral afferent nerve fibers, which send information from sensory neurons towards the central nervous system (Chulder, 2013) and specialized receptors, which retrieve information about two types of touch/sensibility: proprioceptive sense and cutaneous sense (McGlone et al., 2007). Proprioceptive sense (figure 1: B) processes information about the body position, the limb position and muscle forces that the central nervous system uses to control and monitor movements of the body and ensures that a planned movement can be executed fluently. The cutaneuos sense (figure 1: C) can, depending on the intensity of the stimuli, as well as where and who is touching, and the context, be mediated by exteroceptive and interoceptive systems (McGlone & Reilly, 2010; McGlone & Spence, 2010). The exteroceptive systems (figure 1: E) guide somatomotor activity and are also called discriminative touch which responds to both constant and temporal mechanical stimuli. Discriminative touch also responds to the perception of pressure, texture, slip and vibration helping the body to provide information about nonverbal communication of handled objects

(McGlone et al., 2007). The spatial localization of stimuli and the intensity of stimuli are also provided by discriminative touch (Morrison et al., 2010). The interoceptive systems (figure 1: F) regulate feelings and are called affective or emotional touch and percept; pain, temperature, itchiness and recently pleasant touch has been added (McGlone & Reilly, 2010). The interoceptive systems (affective touch) respond to skin-to skin contact such as erotic human touch, parent –infant touch and non-sexual touch (Morrison et al., 2010), as well as low force and slowly moving mechanical stimuli and produce emotional, behavioral and hormonal responses (McGlone et al., 2007). Morrison et al. (2010) divide non-sexual social touch into simple, dynamic and protracted touch (figure 1: M). Where simple touch is brief, intentional contact on a restricted location, dynamic touch involves continuous movement over the skin which can be repeated, and protracted touch involves long and mutual skin-to-skin contact between individuals and includes pressure.

Within the skin there are receptors which respond to these different kinds of touch depending on the sensory axon, which extends information further to other neurons (see p. 10 for details). These axons are classified according to their degree of myelination (myelin is the fatty substance surrounding the axon, see p. 10 for details). The proprioceptive sense is transported via A- alfa axons (figure 1: I) to the brain (see more details of axons and receptors p. 10), whereas cutanoeus sense is transported via three types of axons; A-beta, A-delta and C-fibers (McGlone et al., 2007). Discriminative touch corresponds to A-beta axons (figure 1: J) which are activated from four kinds of low-threshold mechanoreceptors (LTMR): Messiner´s corpuscles, Pacinian corpuscles, Merkel´s disks and Ruffini endings. The first two are fast adaptive (FA) receptors and correspond to temporal stimuli and the last two are slow adaptive (SA) receptors and correspond to constant stimuli (McGlone & Reilly, 2010; McGlone et al., 2007). Moreover, affective touch corresponds to two broad types of axons: the first is A-delta axons (figure 1: K) with LTMR nociceptors (responding to first

sharp pain) and cool receptors (responding to temperature). The second type is C- fiber axons (figure 1: L) with high-threshold mechanoreceptors (HTMR) nociceptors (responding to the second burning pain), warm and cool temperature receptors, itch receptors, C- autonomic receptors and LTMR C-tactile (CT) afferents corresponding to light and pleasant touch.

Figure 1. Overview of the Somatosensory System; Touch



Physiological Aspects of Touch

The following section will focus mainly on the physiological aspects of the cutaneous sense (figure 1: C) and primary affective touch (figure 1: F). However, the physiology of proprioceptive sense (figure 1: B) and discriminative touch (figure 1: E) will be briefly described.

The skin is generally divided into four main layers including different kinds of tissues such as neurons, receptors and vessels etc. (Jepps, Dancik, Anissimov, & Roberts, 2013). Touch to the skin surface happens at the layer epidermis, classically called stratum corneum. The next layer is the viable epidermis, the third layer is called dermis and the last layer within the skin is called hypodermis/subcutaneous tissue. Within these layers there are neurons which are the basic signaling units consisting of a cell body, dendrites and axons (Gazzaniga, Ivry & Mangun, 2009). The cell body contains metabolic machinery that maintains the neuron. The inputs, incoming information, received by the dendrites are transported to the cell body. In contrast, axons make a connection to other neurons by extending information away from the cell body to the next neuron: outgoing information.

In the skin there are mechanoreceptors transforming the stimuli (touch/contact) on the skin into nerve impulses going to the brain (McGlone & Reilly, 2010). The nerves respond to different kinds of touch depending on the nature of their sensory axons and there are four kinds of sensory axons classified according to their degree of myelin (McGlone et al., 2007). Myelin is fatty substance that surrounds axons and determinates the speed with which the axon can conduct these nerve impulses (Gazzaniga et al., 2009). More myelin around the axons makes the signal speed faster and smaller amount of myelin makes the signal speed slower. When the nerve impulses are transmitted towards the brain they arrive at the dendrites and are further transmitted to the cell body, as mentioned. In the cell body the impulses are transmitted further to the next nerve via an axon. Axons that are myelinated

actually have small areas without myelin and these are called the nodes of Ranvier. The nerve impulses from the cell body arrive at the axon and when reaching the nodes of Ranvier, the unmyelinated areas, the nerve impulses, produced by the stimuli, start to jump between these nodes. As a result, the nerve impulses arrive faster at the next dendrites and further to the next neuron and later on the brain. Moreover, the nerve impulses transmitted by unmyelinated axons have no myelinated parts to jump over; therefore, the impulses of these axons are slower and the speed of the signals slowly. Thus, the amount of myelin affects the speed of the signal from the first activated axon to the brain (McGlone & Reilly, 2010). For further detail see e.g Gazzaniga, Ivry, and Mangun (2009).

A-alfa is the fastest and largest axon type and includes neurons corresponding to some proproioceptive sense, for example muscle stretch receptors (McGlone et al., 2007). The second largest axons are called A-beta and they are low-threshold mechanoreceptors (LTMR) and correspond to discriminative touch. Thirdly, the A-delta axon includes receptors corresponding to pain, nociceptors, and temperature, cool receptors. Last, the C-fibers which are unmyelinated and because of that transmit more slowly than the other (the nerve impulses cannot jump between the unmyelinated parts). C-fibers includes nociceptors which correspond to pain, warm and cool receptors corresponding to temperature, itch receptors which correspond to itch, C-autonomic which are autonomic and handle sweat glands and vasculature (etc) and the recently identified C- tactile afferent (CT) receptors, in hairy skin, responding to emotional touch or pleasant touch (McGlone & Reilly, 2010; McGlone et al., 2007).

There are four types of A-beta LTMR corresponding to discriminative touch (figure 1: E and J); (1.) Messiner´s corpuscles (2.) Merkel´s disks (3.) Ruffini endings and (4.) Pacinian corpuscles (McGlone et al., 2007). Messiner´s corpuscles and Merkel´s disks are found within the viable epidermis and dermis (McGlone & Reilly, 2010). Furthermore,

the Ruffini endings are found in the middle of the dermis and the Pacinian corpuscles in the hypodermis. One way of classification of these receptors is by their functions. Messiner´s corpuscles and Pacinian corpuscles respond to a temporary and spatially mechanical stimuli moving on the skin, classically called fast-adaptive (FA) receptors, which means that they conduct fast movements (e.g. McGlone et al., 2007; McGlone & Reilly, 2010). On the other hand, Merkel´s disks and Ruffini endings receptors are classified as slow-adaptive (SA) receptors, which means they continue firing during a constant mechanical stimuli (see more Trulsson et al., 2001). The anatomical location decides the LTMRs skin area where the neurons are sensitive to the touch (receptive field), the nearer the surface the smaller the receptive field will be (e.g. McGlone et al., 2007; McGlone & Reilly, 2010). Since the Messiner´s corpuscles are near the skin surface as well as the Merkel´s disks they have small receptive field. In other words, they have small skin surface area to which they are sensitive and fire. The Ruffini endings and the Pacinian corpuscles are deeper down the skin; therefore, they have larger receptive fields.

However, myelinated afferents do respond to rapid movement and have a fast conducting system (Vallbo, Olausson, & Wessberg, 1999). One characteristic of the myelinated afferents are that many units exhibit a high sensitivity and they give higher impulse rate the faster the stimuli are changing. It is also known that the degree of response from the myelinated afferents and the size of a receptive field may be dependent on stimulus properties and force, the field size increasing with the force (Wessberg, Olausson, Wiklund Fernström, & Vallbo, 2003). In other words, the receptive field of myelinated afferents (and C-fibers afferent) varies in size, shape and complexity between units most likely depending on stimuli parameters (Wessberg et al., 2003).

In both humans and at least some mammals, the system of slow-conducting unmyelinated C-fibers afferents within the skin responds strongly to innocuous skin

deformation (Olausson et al., 2002). Corresponding sensory afferents to CT was first identified within cats (e.g. Zotterman, 1939; Douglas & Ritchie, 1957). Zotterman (1939) found that the signal from touch and from pressure differed within the cat, since light and gentle touch, repeated with short intervals, showed different signals than when the cat was picked by a needle. From this result the question about different kinds of fibers with different sensory functions was raised. The result of Zottermans' (1939) study showed a difference in speed of the signals which indicate that the A fibers had myelinated axons, whereas the C afferents seemed to be unmyelinated. Zotterman (1939) also suggested that the C afferents sub-serve tickle and itch, and that pain applied to the skin is transported to the brain in two different pathways, which have later been shown by, for example, Vallbo et al. (1999) (these neuronal pathways will be described later). Furthermore, Nordin (1990) suggested that these C units were very rare within humans, because the low-threshold C units had only been shown to exist within cats and primates and not within humans. However, Nordin (1990) was the first researcher who showed evidence for the low-threshold C mechanoreceptors within humans, first identified in the supraorbital nerve within the forehead. The C-afferents were classified as tactile machanoreceptors because of their high sensitivity to innocuous skin deformation; they responded strongly to light stroking produced by a finger tip over the skin (Wessberg et al., 2003). At the beginning researchers thought C afferents only existed in the face within humans. However, later research has found evidence against this (Wessberg et al., 2003). The low-threshold C units are now identified within human hairy skin; for example within the forearm, the face, and the legs (e.g. Edin, 2001; Olausson et al., 2002; Vallbo et al., 1999).

