
Affective touch throughout life: From cortical processing in infancy to touch perception in adulthood

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Cover illustration: Baby Astrid in the arms of her mother. Photograph by Emma Jönsson

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Abstract

Affective, interpersonal touch is important for forming and maintaining social bonds. In the hairy skin of humans there is a specific type of nerve fibers called C-tactile (CT) afferents which are optimally activated by a light stroking of the skin, like a caress. These afferents have been suggested to be involved in the detection and relaying of affective touch. In the current thesis stroking touch stimulation, targeting the CT afferents, is used in three papers investigating different aspects of touch processing and touch perception.

In paper I slow (affective) and fast (non-affective) stroking was applied to the forearm of two month old infants while the cortical response was measured using diffuse optical tomography. Analysis of the hemodynamic response of the cortex following slow compared to fast stroking revealed activations in the temporal and insular cortices. These results are coherent with activations previously shown in adults and indicate that the human brain already in early postnatal life can distinguish between affective and non-affective touch.

In paper II and III the perception of stroking touch stimulation was tested in healthy adult subjects. The participants were stroked on the forearm and the inner thigh and asked to rate the pleasantness, eroticism and intensity of the stimulation. Paper II revealed no difference in ratings of stroking on the forearm or the thigh. However, for the first time it was shown that the ratings of eroticism follow the same pattern as previously has been reported for pleasantness rat-

ings, and for the firing frequency of CT afferents. This may indicate involvement of CT afferents also in erotic touch perception. Furthermore, the ratings of eroticism decreased as a function of the duration of the romantic relationship. In paper III a skin sample was obtained together with the ratings of touch perception. In the skin sample the number of hair follicles were counted in order to test the hypothesis that CT afferents are connected to hair follicles, and that the density of hair follicles could have effects on the perception of touch. In this paper, the large sample sizes also allowed assessment of gender differences. Indeed, the results revealed gender differences both in ratings of touch perception and in hair follicle density, where women rated touch as more pleasant and had higher hair follicle densities. The gender difference in hair follicle density was however abolished when controlling for body size. No conclusive evidence for a correlation between hair follicle density and affective touch perception was found.

This thesis adds further knowledge to the growing field of affective touch. Specifically, it adds knowledge on how touch is processed in infancy, and how it is perceived in adulthood. It further also highlights some gender differences in how stroking touch is experienced.

Sammanfattning

Beröring är en viktig del av hur människor och djur kommunicerar och skapar sociala band. Affektiv beröring leder till att känslor uppkommer hos mottagaren. I denna avhandling fokuseras enbart på beröring som leder till positiv affekt, alltså beröring som mottagaren upplever som behaglig.

I den håriga huden hos människor finns speciella nervtrådar som heter C-taktila afferenter. Dessa har till uppgift att uppfatta lätta smekningar av huden och skicka signaler om affektiv beröring till hjärnan. De C-taktila afferenterna reagerar kraftigast på smekningar som är lätta på huden, har hudtemperatur och som har hastighet mellan 1 och 10 cm/s. En beröring med dessa egenskaper har i tidigare studier även visats vara den som människor uppfattar som mest behaglig. I denna avhandling presenteras studier som undersöker hur denna typ av beröring bearbetas i hjärnan hos nyfödda (paper I), om denna typ av beröring kan upplevas som erotisk (paper II) samt om det finns någon koppling mellan antalet hårsäckar i huden och upplevelsen av beröringen (paper III).

Man vet att affektiv beröring har positiva hälsoeffekter på till exempel för tidigt födda barn och man har sett att barn som inte blir berörda uppvisar en nedsatt kognitiv förmåga. I den första delen av denna avhandling undersökte vi hur hjärnan hos 2 månader gamla bebisar reagerade på affektiv beröring i form av långsamma borststrykningar och icke-affektiv beröring i form av snabba borststrykningar. Vi fann

att hjärnan redan så tidigt i livet kan sortera mellan affektiv beröring och icke-affektiv beröring. Detta fynd lyfter ännu tydligare fram vikten av beröring tidigt i livet eftersom kroppen redan då har ett system på plats som kan uppfatta de olika dimensionerna av beröring.

När vi växer upp och blir vuxna så börjar vi också kunna uppfatta och beskriva beröring som erotisk. I del två av denna avhandling undersökte vi om den typ av beröring som tidigare studier beskrivit som behaglig också kan beskrivas som erotisk. Vi applicerade strykningar med en mjuk borste med olika hastigheter på armen hos vuxna och frågade dem hur erotiskt, behagligt och intensivt de upplevde strykningen. Resultaten visade att hastigheterna som optimalt aktiverade de C-taktila afferenterna både uppfattades som de mest erotiska och mest behagliga, vilket kan innebära att systemet av C-taktila afferenter också är viktigt i erotiska sammanhang.

Man vet idag inte hur nervändsluten för de C-taktila afferenterna ser ut, eller hur de är organiserade, men man har i studier på möss sett att nerverna slingrar sig runt vissa typer av hårsäckar. Med hypotesen att detta också gäller för människor och att skillnader i densitet av C-taktila afferenter ger förändringar i hur behaglig en beröring upplevs genomförde vi den tredje och sista delen av denna avhandling. Resultaten visade att det eventuellt finns en svag koppling mellan antal hårsäckar och hur behaglig beröringen upplevs. Dessutom fann vi signifikanta skillnader i hur behaglig beröring upplevs av män och kvinnor, där kvinnor uppfattade beröringen som mer behaglig.

Det är viktigt att förstå hur beröring uppfattas och mekanismerna bakom det så att vi kan lära oss använda beröring på ett bra sätt. Idag kan vi kommunicera och umgås utan att fysiskt befinna oss på samma plats. Även om detta har sina fördelar så har man också sett att beröring kan ha starka positiva effekter, till exempel inom hälso- och sjukvården där beröring kan vara ångestdämpande för patienter med ätstörningar eller som ska genomgå stora operationer och inom skolan där massage i klassrummet kan leda till färre konflikter mellan

eleverna. Beröring är en viktig del i många aspekter av våra liv och därför behöver vi lära mer om dess effekter och vårt behov av beröring.

List of papers

This thesis is based on the following papers, referred to in the text by their Roman numerals.

Paper I: Jönsson, E., Kotilahti, K., Heiskala, J., Backlund Wasling, H., Olausson, H., Croy, I., Mustaniemi, H., Hiltunen, P., Tuulari, J., Scheinin, N., Karlsson, L., Karlsson, H. and Nissilä, I.

Affective and non-affective touch evoke differential brain responses in 2-month-old infants.

Manuscript.

Paper II: Jönsson, E., Backlund Wasling, H., Wagnbeck, V., Dimitriadis, M., Georgiadis, J., Olausson, H. and Croy, I.

