EFFECTS OF SELF MOVEMENT ON ABSOLUTE AND MASKED THRESHOLDS IN THE PACINIAN CHANNEL

by

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EFFECTS OF SELF MOVEMENT ON ABSOLUTE AND MASKED THRESHOLDS IN THE PACINIAN CHANNEL

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ABSTRACT

EFFECTS OF SELF MOVEMENT ON ABSOLUTE AND MASKED THRESHOLDS IN THE PACINIAN CHANNEL

In this thesis, we simulated active touch by measuring absolute and masked thresholds in the Pacinian channel during cyclic self-movement. Based on previous work we hypothesized improvement in the absolute thresholds and increase of masking efficiency compared to passive touch condition. An aluminum contactor (r=0.685) cm) was used for the stimulation of the left middle fingertip of the subjects. The measurements of the psychophysical thresholds were repeated for three conditions: no movement, slow self-movement (0.1-0.2 m/s), and fast self-movement (0.5-0.6 m/s). The slow movement condition (-20.8 dB) and the fast movement condition (-21.8 dB) yielded on average lower thresholds than the passive condition (-17.9 dB). Paired t-tests showed that the differences between the movement conditions and the passive condition were significant (p=0.023 for passive vs. slow; p=0.024 passive vs. fast). Interestingly the threshold shift due to masking increased with self-movement (2.9 dB for passive; 7.9 dB for slow; 9.2 dB for fast). The differences between the threshold shift due to masking for passive and individual movement conditions were significant. According to these results, self-movement significantly enhanced sensation in the Pacinian channel. However the speed of the self-movement did not matter. Forward- masking efficiency also increased due to self-movement. Therefore this enhancement seems to operate at both threshold and suprathreshold levels. Since self-movement involves both proprioceptive and motor signals, the exact source of this enhancement currently cannot be identified.

Keywords: Psychophysics, somatosensation, vibratory stimulus, Pacinian, human, active touch.

ÖZET

ÖZ-HAREKETİN PAÇİNİ KANALINDA MUTLAK VE MASKELİ ALGILAMA EŞİKLERİNE ETKİSİ

Bu tezde, kişi periyodik olarak hareket ederken Paçini kanalının mutlak ve maskeli eşik değerlerini ölçerek aktif dokunma duyusunu oluşturmaya çalıştık. Önceki araştırmalardan yola çıkarak mutlak eşik değerlerinin düşmesini ve maskeleme etkinliğinin artmasını sınadık. Deneklerin sol orta parmak uçları yarıçapı 0.685 cm olan bir aluminyum kontak ucuyla mekanik olarak uyarılmıştır. Psikofiziksel eşik değerlerinin ölçümü üç ayrı durumda tekrarlanmıştır: statik durum, yayaş hareket (0.1-0.2 m/s), hızlı hareket (0.5-0.6 ms/s). Hareketli durumdaki (yavaş: -20.8 dB; hızlı: -21.8 dB) eşik seviyeleri pasif (-17.9 dB) duruma kıyasla daha düşük çıkmıştır. Eşli t testleri hareketli eşik değerlerinin pasif durumdan istatistiksel olarak farklı olduğunu göstermiştir (pasif ve yavaş: p=0.023, pasif ve hızlı: p=0.024). Ayrıca maskeyle oluşan eşik yükselmesi hareketle artmıştır (pasif: 2.9 dB, yavaş: 7.9 dB, hızlı: 9.2 dB). Pasif durum ve hareketli durumlar arasındaki maskeleme etkisi istatistiksel olarak anlamlı çıkmıştır. Bu sonuçlara göre öz-hareketin Paçini kanalından kaynaklanan dokunma duyusunu iyileştirdiği söylenebilir ancak hızın pek etkisi olmadığı görülmüştür. Maskeleme etkisi hareketle artmıştır. Bu da duyudaki iyileşmenin hem eşik seviyesinde hem de eşik üstünde olabildiğini göstermektedir fakat öz-hareket sırasında hem proprioseptif hem de motor sinyaller oluştuğu için bu iyileşmenin tam kaynağı şu an bilinmemektedir.

Anahtar Sözcükler: Psikofizik, bedensel duyu, titreşimsel uyarı, Paçini, insan, aktif dokunma.

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LIST OF SYMBOLS

LIST OF ABBREVIATIONS

Hz Hertz

PC Pacinian Channel

RA Rapidly Adapting

SA Slowly Adapting

FA Fast Adapting

RF Receptive Field

DCN Dorsal Column Nuclei

ML Medial Lemniscal

NP Non-Pacinian

ms Milliseconds

mm Millimeters

 $\mu \mathrm{m}$ Micrometers

dB Decibel

RS Rough-smooth

RR Rough-rough

1. INTRODUCTION

1.1 Motivation and Hypothesis

Tactile sense has as much importance as the other senses during exploration of the environment and performing the life tasks daily. Due to the fact that recognition of objects and communicating with other organisms are mostly carried in a dynamic fashion, we use senses almost always while moving. Previous work has shown that active sensation gives more information compared to passive reception sensory inputs.