Furhtermore, the slightly myelinated A-delta fibers with moderate conduction velocity and unmyelinated C-fibers with slow conduction velocity both include receptors corresponding to noxious stimuli, pain (Weiss et al., 2008). Nordin (1990) found two types of

mechanoreceptors within the C-fibers afferent, one high-threshold mechanoreceptor (HTMR) and one low-threshold mechanoreceptor (LTMR) which correspond to different stimuli. Vallbo et al. (1999) suggested that LTMR C-fibers afferents are a separated set of cutaneous sensory units with different functional characteristics compared to the HTMR C-fibers afferents, now called nociceptors. The sensitivity to skin deformation varied within the two units and the researcher suggested that the thresholds were two separated unit types and had two different kinds of functions. LTMR units respond intense to pin-prick stimuli (noxious) and smooth probe (innocuous) stimuli; however, they did not discriminate between the two as the impulse rates were almost the same. In addition, HTMR units failed to respond to the innocuous stimuli, yet they gave a large response to the noxious stimuli.

These results suggest, that the functions might be as follows: low-threshold units coding light tactile stimuli and high- threshold units coding nociceptive stimuli (Vallbo et al., 1999). The noxious stimuli give rise to two discriminable pain sensations; a short-latency sensation which is transported via the A-delta fibers and is called the first, or sharp, pain and aims at achieving an act to get relatively safe from the source of injury (Weiss et al., 2008). Moreover, a long-latency sensation, transported to the brain via the C-fibers, has a longer lasting attention behavior response to limit further injury, and this is the second, or burning, pain. In short, A-delta stimuli are more often characterized as more painful than the LTMR C-fiber stimulation are.

The responses of the C afferents to stimuli depends on the previous history, with repeated stimuli resulting in shorter response durations and lower instantaneous impulse rates toward the end of the response. In other words, the stimuli leave fatigue, for seconds up to minutes, and make the unit respond less strongly to a subsequent stimulus (e.g. Vallbo et al., 1999; Wessberg et al., 2003). In addition, the receptors respond to different kinds of movement over the skin. For example CT afferents respond to tactile stimuli that are slowly

moving over the skin surface and poorer to rapidly moving stimuli, which indicate a high dynamic sensitivity. The CT afferents are found in peripheral nerves in the hairy skin and not in the glabrous skin, as the palm, and they also respond poorly to vibration which is associated with discriminative touch (Olausson et. al. 2002).

However, it has been difficult to study the function of unmyelinated afferents, like the CT afferents, because when touching the skin all kinds of different receptors respond, both myelinated and unmyelinated axons (Olausson et al., 2002). Therefore, two persons with sensory neuronopathy syndrome have been studied. Sensory neuronopathy means that the unmyelinated axons, A-delta receptors and C fibers, are still intact but the A-alfa and A-beta receptors are damaged. G.L. is one person with neuronopathy and denies any sensation of touch from her nose and down, because permanent of loss of myelinated afferents (Olausson et al., 2008). The other person I.W. reports to have no feeling from the neck and down and has permanently lost his large myelinated afferents. The motor neurons are still intact within both subjects, which mean that they can both move their body, but the sense of touch is lost. Nevertheless, not completely lost; on examination the subjects actually report some kind of sensation of touch. The subject G.L. felt light touch in the forearm but not in the palm, the glabrous skin of the hand (Olausson et al., 2002). Further, she did not feel the vibratory stimuli in the hairy skin, which indicate that the function of CT afferents does not include vibration (Olausson et al., 2008). G.L. did only report a feeling of pleasant touch but not feelings of pain, itch, temperature or tickle. She reported a weaker feeling of pleasant touch than the control subject, without neuronopathy syndrome, reported. However, the reported degree of pleasantness was the same for G.L. and the control group. Nevertheless, G.L. could not tell the direction of the touch for a long distance (100mm in this study) along the forearm, nor detect local vibration. This indicated that some of the discriminative receptors were lost. She had the same thresholds for detecting warm and cold pain, which shows that the

unmyelinated fiber system is intact. On the other hand, she had higher threshold for cool detection which shows partial disturbance of thin myelinated fiber systems. Studying G.L. did not support the previously suggested hypothesis (e. g. Nordin, 1990; Zotterman, 1939) that the CT units sub-serve tickle or itching (Olausson et al., 2002).

However, the results indicate that the CT system does not provide discriminative touch because these receptors lack the precision and consistency to handle that type of touch (Olausson et al., 2002). Moreover, the results did show that CT afferents can provide affective touch and give emotional, hormonal and behavior responses to tactile stimulation. In other words, the A system and the CT system are separate and, as will be described later, have different cortical area connections. The interpretation that CT afferents are a part of an interoceptive system implies that they are a component in the construction of the sense of self – the physiological condition of the body itself. Nevertheless, the function of the CT afferents is still not fully known. The involvement of the cognitive aspects of tactile stimulus has also been raised by Olausson et al. (2002). In addition, more plausible is that CT afferents are involved in limbic functions particularly the emotional aspects of tactile stimulation because of the neuronal activation.

Slowly moving and innocuous skin deformation is common in skin-to-skin contact between individuals as a part of affiliative behavior (Vallbo et al., 1999) which supports the hypothesis that CT fibers are involved in affective touch. Moreover, CT afferents can be a system guarding the persons well-being and signaling reward when being close to a partner, friends, families and loved ones in form of the hormones: endorphins, released for example when grooming, and oxytocin, released for example when touching (McGlone et al., 2007).

A recent experiment was carried out by Lloyd, Gillis, Lewis, Farrell, and Morrison (2013) to investigate where on the body and at what speed the subjects rated the

degree of pleasantness highest. The four different experimental conditions were; (1) stroke the back of the hand (hairy skin) with a velocity of 30 cm/s, (2) stroke the back of the hand with a velocity of 3 cm/s, (3) stroke the palm of the hand (glabrous skin) with a velocity of 30 cm/s, and (4) stroke the palm of the hand with a velocity of 3 cm/s. The hand of the subject was placed within a black box, out of sight of the subject but visible for the experimenter. Then a rubber hand was placed beside the box, in sight for the subject. Before the subjects´ hand was stroked the subject was told to locate the hand position within the box by stopping the experimenters' finger, moving over the box, when above the hand. This procedure was also carried out after the stoking. The experimenter marked the subjective feeling of the position, and noted the actual location (objective measure). The subjects' hand was then stroked by the index finger of the experimenter for two minutes and then the subject rate the degree of pleasantness. The degree of pleasantness was expressed verbally on a 7-likert scale, from (+3) agree very strongly to (-3) disagree very strongly.

At the velocity of 3 cm/s the subject rated a higher subjective feeling of the hand´s position. In other words, the subject´s verbally rated feeling of the hand position was close to where the hand actually was placed in the box (Lloyd et al., 2013). Regardless of the velocity of the finger stroking the subjects' hand no effects were found in the objective measure of the hand position. In contrast, the side of hand being stroked affected the objective measure of where the hand was located; when stroking the hairy skin (back of hand) the performance was better.

The subjective ratings of pleasantness were also higher in the hairy skin, maybe because it is where the CT afferents exist (Lloyd et al., 2013). The stroking/ touch with the velocity of 3 cm/s gave a positive response both when the subject was stimulated in the hairy skin and the glabrous skin. In short, the results of the "study indicate that emotional feelings,

particularly those related to pleasant touch to the body, are a key moderator of subjective body ownership" (Lloyd et al., 2013, p. 6-7).

Neuronal Aspects of Touch

The neural aspects of touch will now be presented. As noted earlier, the focus will still be on the cutaneous sense although the overall (pathways of) somatosensory system and the proprioceptive sense are briefly described.

Moreover, as the distinction between discriminative touch (figure 1:E) and affective touch (figure 1: F) is not always clear-cut in some studies this means that there will be some overlap between the various sections, even though differentiation will be attempted where possible.

Pathways of the Somatosensory System (Figure 1: A)

The first cortical regions involved in the perception of touch are the primary somatosensory system (S1) and the secondary somatosensory system (S2) (Blatow, Nennig, Durst, Sartor, & Stippich, 2007). S1 is located within the postcentral gyrus of the parietal lobe and has an organization of body representations, called somatotopic organization map. Sensory stimulation applied to one side of the body surface, i.e. the skin, is transmitted from the skin via primary afferents (such as A-beta and C-fibers) to the ventral posterior lateral and medial thalamic nuclei and further to S1, where the impulses arrive at the contralateral side of the stimulus.

Moreover, S2 is located in the parietal operculum and has, similar to S1, a somatotopic organization map, even if the organization of S2 seems to be more diffuse or complex than the somatotopic organization of S1 (Blatow et al., 2007). S2 and the ipsilateral S1 are reciprocally connected via corticocortical connections, but recent research suggests direct thalamocortical projections to S2. In other words, the processing of a stimulus

(unilateral to the skin) is first transmitted via thalamocortical connections to the contralateral side of S1 and S2 from where, after some intrahemispheric integration, the information is relayed to ipsilateral S1 and S2 cortices via corticocallosal connections from the S1 to the S1 and the S2, and also from the S2 to the S2 for further intrahemispheric integration (Blatow et al., 2007).

The somatotopic map, both found within the S1 and the S2, is also called the somatosensory homunculus, which means 'the little man' (Pinel, 2009). It receives sensory information from all parts of the body. This has been shown when different areas of S1 have been stimulated, and depending on area stimulated a sensation of touch appears at different locations of the body. In other words, the map in the brain responds to specific areas of the body surface (see figure 2). Depending on how large the representation of the body part is within the map, the sensitivity to stimuli differs – the larger the representation is, the more sensitive the body part is. The somatotopic organization of S2 is located more ventrally to S1 in the postcentral gyrus; however, S2 receives most inputs from S1. The inputs arriving at S1 are mainly contralateral inputs; in contrast, the inputs arriving at S2 are mainly from both sides of the body. Nevertheless, the main part of the outgoing information from both S1 and S2 goes to the association cortex of the posterior parietal cortex.