Unmyelinated Tactile Cutaneous Nerves Signal Erotic Sensations.

The Journal of Sexual Medicine 2015: 12(6), 1338–45.

Paper III: Jönsson, E., Bendas, J., Weidner, K., Wessberg, J., Olausson, H., Backlund Wasling H. and Croy, I.

The relation between human hair follicle density and touch perception.

Accepted for publication in Scientific Reports.

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List of abbreviations

C-LTMR	C low threshold mechanoreceptor
CSSM	Cyanoacrylate skin stripping method
CT	C-tactile
EZQ	Erogenous zone questionnaire
fMRI	Functional magnetic resonance imaging
FOV	Field of view
HbO ₂	Oxygenated hemoglobin
HbR	Deoxygenated hemoglobin
HbT	Total hemoglobin
(HD-)DOT	(High density) diffuse optical tomography
HFD	Hair follicle density
MDMQ	Multidimensional mood questionnaire
ROI	Region of interest
RTS	Rotary tactile stimulator
S1	Primary somatosensory cortex
S2	Secondary somatosensory cortex
STQ	Social touch questionnaire
STS	Superior temporal sulcus
VAS	Visual analog scale

1 Introduction

Our sense of touch is versatile; we used it to determine the structure in materials, to manipulate objects, and to localize insects crawling on our skin. Further, our sense of touch allows us to interact and induce emotions in others (Hertenstein *et al.*, 2006). Affective touch contains a hedonic or motivational component (Morrison, 2016), in other words affective touch evokes feelings in the recipient. Affective touch can have positive or negative connotations, however in the current thesis the focus is exclusively on positive affective components of touch, referred to as pleasantness. Pleasantness itself is not a stand-alone sensation; but is rather a way to describe positive aspects of other sensations, like a “hedonic gloss” applied to them (Frijda, 2010). In the hairy skin of humans there is a system of unmyelinated tactile afferents, called C-tactile (CT) afferents, which has been proposed to signal the pleasant component of touch (Olausson *et al.*, 2008, 2002).

In this thesis, the cortical processing of affective touch in 2 month old infants was investigated (**paper I**), the perception of eroticism and its relation to pleasantness and CT-afferents in adults was explored (**paper II**), and finally a potential connection between hair follicles, touch perception, and gender was examined (**paper III**).

1.1 The importance of touch in development

The first social bond formed in a human’s life is that between mother and the newborn. This early interaction includes gentle caressing of the infant, which can constitute up to 30% of the time mothers interact with their newborns (Stack & Muir, 1992). Research shows that touch in early life is important for normal development (Barnett, 2005; Feldman *et al.*, 2002). The impact of touch deprivation on development is seen, for example, in studies on children adopted from orphanages, preferentially from Romania, where the conditions were very poor in the beginning of the 1990s. These

children show reduced glucose metabolism in some brain regions, including orbitofrontal cortex, prefrontal infralimbic cortex and lateral temporal cortex (Chugani *et al.*, 2001), which might contribute to the cognitive and socioemotional deficits displayed by these children (Wilbarger *et al.*, 2010; MacLean, 2003; Chugani *et al.*, 2001). It is important to note that these children did not suffer only from deprivation of physical contact, but were also deprived of other social stimuli, such as visual and olfactory. In the 1950s, psychologist Harry Harlow conducted experiments with rhesus monkeys where he isolated the monkey infant from its mother only hours after birth (Harlow, 1958). The infant monkey was then placed in a cage with two inanimate mother surrogates, one was made out of wire, the other of wood and covered with a soft cloth. The time the infant monkey spent clinging to the mother surrogates was recorded under two feeding conditions: either the wire mother or the soft mother was providing food. The results show that regardless of feeding condition the infant spent an astonishingly large proportion of the time clinging to the soft mother. Harlow termed this behavior touch comfort, and concluded that love is not only a function of providing the necessities of food and drink, as had previously had been suggested. However, infant animals' need for touch is not limited to primates. Studies on rats show that rat pups reared in isolation display elevated pain responses (Uhelski & Fuchs, 2010) and they also engage in less maternal care of their own pups (Gonzales *et al.*, 2001). The latter effect can be somewhat dampened if the isolated rat pup is stroked with a wet paintbrush across the back, mimicking licking by the rat mother.

Lately, the clinical benefits of touch to infants, especially in the case of preterm infants, have gained attention. Skin-to-skin care, or kangaroo care, was proposed and developed by Edgar Rey in Bogotá, Colombia in the late 1970s, originally to deal with the lack of incubators, and the high incidence of infections and infant abandonment (Conde-Agudelo & Díaz-Rossello, 2014). Most research on skin-to-skin care focus on preterm infants, and a recent Cochrane review

shows that the morbidity and mortality of low-birth weight infants is reduced with skin-to-skin care (Conde-Agudelo & Díaz-Rossello, 2014). Further, preterm infants receiving touch massage gain weight more quickly and can be dismissed from hospital care 3-7 days before non-massaged controls (Mendes & Procianoy, 2008; Field *et al.*, 2011). It is not only the infants who benefit from the touch intervention, studies have also shown that touch increases the mother-infant attachment (Tessier *et al.*, 1998). Therefore, touch interventions could help mothers suffering from postpartum depression, as lack of attachment to the newborn is commonly reported (Feldman *et al.*, 2002; Peláez-Nogueras *et al.*, 1996). A study on 9 month old infants, show that affective touch (slow skin stroking) decreases the heart rate, whereas non-affective touch (fast skin stroking) instead increases the heart rate (Fairhurst *et al.*, 2014). Furthermore, there is an increase in attention to the stimuli for the affective touch, measured as gaze shift from distractor movie to the experimenter or to the brush used to deliver the stroking, compared with non-affective touch.

1.2 Touch in children, adolescents and adults

As we grow up, touch remains important in our daily life (Sehlstedt *et al.*, 2016), and it can have large implications on how we act towards one another. For example classroom massage in elementary school reduces aggressive behavior (Gonçalves *et al.*, 2017). Adolescents with conduct disorder have fewer physically intimate relationships, which might contribute to their disorder, according to a study by Field (2002). In everyday situations, a light touch might influence our behavior. For example, a light touch from the waiter in a restaurant can result in higher tips from the dining customer (Crusco & Wetzel, 1984). The service at a university library is rated as better if the librarian lightly touches the student when returning the library card at the check-out counter, an effect that was particularly pronounced

for female subjects (Fisher *et al.*, 1976). Touch is frequently employed when we experience strong emotions, such as athletic success (Smith *et al.*, 1980), or when we welcome our loved ones at an airport (Greenbaum & Rosenfeld, 1980). Also, touch has important positive effects in healthcare (Airoso *et al.*, 2016). For example touch provides anxiety relief at time of surgery (Lindgren *et al.*, 2013) and for patients suffering from anorexia nervosa, massage therapy reduces stress and anxiety levels, and gives the patients a sense of relaxation (Axelsson & Määttä, 2007; Hart *et al.*, 2001). However, anorexia nervosa patients also report lower perceived pleasantness to stroking touch stimulation compared to healthy controls (Crucianelli *et al.*, 2016).