We initially performed pilot experiments to induce movement during vibrotactile detection tasks. The subjects voluntarily moved their arms while mechanical vibration was applied at the fingertips. Since movement should be continuous in all psychophysical trials we found the most comfortable position of the hand while moving.

My hypothesis was that with movement the sensory thresholds should decrease, i.e. an enhancement. Further experiments were conducted to test whether there is an enhancement at suprathreshold levels by finding the efficiency of forward masking. All experiments activated the Pacinian channel by using large contactors at 250 Hz.

2. THEORY

2.1 Somatosensation

Animals and humans are exposed to different kinds of stimuli in daily life. Sensory organs and receptors help to detect and distinguish the noxious stimuli from innocuous. Somatosensation sometimes behaves as an alarm system too. However the sense of touch has evolved to discriminate fine textures and identify objects in higher organisms. There are several types of receptors and each is specialized to a different tactile modality. The physical signal detected by the receptors is transformed into the trains of nerve impulses in the afferent nerve fibers that innervate receptors before being transmitted to the brain. The information processing in the brain enables us to perceive different features in the stimuli and integrate those to identify objects [1].

Somatosensory system is specialized to provide information about touch, vibration, temperature of the skin and pain. In Addition to these variables we can also construct other psychological properties like dryness and wetness and make size estimates by solely touching. Somatosensation also includes information from inside of the body as well as the skin. Specifically proprioceptors supply information about the position of the limbs in space, muscle length and force. This information is automatically combined with the sense of touch [2].

The sensory information obtained from the receptors is transferred to the nerve fibers that the receptor organ is linked to and the nerve fibres convey the action potentials to the somatosensory centers in the brain. There are three synaptic relay stations between sensory receptors and the cerebral cortex (Figure 2.1). The afferent fibres of the mechanoreceptors in the skin terminate in the gracile or cuneate nuclei in the caudal medulla. Secondary neurons project to contralateral thalamus and terminate in the ventral posterior lateral nucleus. Afterwards the information is relayed to the primary somatosensory cortex (S-I) [3].

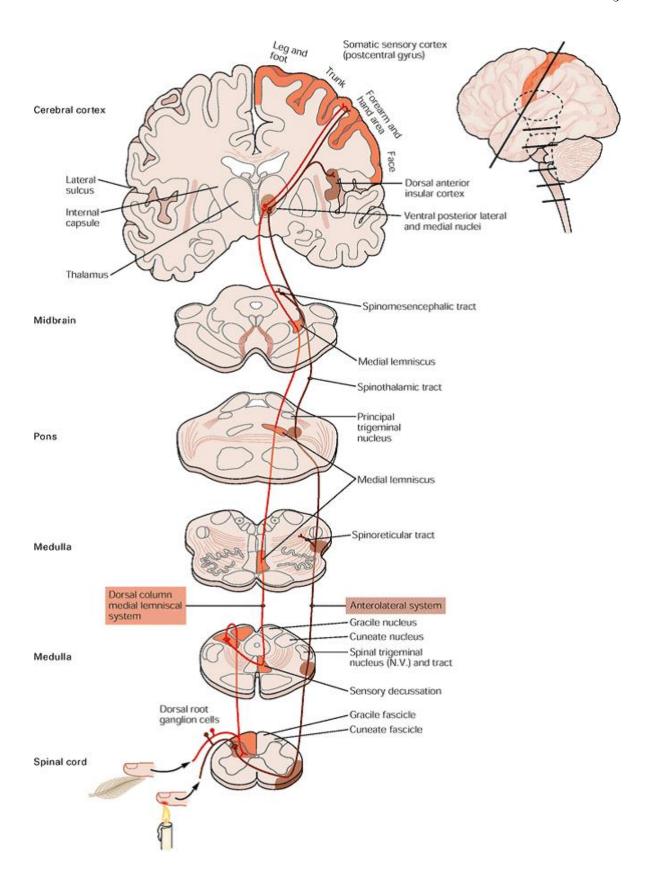


Figure 2.1 Two ascending pathways transmit the sensory information from the skin[3]

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2.2 Structure of the glabrous skin

Skin is the largest organ of the whole body and has a highly complex structure. It acts as a barrier between the internal body and the outer environment. It is safe to say that skin protects the animals from the large physical fluctuations outside [4]. Additionally skin is covered with many sensory organs which help the organism for survival. Several specialized components such as hair, hoofs, claws and nails are also incorporated in the skin. There are three types of skin covering the body: glabrous (hairless), hairy and mucocutaneous skin. Palms and the soles of the feet have glabrous skin, and most of the other parts have hairy skin. Mucocutaneous skin is present at the entrance sites of the body like nostrils [2].