Serino and Haggard (2010) highlight plasticity within 'the homunculus' in S1. When amputation or elongation is performed or when the afferent nerves are severed and do not reach all the way from the skin to S1, then the homunculus shows plasticity. For example, if a person has one hand amputated, the nearby body parts, represented in the homunculus, evolve and take over the place of the amputated body part. In this case, the forearm and eyes evolve and replace the hand represented in the homunculus (see figure 2). However, experiences also affect the plasticity and representation of the homunculus in the S1; e.g. a

blind person who reads Braille has a larger representation of the finger used when reading (Serino & Haggard, 2010).

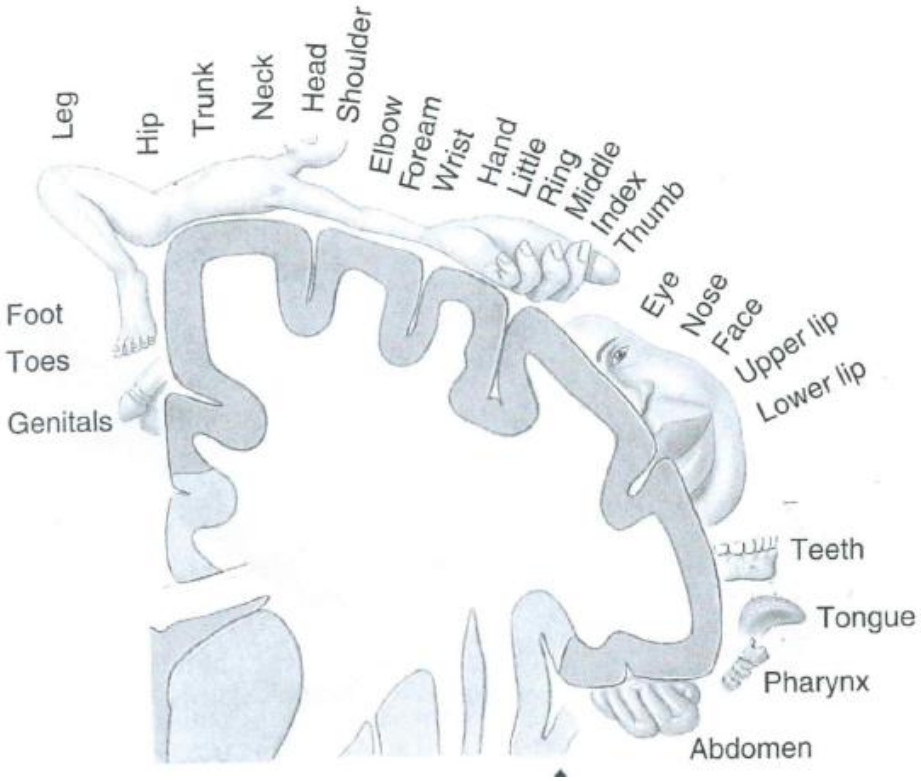
Blatow et al., (2007) studied healthy subjects with unilateral non-painful tactile stimulation produced by a tool on lips and fingers (two body parts especially sensitive to touch, see figure 2). After the stimulus had been applied at a particular body side the subject was told to locate the body site of the stimulation. The subject performed four blocks: (1) stimulus to the left finger, (2) stimulus to the right finger, (3) stimulus to the left part of the lip, and (4) stimulus to the right part of the lip. After the stimuli the subject rested. During all blocks and when the subject rested the subject was scanned with a functional magnetic resonance imaging (fMRI) scanner.

The result from the study showed higher activation within the contralateral side of S1 and S2 than on the ipsilateral side during stimulation to the fingers and the lips (Blatow et al., 2007). Unilateral stimulation of the lips resulted in activation in contra- and ipsilateral S1 and S2 in expected somatotopic locations. The detection frequency of S2 activation was significantly lower than that of S1 activation. Moreover, the location of S1 activation during lip stimulation was localized caudally of S1 activation during finger stimulation. S2 activation was also caudally localized during lip stimulation in relation to activation in S2 during finger stimulation. Further, there was no significant difference between the activation depending on which side was stimulated.

As for the unilateral stimulation of the lips, the unilateral stimulation of the fingers resulted in contra- and ipsilateral S1 and S2 activation in expected somatotopic locations (Blatow et al., 2007). The detection frequency, however, was significantly lower for ipsilateral S1 activation than for contralateral S1 and bilateral S2 activation. S1 activation was located in the postcentral gyrus of the parietal lobe and S2 activation was located more caudally in the parietal operculum and was clearly distinguishable from the activation of S1.

In sum, the ipsilateral S1 produces stronger activation in processing lip stimulation than finger stimulation. In addition, S2 finger and lip representations were found in overlapping regions. The latter suggests a less defined somatotopic representation within S2 than within S1 (Blatow et al., 2007).

Figure 2 - Homunculus



(Figure retrieved from Pinel, 2009, p. 175)

Similar to the visual and the auditory sensory systems, the tactile system has at least two pathways within the brain: one which corresponds to the location of the objects "where" and one which corresponds to the identification of the objects "what" (Reed, Klatzky, & Halgren, 2005). Results from Casellis´ studies (as cited in Reed et al., 2005) of humans with lesions in the ventrolateral somatosensory system like the inferior parietal regions, but with intact S1, show a reduced ability for humans to recognize objects but not to localize the objects within the space. In contrast, humans with lesions in the more dorsal part

of the somatosensory cortices such as the precuneus (part of the parietal cortex) have problems locating and interacting with the objects but not to recognizing them.

As within the visual system the "where" path (locate) is located dorsally within the somatosensory system; from S1 to the posterior parietal lobe (De Santis, Spierer, Clarke, & Murray, 2007). The posterior parietal lobe is identified to process information about the localization of the object in the space, therefore the pathway is called the "where" pathway. The "what" (recognize) pathway is located ventrally within the brain and goes from S1 to S2. Since S2 has been identified to process texture and form to recognize objects it is called the "what" pathway.

In general, integration and interaction between the five sensory systems has been accepted. However, this research area is large and the integrations between the five systems are complex and their discussion is outside the scope of this essay. Nevertheless, brief discussion of the visual and auditory systems integration with the tactile system is of some interest here.

When the tactile information is not limited but gives details and a clear stimulation to the skin or when the tactile stimuli are easy to detect integration between the visual and tactile systems is not needed, since the effectiveness of producing a unimodal, tactile, response is high as well as the ability to discriminate stimuli (Serino & Haggard, 2010). However, visual information, which is not related to an external stimulus, is used to boost the tactile sensation e. g. over the skin when stimuli are more complex. The visual information defines the context of the tactile sensation and the location of the stimulus. It also seems like the receptive fields within S1 decrease when visual information is added, maybe because it is easier to localize the stimulus when using two sensory systems. Serino and Haggard (2010) suggest unimodal brain processing where the different sensory systems are processed within the specific brain region responding to that sense, e. g. touch in S1. Then

Serino and Haggard (2010) suggest that the information is further processed via multisensory brain areas integration where the systems, e. g. visual system and the tactile system, integrate the information in the parietal and pre-frontal cortex. Gallace and Spence (2008) also suggest that the parietal cortex integrates information from the five sensory systems to create a holistic picture of the external world and the stimulus applied to the body.

It is perhaps worth mentioning at this point that the superior colliculus consists of several layers which respond to different kinds of stimuli. Since the early 1980's, research suggests that the superior colliculus integrates and processes multisensory information at the deeper layers and processes unimodal sensory information at higher layers, at least -within cats and primates (Meredith & Stein, 1986). Nevertheless, this is not the focus of the review and will not be further explored.

Yau, Celnik, Hsiao, and Desmond (2014) have studied the contributions of the visual and the auditory systems' pathways to the tactile system pathways using transcranial direct current stimulation (tDCS). To localize objects the researchers used a grating-orientation-identification task where the subject should discriminate the orientation of a grating produced by a machine and when rotate a disk at the top of the machine the grating orientation changed (Zangaladze, Epstein, Grafton, & Sathian, 1999) and in this study the gratings were either vertical or horizontal (Yau, Celnik, Hsiao, & Desmond, 2014). This task was performed at the subjects left finger pad before, during and after application of tDCS over the visual cortex versus the auditory cortex. Application of tDCS over the visual cortex, but not over the auditory cortex, improved the localization of the tactile object temporary but strongly. In contrast, using two equally intense vibrotactile tones as stimuli and delivered these to the subjects left finger (Yau, Olenczak, Dammann, & Bensmaia, 2009) during application of tDCS over auditory cortex and visual cortex, the subject was told to discriminate the highest frequency of the two tones (Yau et al., 2014). Application of tDCS

over the auditory cortex resulted in improvements of the sensitivity of vibration frequencies to the finger but not when tDCS was applied over the visual cortex. Last, the results show that the systems somehow work together and are not separate modalities and that the systems have two pathways processing location and recognition of objects.

Proprioceptive Sense (Figure 1: B)

The proprioceptive sense gives signals about the limbs' positions and movement, also the sense of balance, tense and effort (etc.) and function even though the limbs cannot be seen (Proske & Gandevia, 2012). For example, even when humans close their eyes, or when it is dark, they know where their arms and legs are in space but also in relation to each other. However, the visual and proprioceptive sense do work somehow together, since moving and reaching towards something needs both visual and proprioceptive feedback (Proske & Gandevia, 2012). Using electrical vibration stimuli to the muscles can disorientate the sense of limb position and affect the persons´ movement since the spatial location in the space is disoriented. Moreover, the body map in the brain allows the body to recognize the limbs as part of the body and it discriminates the shape and the exact location of the limbs, both when moving and when holding still.

Proprioceptive information is transported from the area signaling the position of the limbs, through the spinal cord via the medulla and to the cerebellum, then further to the cerebral cortex or primary somatosensory cortex (Stillman, 2002). If the area signals movement the inputs go to the primary motor cortex which in turn sends information to the somatosensory cortex and gives feedback to the limb moved, or that the limb should move.