1.2.1 Touch for romantic couples

Touch is also of great importance for romantic couples. Even when only focusing on non-genital touch in non-sexual situations touch is important for relationship satisfaction (Gulledge *et al.*, 2003). Cuddling not only affects the level of sexual activity but it also makes us feel protected, nurtured and relaxed (van Anders *et al.*, 2013). Affective touch can also influence the physiological states and thereby increase the coupling between partners, i.e. making them more in tune with each other (Chatel-Goldman *et al.*, 2014). The meaning of touch may change over the course of a relationship in a way that touch is more erotic when the romantic bond is formed, whereas in established relationships the touch might instead evoke feelings of security and affiliation (Brennan *et al.*, 1998). The relationship between erotic touch perception and pleasant touch perception was assessed in **paper II**.

1.3 Gender and cultural differences in touching behavior

The need for, and appreciation of, touch is of course very dependent on the person giving and the person receiving it. Even though touch is important for communication and attachment, it is also associated with heavy social and cultural restrictions. In most societies, there are norms concerning who you are allowed to touch, in which ways, and where. A recent study by Suvilehto et al. (2015) shows that there is a positive linear relationship between the emotional bond between the toucher and the receiver, and the total bodily area where touching is allowed. This was true for all five nationalities (Finnish, French, Italian, Russian and British) included in the study. Several other studies also investigated the influence of culture on touch attitude and touching behavior. In a study by Schut et al. (2013) questionnaires were used to gather data on appraisal of touch in four different countries: Italy, France, Germany and Syria. Their results show that Italians score highest in pleasure of touching oneself and touching their partner. Germans and Italians score higher on pleasure of parental touch than subjects from France and Syria (Schut *et al.*, 2013). Robert Shuter (1977) also studied Germans and Italians, together with Americans, where random dyads (male-male, male-female, female-female) in selected neighborhoods were assessed on interpersonal space and tactile interaction. No consistent differences were found for the different cultures or dyads, thus limiting the generalizability of touching behavior (Shuter, 1977). Field also used an observational approach when she studied American and French adolescents at fast food restaurants. Her results show that French adolescents engage in more touching of each other compared with the American adolescents, whereas the Americans perform more self touch and display more aggressive behavior toward their peers (Field, 1999). Setting might also influence the frequency of physical contact as shown in preschool children by Williams and Willis (1978). The children would engage in more touch in outdoor play compared

to indoor play (Williams & Willis, 1978). From preschool through to high school same-gender (i.e. male-male or female-female) pair touch is more frequently observed than cross-gender pair touch. This changes during adolescence and in both college students and adults cross-gender touch is more common (Willis *et al.*, 1978, 1976; Willis & Hofmann, 1975).

1.4 Peripheral processing of affective touch

Two main types of afferents detect light touch to the skin: $A\beta$ and CT afferents. $A\beta$ afferents are thick, myelinated nerve fibers with high conduction velocities, and their main role is to signal the discriminative properties of touch, that is where and how the skin is touched. In contrast the CT afferents are thin and lack myelin, which gives them a slow conduction velocity. This makes them ill-suited for relaying information that requires a fast response from the central nervous system. Instead, the CT afferents are suggested to be responsible for detecting the emotional component of the touch, which allows us to add pleasantness to the tactile experience (Löken *et al.*, 2009; Olausson *et al.*, 2002). Although the two types of afferents detect different properties of touch, the combination of the inputs is crucial to sense the full range of tactile experiences.

The non-human mammalian equivalent of CT afferents, C-low threshold mechanoreceptors (C-LTMRs) were discovered in cat in the 1930s (Zotterman, 1939), and they were later also identified in other mammals (Kumazawa & Perl, 1977; Iggo & Kornhuber, 1977; Bessou *et al.*, 1971). For a long time it was believed that this specific type of nerve fiber had been lost in humans during evolution. This belief was disproved when CT afferents were found in the human forehead skin using the technique of microneurography (Nordin, 1990; Johansson *et al.*, 1988). Later the same method allowed the discovery of CT afferents in the arms and legs of humans (Vallbo *et al.*, 1999). In fact, in the forearm skin the CT afferents are encountered as often

as $A\beta$ s during microneurography (Vallbo *et al.*, 1999, 1993). However, so far CT afferents have not been found in glabrous (non-hairy) skin in humans (e.g. palms of hands, soles of feet). CT afferents are maximally activated by light slowly moving stimuli at skin temperature (Ackerley *et al.*, 2014; Löken *et al.*, 2009; Vallbo *et al.*, 1999). This type of stimulus, often administered with a soft painters brush, elicit faint, but pleasant sensations in patients that lack myelinated afferents, but have intact function of unmyelinated afferents (Olausson *et al.*, 2002). Further, a study by Löken *et al.* (2009) shows that the action potential firing rate, but not the number of evoked spikes, of the CT afferents correlate positively with the ratings of pleasantness perception of the brushing; both the firing frequency and the pleasantness ratings peaked in the range of 1-10 cm/s. Furthermore, it seems the perceived pleasantness of the touch is dependent on the amount of activated CT afferents (Morrison *et al.*, 2010). Morrison *et al.* (2010) investigated affective touch perception in a rare population of patients suffering from a disease called hereditary sensory and autonomic neuropathy (HSAN) type V. These patients have a reduced density of thin, unmyelinated nerve fibers, likely including CT afferents. Following soft brush stroking on the forearm the patients rate touch as less pleasant compared with healthy controls. The temperature of the stimulus also affects the pleasantness ratings as well as the firing of the CT afferents, with the maximal rating and firing frequency obtained when the stimulus is around skin temperature (Ackerley *et al.*, 2014). Taken together, the properties of the CT afferents indicate that this nerve type is tuned toward pleasant human skin-to-skin interactions.