The glabrous skin consists of two layers which are the epidermis and the dermis. Epidermis is the outer part of the skin with 0.05-1.5 mm in thickness and it is important for protecting the underline tissue. It is mainly composed of keratinocytes. Epithelial cells that are generated at the border between the epidermis and dermis move outwards to the epidermis over time. They begin to die during this movement and constitute the hard surface of the outer skin called stratum corneum. The epidermis is connected tightly to the dermis via a complex network of glycoproteins. Dermis has a different structure that is formed by elastic fibres floating in a semi-fluid mixture called the ground substance. It has a varying thickness around 0.5-5 mm. The important components such as fat cells, blood vessels, smooth muscle, sweat glands, the lymphatic supply and, sensory receptors with the nerve fibres innervating them are all located in the dermal tissue of the glabrous skin [2, 4, 5, 6, 7].

Glabrous skin is highly different from the hairy skin as not having hair follicles and associated sense organs (Figure 2.2) It has four types of mechanoreceptors: which are Meissner Corpuscles, Pacinian Corpuscles, Merkel disc receptors, Ruffini endings. The nerve fibers innervating these receptors respectively called RA, PC, SAI and SAII. These mechanoreceptive fibers are classified according to their adaptation and receptive field (RF) properties [8, 9]. SAI and SAII are slowly adapting, while FAI (or RA) and FAII (or PC) are rapidly (fast) adapting afferents. Adaptation signifies the response

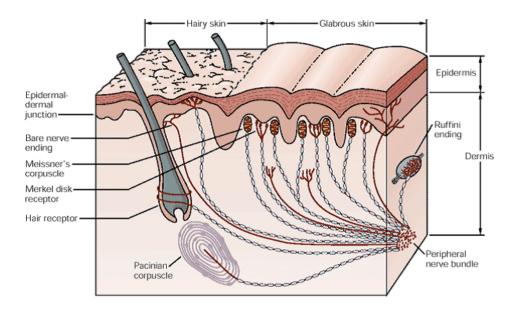


Figure 2.2 Mechanoreceptors in the hairy and glabrous skin of the human hand [3]

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characteristics of the afferent fibres to the sustained skin indentation. FA afferents only generate action potentials during the onset and offset of skin indentation. On the contrary, SA afferents can generate action potential during the static phase of the indentation. Receptive field of a mechanoreceptive fibre is defined by Greenspan and Bolanowski [5] as "the area of skin that, when stimulated, will generate a response in that sensory neuron". Type I fibers have small RF's and type II fibres have larger RF's. Additionally type I fibers have higher innervation densities compared to type II fibers (Figure 2.3) [5]. Johansson R. S. and Vallbo A. B. found that the innervation density of the mechanoreceptors increase in distal direction by recording from the units in the medial nerve. To put in a different way, density is more in fingertips compared to palms [10].

2.3 Sense of touch

The sense of touch originates from the mechanoreceptors in the skin. They are stimulated by a motion across the skin surface or by indentation of the skin. The stress and strain at the mechanoreceptor endings deform the cell membrane and change the permeability of the membrane to ions. Consequently, the ending is depolarized.

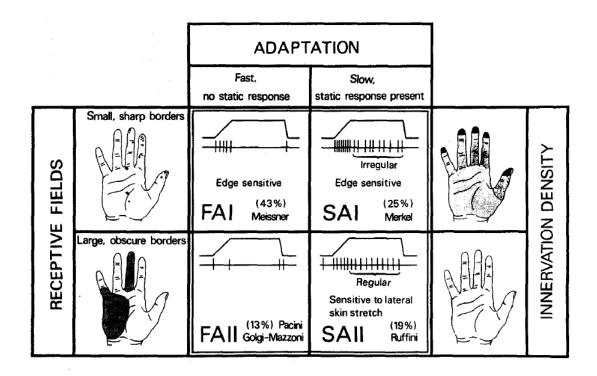


Figure 2.3 Four types of mechanoreceptive fibers and their properties [5]

This is called mechano-electric transduction. If the depolarization is high enough an action potential is generated at the nerve fiber, and this action potential propagates first to the spinal cord. The cell bodies of the mechanoreceptive afferent fibers are located in the dorsal root ganglia. In the dorsal column pathway the axon of the sensory neuron enters the spinal cord and sends collateral up to the dorsal column nucleus. The first synapse occurs there. The secondary neurons cross the midline in medial lemniscus (ML) and synapse in the thalamus. Thalamic neurons projects to the primary somatosensory cortex located in the post central gyrus at the parietal lobe [3, 2, 11]. Tactile neurons and neural assemblies integrate information from different mechanoreceptors. We can distinguish four psychophysical channels associated with the sub modalities of the sense of touch. These channels operate independently to a certain extent. There is little known about how the channels are unified to a single percept.

2.3.1 Four channel model

Based on the receptor systems the psychophysical channels are identified as P channel, NPI channel, NP II channel and NP III channel [9]. Each channel has the neural elements that are tuned to specific features of the stimuli. The correspondence between the channel and the receptor systems is as the following.

- Pacinian channel (Fast Adapting II, Pacinian corpuscles)
- Non-Pacinian I channel (Fast Adapting I, Meissner corpuscles)
- Non-Pacinian II channel (Slowly Adapting II, Ruffini endings)
- Non-Pacinian III channel (Slowly Adapting I, Merkel discs)

Several non-neural constituents are linked to these mechanoreceptors, and they are thought to have metabolic roles as well as shaping the response properties. One major example of these accessory structures is capsule. For example the capsule of the Pacinian corpuscle primarily filters low frequency components in the mechanical stimulus [2, 9].