Cutaneous Sense (Figure 1: C)

In the following section the neuronal aspects of discriminative and affective touch will be described. However, in order to facilitate interpretation of some of the research

to be presented it is necessary to first clarify the distinction between the frequently used terms active touch, passive touch and intra-active touch.

Active, intra-active and passive touch (figure 1: D).

One can differentiate between body parts touching other people or objects and body parts being touched by other people or objects. Both types of stimulation influence and contribute to the perception of the touch experience and activate different brain areas (Bolanowski, Verrillo, & McGlone, 2004). Touching someone or something can also be differentiated from touching oneself and being touched by others. The convention is to describe, touching someone else or something as active touch, because the subject actively touches someone/something and that gives the subject an impression of the person or object being touched. On the other hand, being touched by someone or something else is called passive touch and it evokes a subjective percept that refers to the internal sensation confined to oneself. When one touches oneself the touch is called intra-active touch.

Studying active and passive touch Yang, Wu, and He (2011) used an automated tactile stimuli presentation system which could control a subject´s finger movement orbit and select the location of the stimulus. The tactile system moved the finger with a particular speed on a circular or linear orbit with a tactile pattern. There were 12 different tactile pattern randomly presented 120 times 10 s per trial within two tasks which were carried out while the subjects were scanned by an fMRI scanner. The first task was with the automated tactile stimuli presentation system, so the subjects did not move their finger on the orbit by themselves (passive touch) but the system did. During the first task the tactile pattern was on a primary device from the system. Moreover, the other task was without the tactile system, however, the same orbit; the subjects moved their fingers and explored the tactile pattern by themselves (active touch) on a plastic board instead of the device. As a result, the passive movement (with the tactile system) activated the left primary motor cortex, the left

supplementary motor cortex and left pre-motor cortex, both S1 and S2 on the left side and also the right cerebellum. Nevertheless, the finger movement without tactile system (the active touch) activated almost the same cortical areas. However, there was little more activation within the primary motor area and the right cerebellum, even if there were no significant differences.

Brain activation was also measured when ten right-handed healthy subjects performed six tasks (Zaman, Moody, McGlone, & Roberts, 2001). The first task was to stroke wood with the fingers of the right hand and then rest (1). Next was to stroke velvet with the fingers of the right hand and rest (2), and alternatively stroke the wood and the velvet with the fingers of the same hand (3). Fourth task was to stroke another person to the back of the left hand with the fingers of one's right hand and then rest (4). Fifth, use one´s own finger of the right hand to stroke the back of the left hand of oneself and rest (5). The sixth task was to passively watch another person using the right hand fingers to stroke one´s own right hand fingers and then rest (6).

Stroking wood (1) and stroking wood or velvet (3) with the fingertip of right hand produced activation in the primary motor cortex, the sensory-motor cortex, the supplementary motor cortex and the cerebellum, all contralateral to the hand executed the task (Zaman et al., 2001). However, only stroking the velvet (2) produced activation in ipsilateral sensory-motor cortex. Stroking another person (4) produced activation in the motor and the sensory-motor cortex, similar activation as to the stroking of wood (1) and velvet (2). When the subject was stroked by another person (6) the ipsilateral dorso-lateral pre-frontal cortex (BA45, BA46) was significantly activated as when the subject was stroking another person (4) but not when the subject stroked them (5).

The results indicate that the pre-frontal cortex (ipsilateral dorso-lateral pre-frontal cortex) only activates when the subject interacted with another person (Zaman et al.,

2001). This suggests that the pre-frontal cortex activates when a person is interacting with another person but not when touching oneself.

Furthermore, Yang et al. (2011) also tested the brain activity using fMRI when two subjects discriminated shapes by touching 12 different tactile patterns, first by active touch, touch the patterns by themselves, and then by passive touch, using the automated tactile stimuli presentation system to touch the patterns. The speed of the finger movement was similar in the active and passive conditions. The right finger touched the first pattern for three seconds and then the next for three seconds. After that the subjects had two seconds to decide whether or not the two patterns were the same, this constituted one block. When one block was carried out the subject rested for 30 s and no stimulus was given. In total, there were six blocks given both for the active and passive touch.

The areas mort markedly activated by the passive and active shape discrimination task were: S1 in the postcentral gyrus of the parietal lobe, further, this projected bilaterally into S2, the superior parietal lobe (SPL), the supplementary motor area (SMA) in the precentral gyrus, the prefrontal cortex (PFC), the intraparietal sulcus (IPS), the lateral occipital complex (LOC), the thalamus, the insula and the cerebellum (Yang et al., 2011). However, the posterior parietal cortex, the intralparietal sulcus, the cerebellum, the PFC and the LOC showed more activation during the active touch than the passive touch. These results suggested that the performance of active touch by the finger was greater than that of passive touch, but only when the difference of the two patterns within the block was greater.

Bolanowski, Verrillo, and McGlone, (2004) tested how six blind-folded subjects perceived the size of nine different steel balls when rolling them between the fingers or other body parts. The subject moved the steel balls in circulating movements between the body parts, which the experimenter had chosen, for as long as they wished (usually five

seconds). The nine balls were given in a random order in three blocks, were all nine balls were included in all three blocks. The subject was told to express their subjective experience of the size of the steel balls in a number. The blocks were carried out both with active, passive and intra-active touch. In one condition the steel balls were placed between the right finger pad and the left thumb pad (intra-active touch), another was rolling the steel ball between the right forefinger and the left thenar eminence (group of muscles on palm of hand at the base of the thumb) which is a passive body part. A passive body part means that the different axons and receptors (mentioned in physiology of touch) in the hairy skin is less sensitive to the discrimination of shapes; however, this body part was passively touched by the finger. A third condition was between the right forefinger and the left volar forearm, which is also a passive body part.

Next Bolanowski et al. (2004) tested if both body parts contributed to the perception of the size of the steel balls by letting the subject roll the balls between their right forefinger and another person´s thenar eminence and then the other way around; the other person´s finger and the subject´s thenar eminence. As a result, the researcher found that the passive rolling on the thenar eminence could signal the size of the ball but not the finger rolling to another person´s thenar eminence. However, the result of the study showed that in the absence of an active movement the subject can perform well just by passive touch, even if both the passively and actively touched body parts contribute to the overall perception of the intra-active touch.

In other words, touching something or someone with the fingertip, or hand, produces a different sensation than if the fingertip, or hand, is being passively touched (Bolanowski et al., 2004). In contrast, such a different sensation does not occur when the forearm (or hairy skin of another body part) actively touches another object or person neither when the forearm is passively touched by the object nor person.

Discriminative touch (figure 1: E).

Trulsson et al. (2001) as well as McGlone et al. (2002) studied the somatotopic representation of vibrotactile stimuli, produced by a waveform generator, and microstimuli, produced by a stimulator, applied through a electrode to the digits. The researchers isolated a mechanorecpetive afferent and characterized the function (fast adapting or slow adapting) of that single afferent (Trulsson et al., 2001). The researcher tried to microstimulate the same afferent and later use fMRI to establish the cerebral activation associated with repeated stimulus. However, the researcher also used fMRI to establish the activation of mechanical vibration stimulus to the receptive field of one unit. The microstimulation pulses were carried out by the experimenter and the amplitude increased from zero until the subject felt a sensation. When a stimulus was felt the subject reported the location of the stimulus on the hand surface. Additionally, a new electrical stimulus was applied and if the subject reported the same location the shape, size and quality of that stimulus was described. If the subject did not report the same location the receptive field was not the same and the unit was leaved out. The same process was carried out with vibrational pulses even though they were made by a plastic tip.

Furthermore, the microstimulation was given by the experimenter within 20 trials, where the on period lasted for 16 s, whereof the first 0.5 s included a stimulus and the following 0.5 s did not, and then the off period lasted for 16 s (McGlone et al., 2002; Trulsson et al., 2001). Vibrotactile stimulations were applied to the tips of digit 2 and 5 of the left hand and were applied during 8 s and then the subject rested for 24 s. This sequence was also applied 20 times.

Finger vibrotactile stimulation produced significant activation in contra- and ipsilateral S1, and S2, the posterior insula, the posterior parietal region, the pre-central gyrus (locus 4 & 6 in primary motor cortex) and the posterior cingulate cortex (McGlone et al.,

2002). Moreover, the activation was significantly greater for contralateral activation compared to ipsilateral activation in all the mentioned areas except S2 and the pre-central gyrus. Furthermore, activation within the parietal operculum (S2 is a part of this region) was found in response to intense vibrotactile stimulation. Trulsson et al. (2001) showed a similar result for vibrotactile stimulation. Vibrotactile stimulation activated S1 and S2, the posterior parietal and the insular cortex, the motor cortex and the precentral gyrus (Trulsson et al., 2001).

In addition, during vibrational stimulus the primary somatosensory cortex (S1) response is widespread but over time it concentrates toward the region to which afferents specifically serving that skin region project (McGlone et al., 2002).

Microstimulation of LTMR of A-beta afferents showed most activation in S1 and S2 (McGlone et al., 2002). However, only more circumscribed areas within S1 and S2 were activated (Trulsson et al., 2001).

These results indicate that the responses in somatosensory cortices to rapidly repeated tactile stimuli are not static but change over short periods of time (McGlone et al., 2002). Discriminative touch in the glabrous skin of the thumb showed activation in both S1 and S2 (Trulsson et al., 2001). However, in S1 there were two clusters, one located near the postcentral gyrus (fairly deep on the anterior wall) and the other in the gyral crown, the latter was more varied within the different subjects whereas the first was more stable. This suggests that the brain activation can change, not just over time, but also vary within subjects (Backlund, Morin, Ptito, Bushnell, & Olausson, 2005).

Comparing subjects with hemispherectomy and healthy subjects and their brain responses during discriminative touch indicates – that the brain has capability to change which shows the plasticity suggested earlier (Backlund et al., 2005). Subjects with hemispherectomy have only one cerebral hemisphere and one outcome of that is paresis in

some limb(s) (Pinel, 2009). However, in the study briefly described here, the paresis in each subject does not affect the subjects´ ability to walk (Backlund et al., 2005).