The distribution and structure of the peripheral nerve endings of the CT afferents in humans are unknown. Animal studies have used genetic labeling to elucidate the appearance and distribution of the C-LTMR skin receptors. The target marker for these genetic labeling studies varies. Vrontou *et al.* (2013) used MRGPRB4⁺ as marker for C-LTMRs in mice. They find that the afferents expressing this pro-

tein is activated by massage-like stroking of the skin (Vrontou *et al.*, 2013). Further, the same study show that activating the labeled afferents promotes conditioned place preference, which means that the mice prefer to spend time in the place where the afferents are activated. Li *et al.* (2009) use tyrosine hydroxylase as a marker for C-LTMRs in mice. The axonal branches form longitudinal lanceolate endings in close association with zigzag and awl/auchene hair follicles but no nerve endings are found around the largest hair follicles, the guard hairs (Li *et al.*, 2011). Further, the C-LTMRs are only found in the hairy skin and are most common at the level of the trunk and proximal limbs. This proximal-distal decrease in C-LTMR density is also found by Delfini *et al.* (2013) when they used the protein TAFA-4 as a specific marker for C-LTMRs (Delfini *et al.*, 2013). In contrast to the genetic labeling studies, one study using electrophysiology has reported finding C-LTMRs in the glabrous skin of the rat (Djoughri, 2016).

The association of certain types of hair follicles and C-LTMRs found by Li *et al.* (2011) opens up for the possibility that this is also the case in humans. If the CT afferents are connected to the hair follicles, and CT afferent density is reflected in the ratings of pleasantness (Morrison *et al.*, 2011), then the hair follicle density might correlate to the touch perception. In **paper III** we investigate the potential relationship between hair follicle density of humans and affective touch perception.

1.5 Central processing of affective touch

Studies investigating the brain processing of CT afferents, and the stroking touch stimuli that are known to optimally activate them, have revealed a number of brain areas implicated in processing the affective component in touch. A pivotal study came from Olausson and colleagues in 2002. In this study stroking tactile stimulation was applied to the hairy skin of a rare patient lacking myelinated affer-

ents. The cortical activation, as revealed by functional magnetic resonance imaging (fMRI), is localized to the posterior insula (Olausson *et al.*, 2002). Subsequent studies on healthy adults also identified the posterior insula as an area activated by gentle stroking of the hairy skin (Morrison, 2016; May *et al.*, 2014; Gordon *et al.*, 2013). In fact, Morrison showed in a meta-analysis that the area most likely to be activated by affective touch is the insula (Morrison, 2016). Additional areas that are involved in affective touch processing are the posterior superior temporal sulcus (pSTS) (Davidovic *et al.*, 2016; Bennett *et al.*, 2014; Voos *et al.*, 2013), anterior cingulate cortex (ACC) (Case *et al.*, 2016; Lindgren *et al.*, 2012) and prefrontal cortex (Kaiser *et al.*, 2015; Gordon *et al.*, 2013). Some studies show age related differences in activation. May *et al.* (2014) found an age related difference in activation of the insular cortex, with higher activations in adolescents compared to adults. Björnsdotter *et al.* (2014) found age to correlate positively to secondary somatosensory cortex (S2) activation. Age also correlates with activations near the pSTS, but only in females (Björnsdotter *et al.*, 2014). Further, primary somatosensory cortex (S1) has been suggested to be involved in affective processing, as the activation of S1 is modulated by affective scenarios (Gazzola *et al.*, 2012). However, this view is challenged by others. For example, no effect on pleasantness ratings was found following deactivation of S1 using repetitive transcranial magnetic stimulation (Case *et al.*, 2016). The brain processing of CT targeted touch in early life is however unknown. In **paper I** we investigate the cortical activation following affective and non-affective touch stimulation in 2 month old infants.

1.6 Factors influencing affective touch perception

The perception of affective touch is far from constant, in fact, how touch is perceived depends on the context. For example expectations and the person administering the touch is important for touch perception. Gender of the person administering the touch influences the

ratings of pleasantness. In a study by Gazzola et al. (2012) heterosexual male participants were stroked on the thigh while lying in a MRI scanner. They were given information that they were touched either by a woman or man, when in fact it was always the same female experimenter who performed the touch. The results not only show a significantly lower pleasantness rating for touch supposedly performed by the man, but also show that the activation of S1 is modulated by the perceived sex of the toucher (Gazzola *et al.*, 2012). To limit the effects of toucher identity stroking with a brush is commonly used. A study by Triscoli et al. (2013) show that there is no difference in ratings between touch performed with a brush held by robot or by hand (Triscoli *et al.*, 2013). In a study by McCabe et al. (2008) the pleasantness ratings were modulated by word labels on lotion, which was applied to the skin of healthy female participants. The lotion was labeled either as “rich moisturizing” or “basic”, even though it was in fact the same cream, and it was applied by the same experimenter. The participants rated the pleasantness of the lotion application and the results showed that the “rich moisturizing” was rated as significantly more pleasant. Further, the same study showed that the word labels also modulated the fMRI activations in parietal area 7, insula and ventral striatum (McCabe *et al.*, 2008). A study by Ellingsen et al. (2013) investigated the effect of expectation on pleasantness ratings. They informed the participants that they would receive oxytocin, which would increase the pleasantness of touch. Even though no oxytocin was given, the participants still perceived the touch as more pleasant than controls (Ellingsen *et al.*, 2013).

Input from other senses influences the perception of affective touch. The presence of a disgusting odor (Croy *et al.*, 2014) or images showing an angry face reduces the perceived pleasantness of touch, whereas images of happy faces increase pleasantness ratings (Ellingsen *et al.*, 2014). Age is yet another factor that influences affective touch perception, where pleasantness ratings of stroking touch stimulation increase with age (Sehlstedt *et al.*, 2016). Gender of the participant is rarely

reported to affect the affective touch ratings, but in the few instances where an effect was found females rated touch as more pleasant than men (Croy *et al.*, 2016; Essick *et al.*, 2010). To further investigate this, gender differences in affective touch perception were tested in **paper III**.

2 Specific aims

Paper I: The aim of **paper I** was to test whether cortical processing was different following affective touch and non-affective touch stimulation in early infancy.

Paper II: The aim of **paper II** was to test whether stroking touch stimulation could be described in terms of eroticism, as well as pleasantness, and if there were any differences between skin sites.

Paper III: The aim of **paper III** was to test whether the density of hair follicles in humans related to the perception of touch, and if there were gender differences in touch perception.

3 Methodological considerations

3.1 Ethical approvals

Ethical approval for **paper I** was granted by the joint Ethics Committee of the University of Turku and the Hospital District of Southwest Finland. For **paper II** ethical approval was granted by the regional ethics committee in Gothenburg, Sweden. For **paper III** ethical approval was granted by the regional ethics committee in Gothenburg, Sweden and the ethics committee of Dresden University of Technology. All studies were performed according to the Declaration of Helsinki.