Pacinian channel

Pacinian channel is mediated by Pacinian corpuscles. These corpuscles are located deep in the dermis or sub-cutaneous tissue. They are innervated by Fast adapting II fibres and have onion like capsules with approximately 1mm length (Figure 2.4). This lamellated non-neural capsule acts as a high pass mechanical filter [13]. Pacinian corpuscles can also be found in the hairy skin and in some other body tissues such as viscera or tendons. They respond mostly to high frequencies, optimally around 250-300 Hz. They are also sensitive to distant events through transmitted vibration [14]. The properties of the Pacinian psychophysical channel are largely dependent of the Pacinian corpuscles. This channel is the most sensitive tactile channel and can spatially summate mechanical stimuli. In other words increasing contactor size decreases

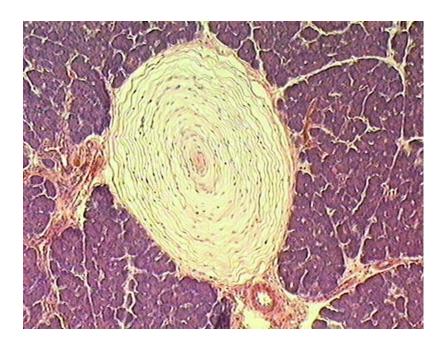


Figure 2.4 Structure of the Pacinian corpuscle [12]

detection thresholds. Additionally successive stimuli are also integrated as temporal summation in the channel.

Non-Pacinian I channel

This channel is mediated by Meissner corpuscles which lie close to the skin surface. They are ovoid in shape and are located in the dermal papillae. Human subjects feel "flutter" when this channel is activated. NPI channel is sensitive to lower frequencies [9].

Non-Pacinian II channel

This channel is mediated by Ruffini endings which are spindle like structures lying parallel to skin surface. They are located deep in the dermis and sensitive to lateral skin stretch. NPII channel mainly has two roles. It perceives object motion on the skin and forces during skin stretch. Additionally hand shape and finger position are also estimated by skin stretch, especially at joints [14].

Non-Pacinian III channel

This channel is mediated by Merkel disc receptors. Afferent fibers come close to Merkel cells and form Merkel cell-neurite complex. A single afferent fiber may innervate many Merkel cells. The psychophysical and neurophysiological studies indicate that this channel is responsible from texture perception. Since SAI fibers are slowly adapting NPIII channel is sensitive to very low frequencies around 1 Hz [15].

2.3.2 The psychophysics of touch

As mentioned above there are four types of the cutaneous receptors in the glabrous skin of the human hand and four types of nerve fibres innervating them. Psychophysical studies are based on stimulating the receptors and taking behavioral measurements to examine the response properties of channels associated with the receptor systems. To understand the cutaneous sense it is important to know the concept of psychophysical threshold. The threshold of detection of a physical stimulus is defined as 'the minimum amount of the stimulus that is needed for the sensory system to elicit a behavioral response'[1]. The researchers measure sensory thresholds at several stimulus frequencies by using sinusoidal mechanical vibrations. In this type of a stimulus the amplitude and the frequency of the displacements can be independently controlled. The threshold-frequency characteristics of the four psychophysical channels is determined by selectively activating the channels by various techniques like changing the frequency, changing the contactor size, by applying masking methods, and changing the skin surface temperature (Figure 2.5) [5]. Highest sensitivity portions above 100 Hz are attributed to the Pacinian channel (Figure 2.5). By masking this channel it is possible to obtain the characteristic of NPII channel which had thresholds lying much above the Pacinian channel. On the other hand low frequencies are primarily sub served by the NPI and the NPIII channel.

In this thesis the effect of self-movement was first studied at threshold level by simply measuring detection thresholds of the Pacinian channel during the experimental

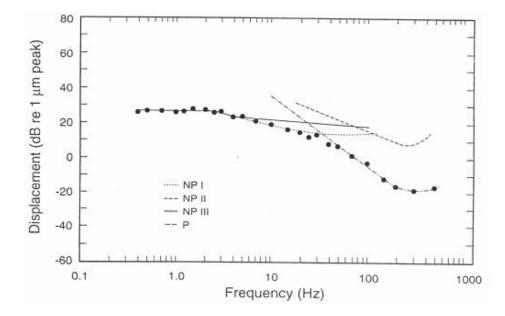


Figure 2.5 The threshold-frequency characteristics of four vibrotactile channels [16]

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task. However, in the daily tasks which involve active exploration by hands, people are mostly subjects to suprathreshold intensities. Since scaling of suprathreshold stimuli is subjective, I indirectly looked at the effect of self-movement at suprathreshold levels by using a forward masking procedure. Masking phenomenon in experimental psychology was discovered very early in the field. Masking is used in old sensory studies including olfactory, auditory, visual, as well as somatosensory. In vibrotactile forward masking, a masking stimulus is applied before the test stimulus. The masking stimulus degrades the detection of the test [17]. Since physiological experiments have shown that the response of mechanoreceptive afferent fibers do not change because of the introduction of the masking stimulus, forward masking is thought to be mediated by the central nervous system. In my experiments the effect of the suprathreshold masking stimulus was altered during movement.