In this study the researcher applied three different stimuli; (1) sliding stimulus, a half-cylinder covered in soft material, (2) a metal tip attached to the skin and pulling in one direction and (3) a rolling stimulus consisted of a wheel (Backlund et al., 2005). These stimuli were applied to the skin of both the paretic side and the non-paretic side of the hemispherectomy subjects and the similar sides of the healthy subjects. The subject was then told to localize the direction of these stimuli; forwards or backwards, up or down. Another stimulus the researcher used was monofilaments touching the skin for two seconds and then the subject reported feeling the stimulus or not. Further, the subject was told to rate the intensity of the monofilament from ‘no sensation’ to ‘the strongest sensation’ on a horizontal line.

Subjects with paresis had difficulties in determining the direction of the sliding and rolling stimuli on their paretic side, even though they performed equally well as the normal subjects on their non-paretic side (Backlund et al., 2005). Nevertheless, discrimination of the direction of the skin pulling at the patients’ paretic side was poorer than within the normal subjects, but not when pulling the skin of the non-paretic side; hence the subjects with paresis performed as well as the healthy subjects. Feeling the monofilaments did not show a significant difference neither between the normal subjects and the subjects with paresis, nor within the subjects’ paretic side and non-paretic side. Finally, the paretic subjects rated the intensity of the stimuli higher both on the paretic side and the non-paretic side in comparison to the healthy subjects, and higher within their non-paretic side versus the paretic side.

This study shows plasticity of remodeling of the brain to have some ability to process complex tactile functions. Previous studies with the same hemispherectomy patients

show activation in S1 and S2 areas when the patients were stroked by a brush and a painful stimulus was applied to the patients, regardless of which side of the patient, paretic or non-paretic side, were stimulated (Olausson et al., 2001). Information about the location and direction is signaled by the LTMR afferents of the discriminative touch; however, it seems like connections to the hemisphere within these patients are still intact, at least with one hemisphere. That may be sufficient for tactile discrimination, because the patient´s ability to discriminate some direction of the stimuli applying to their body (Backlund et al., 2005).

So, overall, there is evidence that S1 and S2 receive information from A-beta axons and have a role in discriminative touch (Olausson, Wessberg, Morrison, McGlone, & Vallbo, 2010).

Affective touch (figure 1: F).

A general problem when studying touch is that it is difficult to know which axons are stimulated by what stimulus. Therefore, different researchers have tested different types of pleasant, neutral and painful (noxious) stimuli in relation to each other for the ability to discriminate different brain areas responding to different stimuli.

Kida and Shinohara (2013) used near-infrared spectroscopy (NIRS) to studying the neuronal activation when stroking the hairy skin of the forearm and the glabrous skin of the hand of thirty- one subjects. The researcher used three different materials to produce sense of touch. A piece of wood stroked over the skin was rated as neutral touch, and a wood stick wrapped in velvet and packed with cotton was rated as pleasant touch and a pointed stylus was rated as painful touch. The subject was told to rate the sense of pleasantness of the different materials on a visual analogical scale (VAS). The different stimuli were presented in 12 trials within blocks where the material, body part and side varied. The NIRS scanner showed activity within the orbitofrontal cortex (OFC), which later has been suggested to be involved with reward processing, and frontal- polar cortice (a part of the prefrontal cortex),

which has been suggested to be involved to monitor and evaluate tactile-induced pleasantness, social behavior and thinking about psychological attributes of people regardless self or others. However, there was no significant difference in activation between the pleasant touch (velvet) and the neutral touch (wood). What was shown was that the OFC and the frontal-polar cortice are involved in the pleasantness produced by gentle touch.

Rolls et al. (2003) studied the neuronal activation within nine right-handed subjects when using velvet as a pleasant touch stimulus, wood as neutral touch and a stylus as a painful stimulus. The different stimuli were rotated over the subjects´ left palm with different intensity and rate of pleasantness.

The fMRI data showed that an affectively pleasant and less intense stimulus activated the OFC greater than a more intense, but still affectively neutral stimulus, did (Rolls et al., 2003). However, the intense (physically strong) and affective neutral stimulus resulted in greater activation of S1 than the pleasant stimulus. The affectively unpleasant pain stimulus did also show greater activity in the OFC than the neutral stimulus, whereas the neutral stimulus showed greater activation in S1 than the painful stimulus. In other words, the neutral stimulus resulted in a significantly greater activation in S1 than the painful and pleasant stimuli did, whereas the painful and pleasant stimuli resulted in a significantly greater activation in the OFC than the neutral stimulus did. These results suggest that there are dissociations between brain areas activated during affective aspects of touch and the non-affective aspects of touch. The dissociation between brain areas may be because the results indicate that the OFC becomes activated by affective stimuli and not the physical strength, whereas S1 is more activated by the physical strength than the affective stimuli. Further, these results provide support for the OFC to have a role in understanding emotions (Rolls et al., 2003). Rolls (2000) suggests that emotion can be stated referred to as being like a reinforcer; rewards (as pleasant touch which animals seek) and punishment (as pain which

animals will avoid and escape). Further, the function of OFC is to decode and represent innate reinforces and learn associations between learned and innate reinforces (Rolls, 2000).

So, during touch experiences subjectively valued as neutral, painful and pleasant S1 becomes activated contralateral to the hand (limb) being touched (Rolls et al., 2001). However, in the pleasant and painful conditions the contralateral OFC is more activated than in neutral touch.

Furthermore, an fMRI scanner was used to investigate the brain areas activated during innoxious tactile stimuli and noxious stimuli (Maihöfner, Seifert, & DeCol, 2011). A plastic projectile produced a tactile or painful stimulus on the skin surface and by applying different kinds of velocities different intensities were produced. The stimuli were given within five blocks lasted 21 s with a stimulus and 21-31 s for rest. The fMRI scanner showed that the innoxious tactile stimulation activated the contralateral S1, the ventrolateral pre-frontal cortex (PFC), the parietal association cortex, the interior parietal lobule, S2, the dorsolateral PFC and the insula and showed deactivation in the OFC and the posterior cingulate cortex (pCC)**.** However, the noxious stimulation resulted in significantly greater activation in the contralateral S1, the ventrolateral PFC, the bilateral parietal association cortex, the interior parietal lobule, S2, the dorsolateral PFC and the ipsilateral insula. Increased activation during noxious stimulation versus innoxious (tactile) stimulation were shown in the ipsilateral anterior insula, and the ventrolateral PFC. Further, the activation in ventomedial PFC, OFC and pCC was equal within the stimulations.

Pain (figure 1: G).

Cutaneous pain is pain deriving from the skin surface and the tissues within the skin serving pain – nociceptors – correspond to both A-delta fibers and C fibers (Jarvis, 2008). In general, pain is mainly divided into acute pain and chronic pain. Acute pain is pain of short duration, often when a person suffers injury and the tissues within the skin get

damaged (Taylor, 2012). However, acute pain tends to decrease when e.g. an injury is healing. When the pain lasts for more than six months it is generally classified as chronic pain. Chronic pain does not generally decrease – like the acute pain, because chronic pain is somehow beyond healing (Brannon & Feist, 2010). There may be no actual apparent tissue damage and the person does not adapt to the pain. Chronic pain does not generally decrease with time and while treatment may help, it is often just for the moment (Taylor, 2012). Chronic pain varies in severity which means that different amounts of muscle groups are involved with the pain. Furthermore, chronic pain is not directly caused by a painful stimulus applied to the skin but acute pain is.

Moreover, pain can also be external and internal. External pain is when a stimulus is applied to the body and internal pain is pain derived from bodily organs within the body. Pain in this context (this essay) is referred to the external stimuli applied to the body surface, pain derived from external stimulation, pain as touch.

Information from A-delta fibers derived within the brain gives a short and sharp pain with a specific location, called first pain (see figure 1: K). The information about pain from C fibers reaching the brain includes a more diffuse and aching pain, which is still felt even after the painful stimulus is gone, called second pain (see figure 1: L). The pain information from both the A-delta and C-fibers is transmitted to the spinal cord which is divided into different layers of nerve cells, also called lamina. The first and second lamina form the substantia gelatinosa (Brannon & Feist, 2010) and retrieves sensory information from different body parts (Jarvis, 2008). The pain sensation goes two ways, one goes from the receptors within the skin to the spinal cord where an action sends out as a response e.g. reflexes (Taylor, 2012). The other sensory way goes via the spinal cord and continues to the brain and thalamus where the perception of pain is experienced.

Pain stimulation on the skin activates nociceptors which transport the impulses to the spinal cord (Taylor, 2012). Within the spinal cord the impulses cross over to the other side and are transmitted through the dorsal horn to the anterolateral spinothalamic tract towards the brain (Jarvis, 2008). From the medulla, at the reticular formation, the impulses are sent to the thalamus (and hypothalamus) and further to the cerebral cortex (Taylor, 2012). Within the cerebral cortex the impulses are identified as pain and the brain localizes from where the pain is coming. When knowing the localization of the pain the brain can send impulses to reduce the pain via the periductal gray in the midbrain which has connections to the reticular formation which in turn has connections to the dorsal horn and the lamina 2 in the spinal cord.

Within the dorsal horn the A-delta and C fibers go different ways (Taylor, 2012). The A-delta transmission, which is suggested to include the sensory aspects of pain, arrives at the thalamus and further to S1 and S2, whereas the C fibers, which are suggested to include the affective and motivational aspects of pain, arrive at another part of the thalamus and further to other areas within the cerebral cortex (Taylor, 2012). Furthermore, the experience of pain depends not just on the nature of the actual physical stimulation and source, but can be modulated by other factors including the context where the individual is, since the information from all senses is put together within the cerebral cortex, and the balance between A-delta fibers and C fibers. Also, negative emotions affect the experience of pain; pain gives negative emotions but negative emotions create stronger feelings of experienced pain. The sensitivity to pain can also depend on the location of the body part in the homunculus, more receptors make the limb more sensitive to touch (see figure 2).