3.2 Participants

For **paper I**, 29 healthy infants were recruited from the FinnBrain Birth Cohort Study. Sufficient data for analysis was obtained from 16 of the infants (6 female, age 56 days \pm 8 days SD). The parents received information at recruitment and when arriving at the testing center they signed an informed consent form. For **paper II**, in total 66 healthy adult volunteers were recruited from the local university in Gothenburg. Twenty (10 female, age 23.5 years \pm 3.2 years SD) of those participated in study 1 and 46 took part in study 2 (27 female, age 26.6 years \pm 6.8 years SD). They all signed an informed consent form and were reimbursed for participating. For **paper III**, in total 138 healthy adult participants were recruited in Gothenburg, Sweden or in Dresden, Germany. Fifty-eight participants (34 female; age 26.2 years \pm 6.3 years SD; N=46 identical to study 2 in **paper II**) took part in study 1, the other 80 (51 female; age 24.9 years \pm 4.1 years SD) were enrolled in study 2. Additionally, 15 participants (8 female; mean age 23.9 years \pm 3.0 years SD) were enrolled in a pretest carried out in Dresden, Germany. All participants signed an informed consent form and were reimbursed for participating.

3.3 Summary of protocols

3.3.1 Paper I

We investigated how the infant brain processes affective and non-affective touch. This was done by applying tactile stroking stimulation with two velocities (3 and 20 cm/s) to the right forearm of the infant. The slower velocity is optimally activating the CT afferent system, which detect emotional components of touch. The fast velocity is suboptimal in activating CT afferents and is therefore less affective. Simultaneously the cortical response in the form of concentration changes of total hemoglobin (HbT), oxygenated hemoglobin (HbO₂) and deoxygenated hemoglobin (HbR) was measured with high density diffuse optical tomography (HD-DOT). The infant was resting in its mother's arms during the experiment and was asleep for approximately 50 % of the experimental session.

3.3.2 Paper II

To test whether CT afferent optimal touch could be described as erotic as well as pleasant two studies were conducted. Both studies used stroking stimulation of the hairy skin and the participants rated eroticism, pleasantness and intensity on visual analog scales (VAS). In study 1 the stimulation was applied both to the inner thigh and the dorsal forearm, in study 2 only the forearm was used. Study 1 additionally tested tactile sensitivity, and both studies collected additional data through questionnaires.

3.3.3 Paper III

To test the influence of hair follicle density (HFD) on touch perception, participants in two studies received stroking stimulation on the forearm and rated the eroticism, pleasantness and intensity of the

stimuli. Skin stimulation was performed at the same site from which the HFD was calculated. The forearm was determined to be a representative skin site for HFD through a pretest in which skin samples from 9 body sites were compared. The large sample sizes allowed testing for gender differences in touch perception and HFD. Due to the highly similar study designs of the two studies the data could also be analyzed as a combined dataset.

3.4 Tactile stimulation and experimental design

3.4.1 Skin stroking

Gentle stroking of the hairy skin with a soft brush at different velocities was applied in all three papers. In **paper I** the brush was handheld and the velocities used were 3 and 20 cm/s. These velocities were presented in a randomized, counter-balanced order, interleaved with resting periods of variable length (mean 31 seconds). In **papers II** and **III** the tactile stimulation was administered by a robotic device, the rotary tactile stimulator (RTS; Dancer designs, St Helens, UK). In figure 1 the experimental setup with a participant and the RTS is displayed. In **paper II** five velocities (0.3, 1, 3, 10 and 30 cm/s) were used. The same velocities were used in study 1 of **paper III**, whereas for study 2 in **paper III** an additional velocity (0.1 cm/s) was used. All velocities in papers **II** and **III** were presented three times for each participant in randomized order. In all three papers the velocities were chosen so that both CT afferent optimal velocities (within the range 1-10 cm/s) and CT afferent suboptimal velocities (lower or higher velocities) were represented.

3.4.2 Monofilament test (Paper II)

In study 1 of **paper II**, the monofilament test was applied to the inner thigh and dorsal forearm to assess the tactile sensitivity. In

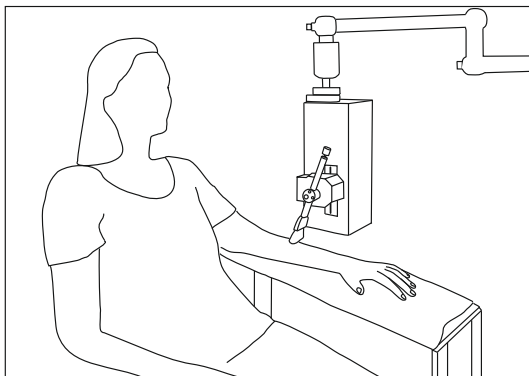


Figure 1: The positioning of the participant and the RTS used in paper II and III.

this test, filaments exerting with different loads were applied to the skin two times, and if the participant could detect both applications the test continued with a lighter filament, otherwise the load was increased. This procedure was repeated for six turning points and the average of the last four turning points was used as the tactile sensitivity threshold.

3.4.3 Two-point discrimination (Paper III)

In study 2, the two-point discrimination test was carried out on the same skin site as the brushing to provide a measure of discriminative touch. The test was carried out using a metal device with two tips with variable spacing (3, 3.5, 4, 4.5 and 5 cm). The participants were asked to report whether they perceived one or two indentations. The examiner carefully touched the skin with the two tips of the device simultaneously. The devices were applied in decreasing order,

starting with 5 cm distance until the participants perceived the two indentations as one in at least one out of five stimulations. The last distance that was recognized correctly in five out of five trials was considered the two-point discrimination threshold.

3.5 Measurements and analysis

3.5.1 Optical imaging and signal processing (Paper I)

The cortical activation following the tactile stroking stimulation on the right forearm was measured with an in-house diffuse optical tomography system. A probe consisting of a flexible silicon sheet with embedded optodes (light sources and detectors) was attached to the infant's head, positioned just above the left ear. Thus covering brain areas of interest, such as the STS and S2 (see figure 2). Optical imaging relies on the scattering and absorption of photons in the different tissue types. The changes in concentrations of the different states of hemoglobin are calculated by relating the intensity of the light from the sources to the intensity of the light that backscatter to the detector. Thus, the detection depth of the method depends on the tissues and the length of the light path. Because of the diffuse nature of the method the spatial resolution is rather low. In adults, optical imaging is best suited to measure activations in the superficial part of cortex, however since the infants in **paper I** were so young it was expected that deeper parts of the brain could be reached, potentially as deep as the insula.

Anatomical landmarks were marked on the infant and stereo camera images of the probe and the anatomical landmarks were taken. This allowed subsequent determination of probe position, and thereby the field of view (FOV). Additionally, following the test session a mesh cap with colored nodes was put on the infant, and stereo images were taken from five different orientations, to create 3D models of the infants' head, with the probe position marked. These models

were co-registered to a representative MR image. The MR image was manually segmented and the light propagation in the different tissues was simulated using a Monte Carlo method to determine the spatial sensitivity profile corresponding to each source-detector pair.