2.4 Kinesthesis

Kinesthesia is the awareness of position and movement by the help of proprioceptors. CNS takes information from both cutaneous receptors and proprioceptors, and integrates that to form the sense of kinesthesia. Proprioceptive system gives us position/movement sense with regard to the information taken from the receptors in joints and muscles. This information is constantly processed without our awareness, but we can realize how important it is when our visual sense is not present or cannot help our daily tasks. For example when one tries to pick up a glass of water, it is important not to exert so much force on the glass, and also hold it so that it will not slip. This task cannot be performed only by visual inputs. Similarly walking requires proprioceptive inputs, we can walk with our eyes closed. However, if one loses the proprioceptive sense he/she should pay attention to the position of the body only through the visual sense and walking is very difficult. Proprioception has two sub-modalities: the sense of immobile status of limb and the sense of limb movement [3]. When a person decides to execute a movement kinesthetic movements develop initially. It seems that the configuration of further sensory inputs is compared and contrasted with these initial templates. While the motor system performs the movement the kinesthetic sensory system seems to lead the other sensory mechanisms. This was considered as a way of thinking unwittingly [18].

Somatosensory system incorporates the cutaneous sense, proprioception and the sense of pain and temperature. A tactual experience gives us a unified percept which includes information about the surface, shape, texture, solidity and temperature of an object, while proprioception signals the static position and movement of our fingers and limbs. Brodmann (1909) divided the cortex according to structure and organization of the cells and numbered each part which is still used today [19]. Proprioceptive sensory information from limbs and muscles is represented in Brodmann area 3a whereas information from skin/touch receptors is represented in area 3b. Sensation, derived from tactile receptors and limb proprioception are both conveyed to the thalamus via the dorsal column-medial lemniscal system. The neural pathway of proprioceptive system is represented in Figure 2.6. Although both tactile and proprioceptive axons are

transmitted via the dorsal columns they remain segregated anatomically. The axons from tactile receptors placed dorsally than those of proprioceptors which are positioned ventrally. Segregation occurs in the gracile and cuneate nuclei where proprioceptive fibers also terminate. In the spinal cord, proprioceptive afferents terminate ventrally in the nucleus of Clarke's column, on motor neurons in lamina IX, and on interneurons in laminae V and VI of the dorsal horn while the neurons for sense of touch terminate in the nucleus proprius in the laminae III and IV [3].

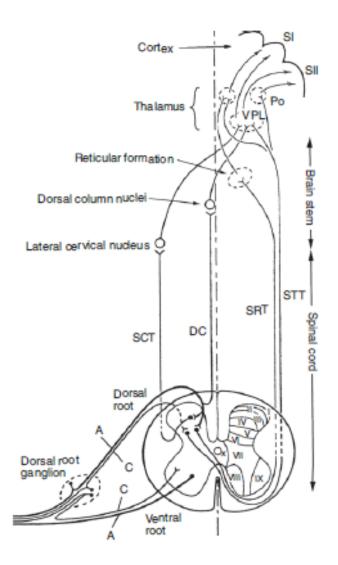


Figure 2.6 Neural pathway of the proprioceptive system [20]

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2.5 Active sensation

Gibson (1962) described active touch as ordinary touching and passive one as being touched [21]. The experiments conducted on passive touch phenomenon have been useful to determine the basic mechanisms of touch. For example, Craig (1968) had shown the spatial summation effect on the human glabrous skin which can be defined as the increase of sensitivity as a function of contactor size [22].

It is important to observe the passive touch processes, because the stimulus condition can be precisely specified. However active touch is more relevant for daily tactile experiences. With active touch, limbs are moved during tactile exploration. Therefore, proprioceptors and motor signals are involved as well as cutaneous inputs. Gibson supported this dichotomy of active and passive sensation by describing the fact that if an observer is exposed to passive stimulation he/she will try to describe this experience in terms of tactile sensations, whereas if the subject is underwent active tactual exploration this description will be in terms of the objects in space. However, it is really difficult to design controlled experiments for active touch in which the stimulus waveform can be specified at the level of micrometers (fine tactile discrimination). Therefore one of the important contributions of this thesis is that protocols used for passive touch experiments were combined with movement in a controlled way in humans. Previously these types of experiments were mostly done with rat vibrissa system in behavioral tasks. This system does not exist in humans.

2.5.1 Vibrissal active touch

Rats are nocturnal animals and do not depend on visual inputs as much as olfactory inputs and tactile inputs especially from whiskers. Therefore rat whiskers were thought as a good modeled system for human fingers. Like our fingers rats move their vibrissae to get information from external environment. Therefore they constantly used active touch. Active touch capacity of rats enables them to solve very complex perceptual

tasks. These tasks include texture, shape, and position discrimination.