Before neuroimaging techniques had evolved Melzack and Wall (1965) developed a theory of how the pain was transmitted and interpreted, called the Gate Control Theory of Pain (GCT) (Gurung, 2014). The main aspect of the theory was the hypothesis that

there exists a control mechanism, which the researchers referred to as a ‘gate’, in the spinal cord that allows an interaction between bottom up information from the peripheral sensors and top down processes, signals from the brain.

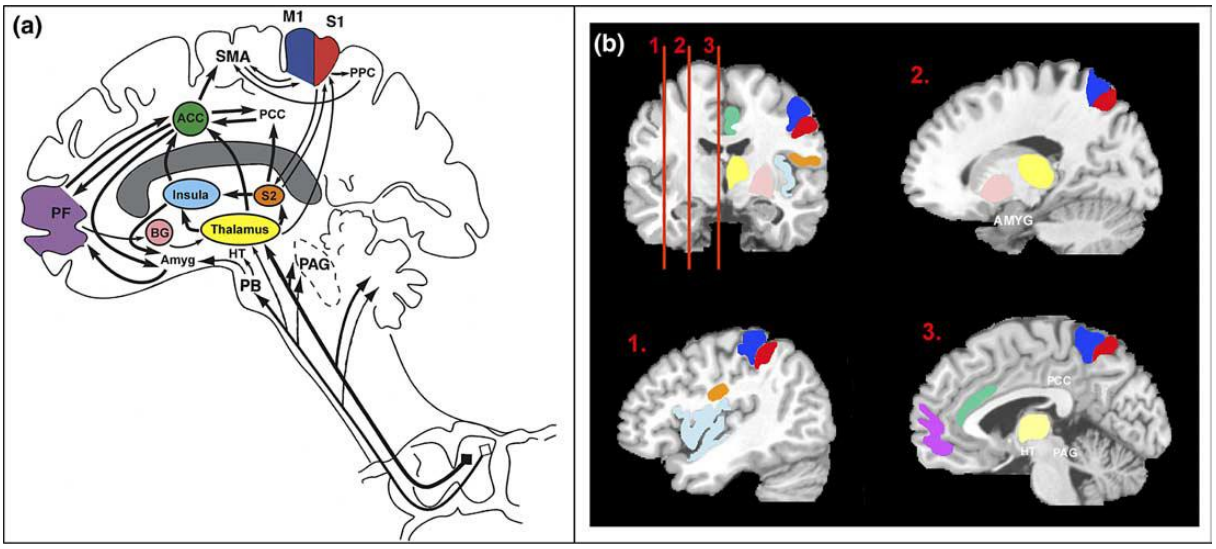
Melzack and Wall (1965) suggested that the main part of the individual´s actions to reduce pain was executed within the dorsal horn and lamina 2 which were affected by the brain (Gurung, 2014). The gate was suggested to exist within the dorsal horn, in the spinal cord, where the impulses from the peripheral neurons arrived and were further transported to the brain. Within the dorsal horn there were four different types of fibers dealt with the pain impulses; A-beta fibers, A-delta fibers, C fibers and interneuron – which were the gate neurons. The GCT claimed that the A-beta fibers transmitted the fast and sharp pain to the brain. They also activated the gate neurons; means they closed the gate in the spinal cord and the information transported from the dorsal horn to the brain was stopped, which gave a result of no perception of pain (Gurung, 2014). On the other hand, the A-delta and C fibers transmitted the slow and aching pain impulses to the brain and prevented the gate neurons to close and when happened; the brain percept pain. In contrast to current research indicating that it is only the A-delta (fast pain) and C-fiber (slow pain) which transmit pain impulses (e.g. Weiss et al., 2008).

In short, when the gates are open they transport the pain impulses to the brain via the spinal cord (Brannon & Feist, 2010). When the gates are closed the pain impulses are neither transmitted to the spinal cord (the impulses are inhibited) nor to the brain, and because of that the person does not experience pain. To close the gates the A-beta fibers must be stimulated which prevented the pain enters the brain. Since, when a person feels pain he/she rubs or scratches the place on the skin where the pain comes from, which stimulates the A-beta fibers which in turn activate the interneuron and close the gate (Gurung, 2014). If the A-beta fibers are not stimulated then impulses from the brain or activation in the spinal

cord can close the gates. Later research has confirmed that electrical stimulation to specific brain areas can inhibit the pain sensation as well as psychological factors (Gurung, 2014).

Apkarian, Bushnell, Treede, & Zubieta (2005), on the other hand, explain the transmission of the pain perception in more neuronal terms. They suggest that the pain impulses are transported from the skin and its receptors via the spinal cord to the brain. When the impulses arrive at the cerebral cortex there are both cortical and sub-cortical areas involved in the perception of pain. As mentioned before the pain takes two pathways, but Apkarian et al. (2005), in contrast to Taylor (2012), explain the pathways from thalamus further into the brain. The thalamus receives the pain impulses first and from the thalamus the impulses are transmitted further to S2, the insula, S1 and the anterior cingulate cortex (ACC) (Apkarian et al., 2005). Furthermore, from S2 the impulses are transmitted also to the insula and S1 but also further to the posterior cingulate cortex (pCC). The impulses reaching the insula are transported to the ACC and the amygdala and when reaching the amygdala the impulses are transmitted further to the prefrontal cortex (PFC). In the PFC the impulses are transported again to the ACC and to the basal ganglia which transmit the information back to the thalamus. The ACC sends the impulses to the supplementary motor area (SMA) and the pCC and also back to the PFC and, as written before, the amygdala. The SMA then sends and retrieves impulses from the primary motor cortex (see figure 3).

Figure 3. Pain Pathways



(Figure retrieved from Apkarian et al., 2005, p. 473)

Studies on pain have been carried out on healthy subjects as well as subjects with clinical pain (chronic pain). However, there are different kinds of pain sensation and pain stimuli, such as heat, cold and electrical shocks to the skin, which have been used in different studies (Apkarian et al., 2005).

There are several things affecting the experience of pain which in turn affecting the brain activation. Pain can only be measured subjectively, which means everyone experiences pain slightly different (Taylor, 2012). Pain can be affected by factors like gender and genetics (Apkarian et al., 2005). Another factor affecting the detected activity within the brain is the imaging technique used, since the imaging techniques differ in sensibility to different areas within the brain and also how deep or low the activation is within the cortex. Analyses from pain studies used electroencephalography (EEG) and magnetoencephalography (MEG) show activation in S1, S2, IC, ACC and frontoparietal operculum. Hence, differences in activation using EEG and MEG can be a result of that MEG

is more sensitive to activation in S1 and S2, whereas the ACC activation is easier to detect with the EEG.

Things like emotions and expectations are other factors which can affect the activation in the brain. Studying the activation during modulation of pain as Phillips et al., (as cited in Apkarian et. al., 2005) did the S1, the ACC, the IC and the thalamus were activated and when subjects were distracted from the pain activation were found in the periaqueductal gray (PAG), the OFC (within the PFC) and parts of the ACC. A negative emotional state enhanced the pain- evoked activity in ACC and IC which are parts of the limbic system that were activated. Besides, the expectation of pain (in the absence of a painful physical stimulation) causes activation in regions as S1, ACC, IC PFC and PAG and cerebellum.

Pain caused by different kinds of stimuli activates both similar and different cortical and sub-cortical regions in the brain, as well as produces different kinds of experiences. In a comprehensive review, Apkarian et al. (2005) report that heat pain studies overall show activation within S1 and S2. This activation suggests that these regions are involved with the perception of the sensory features of pain as mentioned before. The ACC and the IC also gets activated during heat pain studies but are suggested to be involved with the affective part of the pain. On the other hand, the PFC and parietal association areas activation may be related to the cognitive components of the pain, such as memory. Sometimes the primary motor cortex and the pre-motor cortex are activated during heat pain and are suggested to be related to the movement reducing pain or the movement causing the pain. Other sub-cortices which are also activated during (temperature/heat) pain studies are the thalamus, the basal ganglia and the cerebellum.

Overall, studies on pain show activation within S1, S2, the ACC and the IC, nonetheless, the exact location of activation within the brain during the different pain stimuli varies (Apkarian et al., 2005). Heat studies, for example, suggest the ACC are involved in the

cognitive-evaluative stages of pain processing; such as affective reactions to pain. In contrast, cutaneous pressure (e. g. stylus picked on the skin (Rolls et al., 2003)) studies suggest the posterior part of the IC to be more related to sensory aspects of pain, whereas the anterior part of IC (which is more connected to the PFC) has an important role in emotional, cognitive and memory related aspects of pain.

Networks of structures have been identified in studies where neuroimaging techniques have been used (Apkarian et al., 2005). The structures are somatosensory structures (S1, S2, IC), limbic structures (ACC and IC) and associative structures (PFC) and these receive parallel inputs from multiple nociceptive pathways. Healthy subjects tend to transmit nociceptive information through the spinothalamic pathway; the thalamus, S1 and S2, the IC and the ACC. In contrast, the activation within the PFC seems to increase within subjects with chronic pain, which may be because the pathways goes outside the spinothalamic tract and activates the PFC. The nociceptive information which is transmitted through these pathways becomes more important for subjects with chronic pain than for healthy subjects. The activation of PFC suggests that chronic pain state has stronger cognitive, introspective and emotional components than acute pain condition has.

In addition, the first brain regions activated in response to pain are S2 and then the IC. In contrast, within tactile stimulation S2 gets activated after S1 (Apkarian et al., 2005). This suggests that S2 and the IC are primary regions for nociceptive (painful) inputs to the brain.

As mentioned briefly before, nociceptive cutaneous stimulation activates the brain through two types of afferent nerves; slightly myelinated A-delta fibers with moderate conduction velocity, and unmyelinated C-fibers with slow conduction velocity (Weiss et al., 2008). Weiss et al. (2008) investigated the neuronal responses transported by these two afferent nerves by stimulating tiny skin areas. The C-fibers stimulation is often characterized

as more non-painful than A-delta fibers stimulation is, whereas A-delta fibers stimulation is more often characterized as painful than C-fibers stimulation is. The C-fibers system inputs seem to be interoceptive (as mention in physiology section, p. 16) and homeostatic, which means the CT afferents integrate signals from the internal states (the body) and the external inputs (environmental stimulation) and have a vital role for maintaining a bodily balance – homeostasis (Olausson et al., 2010).