Low-frequency oscillations and drift were reduced by subtracting a low-pass filtered version of the signal from the signal. Motion artifacts and episodes where the infant was moving or crying, as marked in the videos from the experimental sessions, were removed. The signal was then averaged and source-detector pairs with low signal-to-noise ratio were removed from analysis. To reconstruct images from the optical data, an image reconstruction algorithm based on the perturbation Monte Carlo method was used. Finally, the concentration changes of HbT, HbO₂, and HbR were calculated from the processed signal. The resulting images of HbT, HbO₂ and HbR were smoothed using a Gaussian blur operation across all subjects. Subsequently, the areas where the slow and fast brushing produced different responses in the time window 2-8 seconds post-stimulus were identified. These areas were used in the statistical testing.

Statistical testing Two analysis approaches were used to determine which brain regions were activated by the stimuli. The first approach entailed finding the voxel with the largest difference in HbT between fast and slow stroking. The 27-neighbourhood of the seed voxel was then assessed and voxels having an absolute value of one quarter of the maximum value or more were added to the cluster. When all voxels fulfilling this criterion were found the center of gravity was calculated for the cluster using a weighted average. In the second approach the voxels with statistically significant different HbT values were included in the cluster. The statistical threshold was set to $p=0.02$. The center of the cluster was calculated as the average of the voxel coordinates. The time courses of the responses were calculated as the average of the HbT response in the cluster. The concentration values were also used to determine the cluster-wise HbT, HbO₂ and



Figure 2: Experimental setup for paper I with the HD-DOT headgear attached to the head. The white dots on the probe and the black and white stickers on the skin were used to localize and coregister the obtained data.

HbR values, which were then compared between fast and slow brushing using Student’s t-test. Due to the number of tests the estimated factor for multiple comparison correction was set at 80. Furthermore, a region of interest (ROI) analysis was carried out for the voxels within the FOV that belonged to S1. In this region, the mean values for HbT, HbO₂ and HbR were calculated. The anatomical locations of the resulting activations were determined with visual inspection of the activation cluster overlaid on the representative MR image.

3.5.2 Subjective ratings of tactile perception (Paper II and III)

Following each skin stroke in **paper II** and **III**, the participants were asked to rate three aspects of the stimulation: how erotic it felt, how pleasant it felt and how intense it felt. The anchor points were “not

erotic at all” to “extremely erotic”, “extremely unpleasant” to “extremely pleasant” and “not intense at all” to “extremely intense”, respectively. The ratings were done on VASs that appeared on a screen. The ratings were automatically translated into numerical values for use in the analysis. The participants were assured that the experimenter would not supervise the rating procedure.

Statistical testing Mean ratings of eroticism, pleasantness and intensity for each of the five velocities were produced in both **paper II** and **III**. These means were then analyzed with repeated measures ANOVAs, with skin site as a within-subject factor in **paper II**, study 1 and with gender as a within-subject factor in **paper III**. Furthermore, in **paper III** two touch variables were computed from the touch ratings: overall pleasantness/eroticism/intensity and pleasant/erotic touch awareness. The overall variable was calculated as the mean of all pleasantness/eroticism/intensity ratings. The touch awareness variable is a measure of the shape of the rating curve and was calculated by subtracting the rating value for 30 cm/s from the peak rating value (3 cm/s for pleasantness, 1 cm/s for eroticism) and then dividing by the overall pleasantness/eroticism (Croy *et al.*, 2016).

3.5.3 Questionnaires and background data (Paper II)

In both study 1 and 2 of **paper II**, the attitude toward interpersonal touch was measured using the Social Touch Questionnaire (STQ (Wilhelm *et al.*, 2001)). In study 1 the participant further reported their current mood using the multidimensional mood questionnaire (MDMQ (Steyer *et al.*, 1997)). In study 2 the digital version of the erogenous zone questionnaire (EZQ (Turnbull *et al.*, 2014)) was used to measure how “hot” it would feel to be touched by another person on different body sites. Further, in study 2 the participants provided background information such as relationship status, relationship length, frequency of being/wanting to be sexually active,

and frequency of intimate (non-sexual) body contact on a self-devised questionnaire.

Statistical testing The questionnaire and background data was analyzed with t-tests and correlations.

3.5.4 Hair follicle density: Cyanoacrylate skin stripping method (Paper III)

To measure the HFD the cyanoacrylate skin stripping method (CSSM) was used (Otberg *et al.*, 2004). An area was marked on about the middle of the forearm, on the dorsal side. The skin area was shaved and a drop of cyanoacrylate glue was placed on the skin and a glass slide was put on top. By gently pressing the glass slide a thin film of glue was formed, and after about a minute of polymerization the glass slide was lifted off the skin. The sample consists of a thin sheet of horny cells, hair shafts, and casts of the follicle (Otberg *et al.*, 2004). The HFD was determined by manually counting the number of hair follicles in 1 cm² using a light microscope.

Statistical testing The correlation between HFD and touch ratings was tested using linear correlation analysis, as well as in partial correlations with inclusion of height and weight of the participants. Gender difference in HFD was tested with a t-test.

4 Summary of results

4.1 Paper I

The two analysis methods returned two different activation clusters for slow compared to fast stroking stimulation. In the first analysis approach, a cluster was formed from the neighborhood of the voxel with the largest difference in HbT concentration. This approach returned an activation cluster for the slow compared with fast brushing in the temporal cortex, expanding towards the insula, superior temporal sulcus and parietal operculum. The center of gravity for this cluster was located in the middle temporal gyrus and the cluster size was 14 cm³. The time course for HbT in the cluster increased and peaked at 8 seconds post stimulus onset for slow stroking. The HbT concentration after fast stroking instead showed a decrease. Furthermore, the HbT response to fast brushing was more superficially located than the response to slow brushing. The maximum difference between fast and slow brushing was obtained at 12.5 mm depth. The second analysis approach marked the voxels with significantly different HbT concentration after slow and fast stroking stimulation activated. This approach returned an activation cluster in the insula. In this area, the activation from slow brushing was significantly larger than the activation from fast brushing from 4 to 8 seconds post-stimulus. The cluster spanned 1.1 cm³ at significance level $p=0.02$. For the ROI analysis of S1, no statistical significant response or difference between slow and fast stroking was found.