Welker (1964) was one of the first scientists who realize that rats scan their environment with their whiskers to detect, localize and perceive objects and their spatiotemporal organization [23]. Szwed and his colleagues (2003) induced artificial whisking in anesthetized rats and recorded from first order neurons in the trigeminal ganglion. These neurons offer a rich repertoire of responses during active touch, which could not be deduced from their responses to passive deflection stimuli [24].

Vibrissal system of the rat is composed of nested feedback loops that have a closed cycle at the level of brainstem and extend to neocortex level (Figure 2.8). The motor nuclei which control the movement of each vibrissa and secondary sensory nuclei are included by the brainstem sensorimotor loop. Sensorimotor integration is mediated at the lowest order by this circuit [25].

At this time it is difficult to verify these feedback loops in the human because they require invasive experiments. Therefore there is limited amount of work in the literature which has physiological data on active touch in humans.

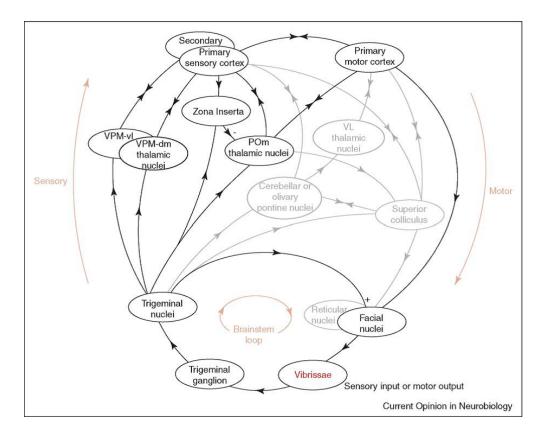


Figure 2.7 Nested sensorimotor loops of vibrissal system of the rat [25]

2.5.2 Effect of movement on tactual perception

centers involved.

Human experiments on active touch were mostly designed as cognitive tasks. Two ideas came along together regarding the effect of movement on the sense of touch. One suggests that active movement enhances tactile sensation whereas the other suggests that during movement the sensory capacity is actually decreased. This contradiction may be because of the complexity of the tactile tasks, and associated neural

Gibson (1962) used raised edge objects for testing identification during active and passive touch. He found that that the mean frequency of correct matches for passive touch is 49% and for active touch 95% [21]. Touching an object instead of being touched lead to an improvement in tactile object recognition according to his paper. Since active touch also involved kinesthesia, it may have caused the improvement with

the help of proprioceptors [26]. Furthermore, it was suggested that muscles controlling the hand may be active even if the hand was held immobile, as during normal postural maintenance or isometric muscle contractions.

According to Magee and Kennedy (1980), active touch requires division of attention between sensory and motor tasks [27]. Their subjects performed worse when they voluntarily moved their hands compared to involuntary movement induced by the experimenter. This experiment shows that the motor signal may be detrimental for the recognition tasks. Additionally this decrease in performance may be due to the extra load of cognitive processing during the planning of movement.

However, in another study, Brisben and his colleagues (1999) studied the detection of vibration through an object grasped in the hand, and found that voluntarily exerting the grasping force was effective for lowering thresholds in the palm. Furthermore they added that the difference between the thresholds were not so much to be considered as practically significant (4dB at 40 Hz and 2 dB for 300 Hz) [28]. This study did not involve movement, so the active touch process was not fully operational.

Güçlü and Murat (2007) studied active and passive sequential processing and showed that proprioceptive inputs did not improve the counting performance. This task used suprathreshold tactile bumps and probably used higher order cognitive processes during counting [29].

Another study showed that the perception of suprathreshold electrical stimuli is diminished during motor activity. It was concluded that the additional peripheral feedback from the elbow was the source of the gating effects seen during the task of this study. However, the stimuli and the tasks used in this study are very different than mechanical vibrations occurring during passive and active touch. Therefore, these studies [30, 31] are not really informative for understanding tactile sensation during voluntary movement. In this thesis, voluntary movement was performed during a vibrotactile detection task which used mechanical vibrations. The results were interpreted on the basis of the psychophysical theory outlined above.

3. METHOD

3.1 Participants

Ten volunteers who were Boğaziçi University students participated in the experiments. 5 of the subjects are mails and 5 were males. Their ages were between 20-30 years old. The subjects did not have any medical conditions which could interfere with the experiments. The procedure was approved by the Ethics Committee for Human Participants of Boğaziçi University and it did not pose any harm to the participants.