The result of Weiss et al. (2008) study indicates that the ACC, the posterior operculo- insular cortex, the SMA and the thalamus are associated with the processing of C-fibers input in relation to the baseline. Moreover, when reporting the feeling of stimuli S1 was activated contralaterally to hand movement. Comparing A-delta fiber input with the baseline activation in the ACC, the SMA and the thalamus were observed, as well as S1 contralaterally to the hand moved. Nevertheless, when comparing A-delta input response and C-fiber input response a complex network of structures, including those known to be involved in processing somatosensory and nociceptive information, were activated. However, the authors reported that they cannot be sure that only the C-fibers or A-delta fibers were activated, as both could have been activated simultaneously. On the other hand, there was a significant difference in large cluster of activated voxels including parts of the right anterior insula, right frontal operculum and right inferior frontal cortex (Weiss et al., 2008).

Pleasant touch (figure 1: H).

As mentioned, there is a problem in knowing which axons are activated during studies of touch. In affective touch it is important to discriminate the activation of A-fibers and C-fibers; therefore, subjects with neuronopathy have been studied. Two persons, G.L. and I.W., have been tested because of their loss of myelinated afferents; however, they experience some touch (see p. 15 in physiology). So, by studying their brain activation during

different kinds of touch the distinction between discriminative touch and affective touch can be clearer.

The insular cortex is one part of the brain which seems to have a role in affective touch. It may be because the insular cortex is considered as a gateway from the sensory systems to the emotional systems of the frontal cortex (Olausson et al., 2010). The lack of activation in S1 and S2 areas within the neuonopathy subject G. L. shows that the CT afferents mainly have excitatory projections to emotion- related cortical systems, just like the insular cortex. The peripheral afferents, A-delta and C-fibers, of the affective touch are suggested to project to thalamocortical relay nucleus which in turn project to the dorsal part of the posterior insular cortex. In the interoceptive system the CT afferents integrate signals from the internal states and the external inputs which are vital for maintaining a bodily balance. Moreover, the unmyelinated fibers have access to brain areas which control hormonal, autonomic, affective and behavioral responses which in turn can adjust the action of the organism. Later on, within the insula (more anterior in the posterior region) a re-representation of the bodily state may progress an integration of emotional salient inputs from multiple sensory systems and emotionally salient inputs from limbic cortical regions, such as the ACC and the OFC. This re-representation may report the integration of the bodily balance with the sensory environment, social conditions and motivational conditions.

It is easier to observe brain regions only responding to C-fibers when studying G.L. and I.W. (Olausson et al., 2008). When stroking I.W. left forearm (the dominant arm) with a velocity of 4 cm/s and a distance of 15 cm activation in contralateral right posterior and ipsilateral mid-insular cortices and contralateral superior temporal gyrus were observed (Olausson et al., 2008). Further, caressing in I.W. deactivated the area of the arm represented in S1 contralateral to the stimulus. However, G.L. had a deactivation in contralateral S1, bilateral S2, ipsilateral insular cortex, bilateral ACC, motor cortices, the parietal association

cortex, the prefrontal cortex and the thalamus. CT afferents activate insula and deactivate contralateral S1 which indicate that CT underpins affective (pleasant) aspects of tactile stimulation and not discriminative system, as the deactivation in S1 shows. In addition, the deactivation in ACC and S1 indicate that CT reduces pain (Olausson et al., 2008).

Impairment (or loss) in one sense gives the opportunity for other senses to evolve more which produces changes in the brain (Čeko, Seminowicz, Bushnell, & Olausson, 2013). This plasticity is also shown within the homunculus when e. g. amputation or elongation has been carried out (Serino & Haggard, 2010). The neuropathy subject G.L. (mentioned earlier) showed thinner cortex in different areas than healthy subjects did (Čeko et al., 2013). This was showed when 12 healthy subjects and G.L. participated in a magnetic resonance imaging (MRI) scan session. The primary somatosensory cortex was significantly thinner on her left side and had a similar trend on right side. Nevertheless, the insula and cingulate cortex were significantly thicker than within healthy subjects, with the most difference in right anterior insula (aINS). More, the aINS within G.L. had stronger functional connectivity with the right temporal pole and right, left mid/posterior parts of the insula than within healthy subjects. She had also weaker functional connectivity between aINS and parts of the temporal lobes and cerebellum. Moreover, G.L. had increased functional connectivity of the insula with the visual cortex and the left S1; however, she displayed decreased connectivity with parts of the parietal and temporal lobe, cingulate cortex and cerebellum. This functional connectivity differences suggests an adaptive plasticity as compensation for large-fiber afferent somatosenory denervation. On the other hand, grey matter, white matter and cerebrospinal fluid did not differ significantly between G.L. and the healthy subjects. G.L. uses her vision to know if she touches something in her surrounding, maybe explaining why the connection between insula and visal cortex is stronger.

Sensation, such as pain and temperature, transported by A-delta fibers and C-fibers, including CT, reveal activation in the contralateral posterior insular cortex but not in the somatosensory cortices (Björnsdotter, Löken, Olausson, Vallbo, & Wessberg, 2009). Brushing healthy subjects' forearm and thigh activates S1 – postcentral gyrus- with some differences between the arm and thigh (more lateral and inferior activation of S1 when brushing the forearm than the thigh) and bilateral activation of S2 with no significant difference. Healthy subjects as well as G.L. showed different activation when being soft brushed and when resting. Soft brushing showed activation in the contralateral (left) insular cortex, most parietal regions, in contrast to resting which did not show such activation. Forearm brushing showed more anterior activation in the insular cortex than the brushing of the thigh, both within the healthy subjects and G.L. with neuronopathy. The activation shows the somatotopic organization of the forearm and the thigh; the forearm more anterior to the thigh (see figure 2). The CT system contributes to the maintenance of the physical integrity and well-being (homeostasis) by relaying information about the affective tactile status of the body. From this arises the suggestion that the CT system has an important role in the sensory underpinning of social behavior and in the foundation of self-awareness (e. g. McGlone et al., 2007; Olausson et al., 2008). Maybe CT system serves a function where a gentle touch within the face evokes different emotional and motivational responses than a gentle touch on the arm does, thus signaling various affective aspects with corresponding social implications (Björnsdotter et al., 2009).

When using human skin-to-skin contact, significant differences in the ratings of pleasantness was shown between a moving hand on the skin and a hand with a rubber glove moving over the skin. The moving hand without a glove was rated as more pleasant than the hand with a glove (Lindgren et al., 2012). The result also showed a significant higher activation in the contralateral somatosensory cortex and in (or near) the bilateral insular

cortex during a moving stimulus versus a stationary stimulus. In contrast, the rubber hand moving stimulation gave a significantly higher activation within the cerebellum, whereas the human hand moving gave strongest activation in the pregenual anterior cingulate cortex (pgACC). Last, the moving hand stimulation was rated as most pleasant and showed activation in the pgACC, the stroking of the forearm (both with glove on the human hand and without) activated bilateral insular cortex, whereas there was no significant difference within the stationary stimulation of the forearm. The pgACC is therefore suggested as being involved with rewarding pleasant stimulations.

In general, it seems like discriminative touch mainly activates the primary somatosensory cortex (S1) and the secondary somatosensory cortex (S2), whereas the affective touch mainly activates the orbitofrontal cortex (OFC), the anterior cingulate cortex (ACC) and the insula cortex (IC).

To sum up the essay, the somatosensory system touch includes different types of touch. Proprioceptive touch, transported to the brain via A-alfa fibers, corresponds to limb position and gives a sense of balance. Cutaneous sense; discriminative and affective touch, is transported to the brain via A-beta respective A-delta and C-fibers. Discriminative touch corresponds to constant and temporal stimuli and provides information about handled objects, and activates mainly the somatosensory cortices. Within the somatosensory cortices a somatotopic organization map is identified, even if the map within secondary somatosensory cortex seems to be more diffuse and complex. Affective touch responds to skin-to-skin contact and slow mechanical stimuli. It also provides emotional, hormonal and behavioral responses which can adjust the action of the organism.

Pain and pleasant touch are two types of affective touch. Research from the 60’ developed a gate control theory of pain which suggests a gate control mechanism within the spinal cord which allows top-down processing. Further research has confirmed that

psychological factors can inhibit pain, but not the other parts of the theory. Pleasant touch (light touch) activates C-tactile (CT) fibers which correspond to gentle touch. When CT fibers get activated it can inhibit pain, since gentle touch produces activation in insular cortex and deactivate primary somatosensory cortex and anterior cingulate cortex, which indicate inhibition of pain.

Plasticity within the brain is shown within subjects with loss of myelinated fibers, subjects with paresis as well as within subjects who have e. g. amputated a limb.

Brain areas suggested to be involved in affective touch is the insular cortex, orbitofrontal cortex, cingulate cortex and prefrontal cortex. The insular cortex seems to have a role as a gateway from the sensory systems to the emotional systems of the frontal cortex. The orbitofrontal cortex seems to have a role in understanding emotions. The cingulate cortex is suggested to be involved with rewarding pleasant stimulations. Finally, the prefrontal cortex is suggested to activate when interacting with another person, but not when touching oneself.

Discussion

The somatosensory system retrieves information about touch applied to the skin, and the information is transported to the primary somatosensory cortex (S1), part of the postcentral gyrus, and to the secondary somatosensory cortex (S2), part of the parietal operculum. Depending on the tactile stimuli and its need to be localized or recognized the information is transmitted two ways; the ventral “what” pathway and the dorsal “where” pathway.

The somatosensory system retrieves information about two types of touch; (1) proprioceptive touch which for example signals the sense of limb position and movement through A-alfa fibers to the brain, and (2) cutaneous touch which gives information from the

exteroceptive, discriminative touch, and interoceptive, affective touch, systems. Receptors within the skin, which consists of four main layers, transform the stimuli applied the skin into electrical signals which transports to the brain via different types of axons. Discriminative touch transport electrical signals via A-beta fibers and affective touch via a-delta fibers and C-fibers. The C-tactile fibers (CT), found in hairy skin within humans, are suggested to have a vital role in social touch and give emotional, hormonal and behavioral responses to touch.