4.2 Paper II

The results from the two studies in **paper II** both showed that the subjective ratings of eroticism reached their maximum values for stroking stimuli at velocities within the CT afferent optimal range. This was also found to be true for the pleasantness ratings, confirming

previous studies. However, the ratings of eroticism were highest for 1 cm/s, whereas the ratings for pleasantness were highest for 3 cm/s (Ackerley *et al.*, 2014; Löken *et al.*, 2009). As previously reported, the intensity ratings increased linearly with the stroking velocity (Ackerley *et al.*, 2014; Löken *et al.*, 2009). This led to the conclusion that to obtain high ratings on perceived eroticism the stimulus has to evoke a high activity in the CT afferents (i.e. highly rated on pleasantness) but low activity in the $A\beta$ afferents (i.e. low intensity). In fact, it was found that a linear combination of the pleasantness and intensity ratings predicted the eroticism ratings, according to equation (1).

$$\text{eroticism rating} = 1.5 \cdot \text{pleasantness rating} - \text{intensity rating} \quad (1)$$

The data from study 1 failed to detect any effect of skin site on the rating behavior, i.e. the ratings following stroking stimulation on the inner thigh did not differ from those applied on the forearm on for any of the three rated properties (eroticism, pleasantness and intensity). However a difference in tactile sensitivity was found between the two skin sites, with the inner thigh having a higher tactile threshold than the forearm, in line with previous knowledge (Ackerley *et al.*, 2014). The MDMQ revealed no correlation with overall eroticism ratings, nor did the STQ for either study. A positive correlation was found for the overall EZQ score and the overall eroticism ratings from study 2. The EZQ also revealed that imagining touch to the inner thigh felt more erotic than touch on the forearm, something that was not found in study 1 for actual touch stimulation on those skin sites. The partnership and sexuality questionnaire in study 2 revealed a positive correlation between frequency of intimate body contact and appreciation of such touch, but no correlation was found between appreciation of intimate body contact and overall eroticism ratings. There was a positive correlation between mean eroticism rating and the frequency of sexual activity, and a negative correlation between frequency of sexual activity and duration of relationship.

4.3 Paper III

The results of **paper III** showed that HFD was related to body size; it significantly correlated to weight in study 1 and to weight and height in study 2 and in the combined dataset. Women had a higher HFD than men, but this difference was not significant after inclusion of height and weight as covariates. The ratings of pleasantness and eroticism followed the expected inverted U shape, and intensity ratings followed the expected linear shape, as a function of stroking velocity. The ratings of pleasantness peaked at 3 cm/s stroking, and for eroticism the peak was for 1 cm/s, replicating findings from **paper II**. In both study 1 and study 2, as well as in the combined sample, women rated touch as significantly more pleasant and more erotic than men, in both studies as well as in the combined dataset. There were no gender differences in pleasant and erotic touch awareness, indicating that the shape of the curve did not differ between genders. In study 2, intensity was rated higher and the two-point discrimination threshold was lower for women than for men. HFD did not correlate to any touch measures, except for pleasant touch awareness in study 2, where a higher HFD indicated higher pleasant touch awareness, i.e. a sharper bend of the curve.

5 Discussion

5.1 Paper I

In **paper I** we wanted to test how the infant brain processes slow, CT optimal stroking touch, compared with fast, CT suboptimal stroking touch. This was done by applying brush stroking at 3 and 20 cm/s to the forearm of the infant while measuring the cortical activation with diffuse optical imaging. In adults, slow stroking has been described as more pleasant than fast stroking (Löken *et al.*, 2009), and the CT afferent system has been suggested to signal this emotional component of touch (Olausson *et al.*, 2002). This means that the slow stroking carries a higher emotional load, i.e. is more affective than the fast stroking. The results of **paper I** show that the infant brain is activated differently by slow relative to fast touch. This fits well with the existing literature, highlighting the importance of affective touch in early life. Using two different analysis approaches we found two activation clusters in the infant brain, one located in the temporal cortex and one in the insula. The finding of activation in the temporal cortex fits well with the existing literature, as activation of the STS has been reported on numerous occasions as a response to slow stroking. The activation of STS after stroking tactile stimulation has been found to positively correlate with the rating of pleasantness (Davidovic *et al.*, 2016) but correlates negatively with autistic traits in healthy adults (Voos *et al.*, 2013). The STS is suggested to be involved in processing of other socially relevant stimuli (Beauchamp, 2015) such as faces and voices, language, faces and biological motion (Deen *et al.*, 2015), and social inclusion (Bolling *et al.*, 2013). Unexpectedly the simulations of light propagation in the brain of infants at this age showed detection depth that allowed detection of activations in the insula. To our knowledge, this is the first time diffuse optical imaging has been reported to be able to reach as deep as the insula. We attribute this breakthrough to the combination of rapidly devel-

oping technology, very young subjects and the fact that there is a pocket of cerebrospinal fluid adjacent to the insula at this age. Using the second analysis approach we found the activation to be located in the insula, with the center of the cluster at 24 mm depth. The insula is of great interest for affective touch studies, as previous reports identify it as a key area for the processing of CT targeted touch (Morrison, 2016; Kaiser *et al.*, 2015; Olausson *et al.*, 2002). The insula is proposed to be a processing hub for interoception (Craig, 2002) and part of the salience network (Uddin, 2014).

However, it is important to point out that the DOT method has low spatial resolution and does not give any anatomical information. It is therefore not possible to get exact localizations of the activation clusters, as would be the case with, for example, fMRI. In **paper I** we used a representative MR image of an infant in which we performed the simulations of light propagation and co-registered the HbT, HbO₂ and HbR images to. Individual differences and rapid growth of the brain this early in life also makes more precise localization of neural activation challenging, as does the immaturity of the hemodynamic response function in infants. In this paper, we prove the hypothesis that an intact sensory system for affective touch is in place already in early postnatal life. This could have implications for the care of newborns; in particular pre-term infants who often are denied human touch due to infection risks. It could also have implications in the care of post-partum depressed mothers, where a touch intervention between mother and child could help form the attachment that sometimes is compromised.