3.2 Experimental set-up

3.2.1 Apparatus

The apparatus (Figure 3.1) was similar to the one used by Güçlü and Öztek (2007) [32]. There was a digital to analogue converter card (Iotech, USA) to produce the vibration waveform. The signal was amplified to drive a mechanical shaker modified from a speaker. The amplitude level at each trial was controlled by a digital attenuator (TDT, USA). Mechanical displacements were applied by a cylindrical aluminum contactor. Contactor radius was 0.685cm. The sinusoidal displacements of the contactor were calibrated by a Photonic Sensor (MTI-2100, MTI Instruments Inc, Albany, NY, USA). Sounds were masked by white noise applied to the participants through headphones. During the experiments only the Pacinian channel was activated by 250 Hz vibrations. The behavioral responses were recorded by a response box. The hands of the participants on a thin platform are supported by a sling. The hand was attached to the platform by medical tape. The movement speed was measured by the integrated output of an accelerometer (B&K, Denmark). The experiments were conducted in a soundproof and vibration insulated booth. The participants could be observed through a small window and their hand position was monitored by a hand

camera. Additionally, skin surface temperatures were measured.

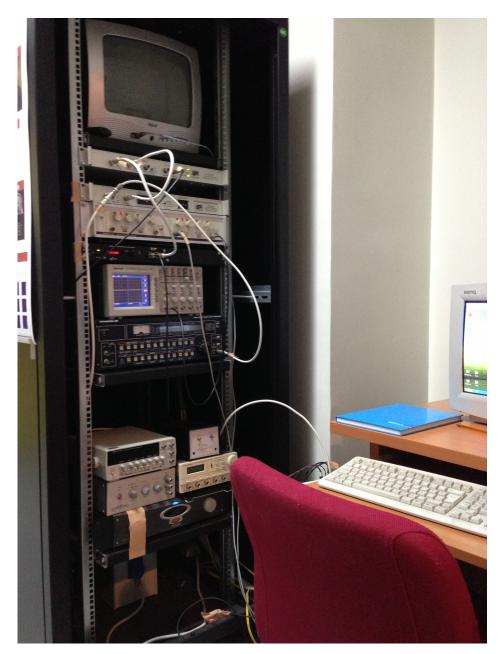


Figure 3.1 The apparatus used to conduct the experiments.

3.2.2 Stimuli

The stimuli were bursts of sine waves superimposed on a 0.5 mm static indentation. The burst stimuli began and ended as cosine-squared ramps with 50-ms rise and fall times. The duration of the test stimulus was 500-ms as measured between half-power points of the burst. The frequency of the test stimulus was 250 Hz. In the

masking experiments, a forward masking stimulus of 250 Hz was applied before the test stimulus at each trial. The intensity of the masking stimulus was 30 dB above the threshold for each participant. The duration of the masking stimulus was also 500-ms, and there was a 150-ms gap between the masking and test stimulus. The timing diagrams for absolute and masked threshold experiments are given in Figure 3.2 and Figure 3.3.

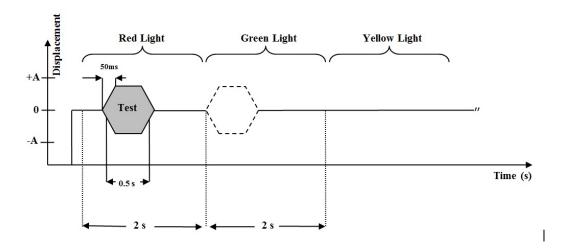


Figure 3.2 Timing diagram for absolute threshold detection experiments.

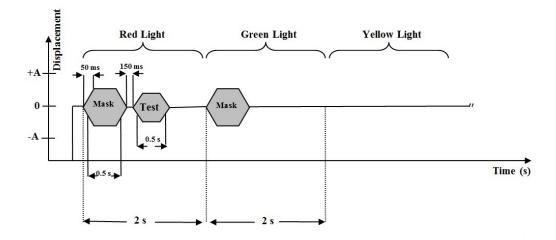


Figure 3.3 Timing diagram for masked threshold detection experiments.

3.3 Procedure

The left hand of each subject was immobilized by modeling clay on a rectangular rigid platform about the size of a human hand. The hand was further secured by elastic bandage cloth wrapped around the platform. The left middle fingertip was stimulated by the contactor probe through a hole in the platform. The height of the contactor probe was adjusted by a micromanipulator fixed to the platform. Two experiments were performed. In first experiment, absolute detection thresholds were measured for three conditions. In the first condition the arm was stationary. In the second condition the subject voluntarily moves his/her arm in the range of 0.10-0.20 m/s after training with a metronome. In the third condition the participant moves his/arm at a fast speed in the range of 0.5-0.6 m/s. The second experiment was similar to the first except the threshold of the Pacinian channel was measured with forward masking.

In control experiments we observed the effect of vibrations coming from the surface of the platform and we saw that the vibrations are weak enough that does not have an effect on the threshold measurement.

Two-interval forced choice method was used as the detection task in the experiments (Figure 3.5). The participant decided whether the test stimulus was in the first or second interval. The mask stimulus occurred in both intervals. However, the interval of the test stimulus was randomized. Each interval was of 2 seconds and queued by a red or green light. (Figure 3.2, Figure 3.3).

The intensity of the test stimulus was altered by using up-down rule which tracks thresholds at 75% correct probability of detection (Figure 3.4) [33]. According to the up-down rule, when an incorrect response is given, the attenuation decreases by 1 dB step. When three correct responses are given (not necessarily consecutive), the attenuation increases by 1 dB. The experiment was automatically stopped when the stimulus level was within \pm dB range for the last 20 trials. Roughly 40-60 trials were needed to reach the threshold.