The cutanoeus touch can be applied in three different ways; actively, passively and intra-actively. Active touch is when a person is touching someone/something, passive touch is when a person is being touch by someone/something and intra-active touch is when a person touches oneself. Active touch is associated with better performance than passive touch and activates the PFC. Moreover, when a person use the fingertips or the hand to explore/touch someone/something actively another type of sensation is perceived than when passively touch the same thing. In contrast, this is not found when touching the forearm or another part of the body skin which is hairy.

If a stimulus is less physically intense and rated as pleasant the OFC is activated, in relation, when a stimulus is more physically intense and rated as neutral touch S1 is activated. People with paresis on one side rate the intensity of a stimulus higher on both the paretic side and the non-paretic side than healthy subjects do. However, the paresis cause difficulties determine the direction of sliding and pulling stimuli which is discriminative touch.

The Gate Control Theory gave a working hypothesis that gates existed within the dorsal horn, in the spinal cord, that regulate the transmission of pain to the brain. When A-beta fibers were activated the gates closed and when the A-delta or C-fibers were activated the gates opened and transmitted the perception of pain to the brain. The theory also stated that the person could inhibit the pain perception with psychological factors, which resent

research somehow have confirmed. However, resent research have found that it is mainly the A-delta and C-fibers that are activated by pain stimuli.

The main regions in the brain activated during painful stimuli applied to the skin are S1 and S2 but also the OFC, the insula and the ACC. Interestingly this is also the main areas activated during touch rated as pleasant, above all the OFC and ACC.

Overall, the discriminative touch actives S1 and S2 and are transmitted to the brain by A-beta fibers, whereas the affective touch actives the OFC, the ACC and the insula cortex. Depending on which type of affective touch the A-delta and the C-fibers get activated. Pain activates both types of fibers and pleasant touch activates CT afferents in the C-fiber system.

Further Research Directions

Blatow et al. (2007) showed that the somatotopic organization within the primary somatorsensory cortex was easier to distinguish than the somatotopic organization within the secondary somatosensory cortex. The organization within secondary somatosensory cortex was suggested to be more diffuse than the primary somatosensory cortex map, because it showed more overlap between the body part representations. The researchers indicate that S2 somatotopic organization was less define and even more complex than S1 organization (Blatow et al., 2007). Further research is needed to clarify the somatotopic organization within S2; why there are more overlapping areas, and why it is harder to define the organization. Moreover, if S2 somatotopic organization is more complex; why is it more complex than the organization within S1? Maybe the diffusion about S2´s organization depends on the deeper location in the brain, maybe not.

The CT afferents need to be better understood both physiologically and neurologically. First, further characterization of the function of the CT afferents is needed and how the pathway from the dorsal horn, in the spinal cord, goes to the brain, and where in

the brain the CT inputs are interpreted (Olausson et al., 2010). Second, it has been identified that CT afferents generally respond to pleasant and gentle touch, but what inputs actually activate the CT afferents more exactly need to be further examined. Further, Olausson et al. (2010) suggest that CT stimulation can be used to treat chronic pain in the future, if the relationship to experienced pain would be more characterized. Lindgren et al. (2012) report the pgACC involvement in human skin-to-skin contact which is also perceived as pleasant touch. This contribution of brain areas responding to pleasant touch can help future research to address the importance of pleasant touch in clinical settings, especially the effects of human skin-to-skin contact (Lindgren et al., 2012).

Moreover, the more exact locations of the CT afferents on the body need to be identified. Today it is known that the CT afferents are found in human hairy skin but not in glabrous skin (e. g. Olausson et al., 2002). What is also known is that the CT afferents exist in arms, face and legs but there are no further knowledge about to which extent the CT afferents exist and that needs to be clarified (Morrison et al., 2010).

Variables and texture affecting the experience of pleasantness are also some future directions to study (Klöcker et al., 2013). Klöcker et al. (2013) had an example to study the objective effect of different physical factors on the perception of pleasantness; for example, the effects of temperature of a stimulus when a subject uses ones' finger to explore it and how the temperature affects the ratings of pleasant perception. Essick et al. (2010) agree with Klöcker et al. (2013) that the roles of temperature on the ratings of pleasantness need to be addressed, also the receptors corresponding to temperature and their relation to the affective touch. Olausson et al. (2010) suggest the responsiveness of CT afferents should be examine in relation to cool stimulation compared to both warm and neutral temperature stimuli in a social context.

Examination of the effects of dominant and non-dominant hands (body parts) within affective touch and the emotional process are another factor that can be something to further analyze (Kida & Shinohara, 2013). This has been more studied within discriminative touch, but is not fully understood either within affective or discriminative touch.

All possible interactions between brain areas when processing information are still not clear. Earlier in the text (neuronal aspects) the integration between somatosensory system and visual and auditory systems has been stated (Yau et al., 2014). However, the extent to which these systems, and others, work together when processing multisensory stimuli are still uncertain and need to be explored (Sathian et al., 2011). How the systems and interactions between the systems are maintained and modulated need to be addressed according to Yau et al. (2014).

Furthermore, it is important to understand the complexity of activation within the brain during touch. Studying the different kinds of touch does not at present guarantee that only the afferents thought to be activated are actually activated. The afferents are included in a complex system and when studying touch it is easy to activate different afferent types simultaneously (Olausson et al., 2002). So, future research should investigate the brain areas activated during different types of touch more closely. Rolls et al. (2003) mention the investigation of the orbitofrontal cortex and anterior cingulate cortex activation during pain and pleasant touch. Questions such as; ‘which brain areas are actually activated by pain versus pleasant touch?’ ‘what do these brain areas work with?’ and ‘why do they get activated by that kind of touch?’ need to be clarified in the future.

Touch is somehow known and studied mainly within a laboratory setting but touch is something humans use as e.g. a communication system (Gallace & Spence, 2010). So, touch is used in a social context and on a daily basis. Therefore, studies in human natural environment should be carried out (Field, 2010). As mentioned, expectations and emotions

are factors that affect the experience of touch, especially pain (Apkarian et al., 2005), but also the social context affect how a person perceives touch (e.g. McGlone & Reilly, 2010). Considering these aspects, the social context is important for how a person experiences touch and the subjective experience affects which brain areas get activated during the touch, therefore naturalistic studies should be carried out.

Olausson et al. (2010) and Lindgren et al. (2012) suggest that the pleasant touch should be further examined because it can potentially be used effectively as treatment in clinical settings to reduce stress, anxiety and pain.

Why Is It Important To Know More About the Sense Touch?

Well, touch is important to understand because…

Moving around in the world humans (and other animals) use their sense of touch to interact with the external environment (Olausson et al., 2010). Touch is necessary to manipulate objects and feel the objects shape and weight, which help the person to form an opinion about how much strength needed to lift/hold (etc.) the object. CT afferents are suggested to have a vital role in social context – to maintain social bonds and to form both new and old relationships.

Debrot, Schoebi, Perrez, and Horn (2013) found that touching a partner in a close relationship has both a short-time and a long-time effect. The subjects reported affective state, which were if the person has been touching their partner or had being touch by the partner, and if the person felt a sensation of intimacy. The subjects reported this in a computerized diary every day for a week whenever an automated, pre-programmed computer/phone signal prompted the participants to answer the questions. Touching the partner and being touched by the partner was associated with increased affective state (short-time effect) whereas retrieved touch in everyday life was associated with increased long- time effects of well-being for six months after the experimental week. Moreover, touch enhances

the feeling of intimacy within the relationship which affects the mood of the persons and also the quality of the relationship.

Research has also shown that touch may increase the likelihood that the person touching gets what he/she wants. For example when a waitress touches the customer when asking what drink they would like to order, the customer is more likely to give a tip (Guéguen & Jacob, 2005) – touch that Morrison et al. (2010) call simple touch (see figure 1: M). In addition, students who were touched on the forearm by the teacher during a corrective exercise and when asked if the student wanted to explain the exercise on the blackboard, the touched students were more likely to volunteer (Guéguen, 2004).

Partners who were married or had lived together for at least six months performed an experiment (Grewen, Anderson, Girdler, & Light, 2003). In the experimental condition the couples sat together and touched each other while talking about an experience they experienced together, and then they hugged for twenty seconds. After that they were separated and were told to perform a speech, in front of a stranger, about something in the relationships which makes the subject angry or sad. The control group rested alone while the couples were together and stood alone for twenty seconds. The results indicate that the subjects within the experimental condition showed significantly lower blood pressure and heart rate when performing the speech in relation to the subjects within the control group (Grewen et al., 2003). Interacting positively with a close person has an effect on blood pressure and heart rate responses to a stressful stimulus, such as performing a speech. This is touch that Morrison et al. (2010) refer to as protracted touch – a hug (see figure 1: M).

Thus, finally, touch is important because it affects human behavior and how we interact with the external world. Through touch we can easier get what we want, and also decrease physical responses in stressful situations.

Conclusion

The aim of this essay was to give an overview of the sense touch including a discussion of the relevant neuronal correlates, mainly focusing on affective touch. It seems like the brain areas orbitofrontal cortex, cingulate cortex, prefrontal cortex and the insula cortex have a vital role in processing affective touch, such as pleasant touch and pain. On the other hand, the somatosensory cortices seem to be more active and have a role in processing discriminative touch and touch rated as neutral.

In order to understand the somatosensory system more deeply further research is needed, primary on the affective touch. The neuronal correlates of discriminative touch have been studied more carefully than the neuronal correlates of affective touch. However, C-tactile fibers are fibers that need to be more studied in order to understand affective touch deeper.

Finally, to know more about the sense of touch through future research is important, because touch has a vital role for humans (and other animals) to interact with the external world. Touch also works like a non-verbal communication between people and it affects the perception of stressful events, as well as increases the likelihood of getting what the person wants.

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