5.2 Paper II

In **paper II** we investigated the involvement of CT afferents in erotic touch perception by applying touch with different stroking velocities on the forearm and on the inner thigh of young healthy adults. The results from both studies in **paper II** showed that stroking at CT

optimal velocities was perceived as more erotic than CT non-optimal velocities. This indicates involvement of the CT afferent system in non-genital erotic touch. The rated pleasantness of stroking touch follows an inverted U-shape, where the velocities optimally activating CT afferents (1-10 cm/s) are rated as more pleasant than slower and faster velocities (Ackerley *et al.*, 2014; Löken *et al.*, 2009). The inverted U-shape was validated for pleasantness in **paper II** and it was shown that the curve shape was also valid for eroticism. However, the ratings of eroticism peaked at 1 cm/s rather than at 3 cm/s, which is the case for pleasantness. In fact, linear combination of the ratings of pleasantness and intensity predicted the eroticism ratings, such that a high pleasantness rating and a low intensity rating yielded a high eroticism rating. This highlights the importance of the combination of input from different types of tactile afferents. Furthermore, **paper II** showed that touch to the inner thigh and to the forearm did not differ in ratings of pleasantness or eroticism. Previous research shows that when imagining touch, the inner thigh is thought to be more erotic than touch to the forearm (Turnbull *et al.*, 2014), but this was not observed in **paper II**. This likely reflects the context dependence of touch perception, where a light stroking by a brush in a laboratory environment is a poor replication of the same stroking performed by one's partner in a more private setting. Finally, **paper II** also showed a negative correlation between erotic touch perception and the duration of romantic relationships. Potentially this reflects a shift in meaning of touch as the emotional bond matures in the relationship. In the beginning of the relationship, during the formation of the romantic bond, touch carries a higher erotic load, whereas in a later stage of the relationship touch might instead signal affiliation and security that helps to uphold the bond.

5.3 Paper III

In **paper III**, the hypothesis that CT afferents are connected to hair follicles, and that the hair follicle density thus could be reflected in the perception of stroking touch was tested. This hypothesis could not be confirmed, as only a weak correlation was found for the relation between HFD and pleasant touch perception. The lack of effect on touch perception could be due to the rather unspecific skin stripping method. The method we used did not let us separate between the different types of hairs, nor which stage of the hair cycle the follicles were in. Furthermore, we do not know the exact connection between hair follicles and the CT afferents, or even if there is one. A possible scenario could be that the CT afferents use the hair follicle, or trophic factors released from it, as a beacon that guides the afferent during development. This could also explain why the CT afferents are not found in the glabrous skin. Another possible reason that the relation between HFD and pleasant touch perception was weak is because the relation might not be linear. Instead it is possible that a staircase model, i.e. that a certain number of hair follicles is required to see a difference in ratings of pleasantness, better describes the relation. If so, our sample of healthy participants would likely not be enough to fully explore the relation between HFD and pleasant touch perception. To do this one would have to look into different clinical populations, such as alopecia patients who suffer from excessive hair loss, hypertrichosis patients who suffer from excessive hair growth or perhaps obese patients (where the HFD would be expected to be lower).

Furthermore, **paper III** showed gender differences in HFD, two-point discrimination and in ratings of touch perception. The gender difference in HFD arises from differences in body size between men and women, as has previously been reported also for two-point discrimination on the hands (Peters *et al.*, 2009). Taken together, these gender differences indicate that women are more sensitive both to

discriminative and affective aspects of touch. However, the differences in ratings of affective touch perception might also arise from top-down gender differences, including differences in interpretation of the VAS labels. **paper III** further confirmed the shape and peak of the rating curve for eroticism that was reported in **paper II**.

5.4 General discussion

The touch we receive in early life shapes us and our ways of touching others. From early childhood and throughout life, touch remains a core feature in human interaction. As shown in this thesis, affective touch is processed differently than non-affective touch in early post-natal life. Other studies have shown that heart rate in infants is modulated by affective touch (Fairhurst *et al.*, 2014). In a recent fMRI study on affective touch, reward processing cortical areas show stronger activations in adolescents compared to adults (May *et al.*, 2014). The authors conclude that adolescents have a different touching behavior. This could be a function of a change in the meaning of touch in puberty. From being a part of a social group in childhood, the adolescents start using touch as a means of creating their own social group and to find a partner. During puberty it is likely that we also start thinking of touch as something that can be erotic. In this thesis, I show that the word eroticism can be attributed to CT afferent optimal touch, in a similar manner as pleasantness. The feeling of the stroking touch is probably highly similar in adults and children (potentially slightly different as the hair follicle density in children should be higher than in adults), but the interpretation changes – allowing affective touch to be described also as erotic. As shown in **paper II**, the eroticism ratings decreased as a function of romantic relationship length, indicating the interpretation of touch has changed as the relationship matures.

The type of touch used in this thesis is described as pleasant in a number of studies, and in **paper II** and **III** in this thesis, also as erotic.

It is important to point out that the ratings of perceived pleasantness and eroticism are highly subjective. Great care was taken to give the information to the participants in a consistent way, however factors such as for example social desirability might still have influenced the rating behavior. Social desirability is a phenomenon in which the participant attempts to give the expected answer on questionnaires, according to the social norms surrounding the questions (Grimm, 2010). In the case of VAS ratings in this thesis social desirability might have resulted in participants rating the touch in a way that did not reflect their actual experience. Another factor that might have influenced the results was the interpretation of the rating scale labels. No definitions of the labels were given, so it is likely that there was an inter-participant difference in the interpretation. Possibly this interpretation difference was gender dependent, which would explain the gender differences found in **paper III**. The laboratory environment in which the data was collected is far from the normal social touch interactions we experience, which might make broad, context dependent labels, i.e. eroticism, hard to evaluate and rate.

Pleasantness and eroticism are unlikely to be the only terms that can be used to describe the CT afferent optimal touch. Words such as security, calmness or acceptance would plausibly also produce the same inverted U-shape. Touch has indeed the power to induce calmness and relaxation in the receiver, as has been shown in different patient groups (Lindgren *et al.*, 2013; Hart *et al.*, 2001). Slow, CT afferent mediated touch, activates areas implicated in affective processing and reward, potentially releasing neuropeptides such as oxytocin (Walker *et al.*, 2017) which further results in a calming sensation. The function of the CT afferent system could in summary be described as a way for humans, and other mammals, to create affiliation and to express the physiological state that one is in.

5.5 Applications

The study of affective touch, how it is perceived and the effects of it, is important to understand how humans communicate and form affiliations. Touch is one of the channels of communication that have received the least attention. However, touch has large impact on our everyday life. In many healthcare settings touch has been found to have positive effect, making the patients feel relaxed and less anxious. Further understanding the mechanism behind these positive effects could help us better use this powerful way of communication in an adequate way. Potentially, insights into and better understanding for conditions with altered tactile sensitivity, such as autism spectrum disorders could also be achieved.

6 Conclusion

The current thesis has added new knowledge to the growing field of affective touch. First, it was shown that cortical processing of affective touch differed from processing of non-affective touch already in early postnatal life, which can help us understand the positive effects of skin-to-skin care and further investigate the importance of touch for social bonding and neural development. Second, important discoveries about the relation between pleasant and erotic touch were made. These findings can prove to be of use in the study of sexual dysfunctions and in studies concerning romantic couples. Third, gender differences in ratings of touch perception were found, which opens up for new studies on the origin of this difference. In designing future studies in the field of affective touch this gender difference should be taken into account.

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