Full contact was sustained by the help of the indentation between the contactor probe and the skin. Furthermore, the hand and finger position was continuously monitored by a camera and the skin surface temperature was measured. Since the Pacinian channel can be affected by temperature, I ensured that the skin surface temperature was in a relatively narrow range (30-36 ° C). The participant responded after two intervals when the yellow light was on. If the response was correct the yellow light blinked. The participant and hand position are shown in Figure 3.5.

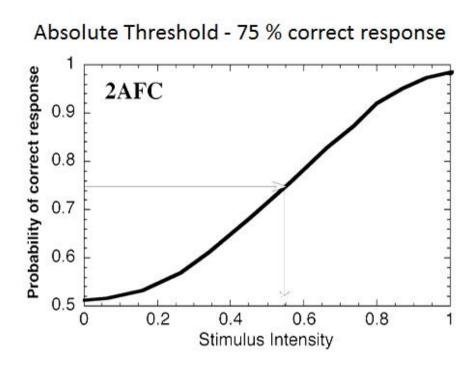


Figure 3.4 Psychometric function for two interval forced choice paradigm [34]

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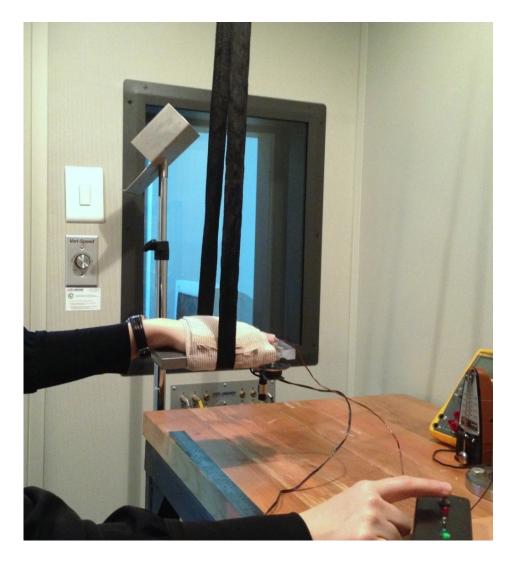


Figure 3.5 Experimental set-up and procedure represented.

3.4 Analysis

All equipment control and data acquisition were performed in MATLAB (Math-Works, Natick, MA, USA). Statistical analyses were done in MS Excel. The detection thresholds were peaked in dB units referenced to 1μ m peak displacement amplitude. Each task was repeated four times for each subject. Normality of each data set was tested by the Lilliefors test. Normality could not be rejected for all conditions except fast movement condition of masked thresholds. Paired t-tests were performed on micrometer averages of those measurements. Pearson correlations were calculated between displacement thresholds and movement speeds. Additionally, I looked at the correlation between the thresholds and the skin surface temperature.

4. RESULTS

4.1 Measurement of absolute detection thresholds

Absolute detection thresholds of each subject were measured at 250 Hz four times. The averages of those measurements were used for statistical analyses. The data from all subjects are given in Figure 4.1 to Figure 4.10. The mean thresholds of the subjects are represented with blue diamonds on the graphs. The threshold values are given in dB referenced to $1\mu m$ peak displacement amplitude. Detection thresholds of seven of ten subjects showed a decreasing trend with movement. S4, S5 and S9 have increasing thresholds. The average threshold in passive movement condition was 0.128 μ m, the average threshold in slow movement condition was 0.091 μ m and the average threshold in fast movement condition was 0.081 μm (Table 4.1). Mean micrometer values showed the decrease of detection thresholds clearly. The averages of the absolute detection thresholds for ten subjects were -17.889 dB for passive condition, -20.787 dB for slow condition and -21.825 dB for fast condition. According to paired t-test the increase from passive condition to slow (p=0.023) and from passive condition to fast (p=0.024) is significant. There is no statistical significance between the mean thresholds of the slow and fast movement conditions (p=0.131). The two graphs on Figure 4.11 and Figure 4.12 give the average threshold values in μ m and dB respectively. There was an approximately 3-4 dB threshold difference between passive and movement conditions (Figure 4.12).

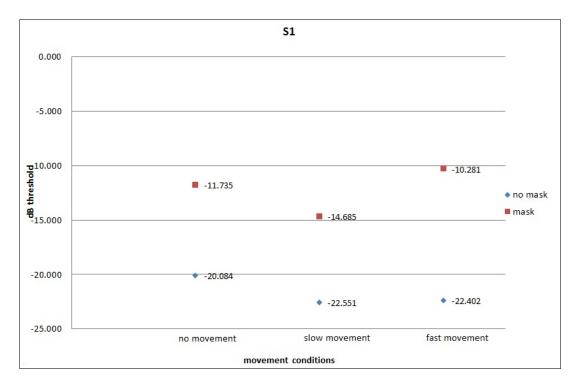


Figure 4.1 Graph of the 1st subject's data.

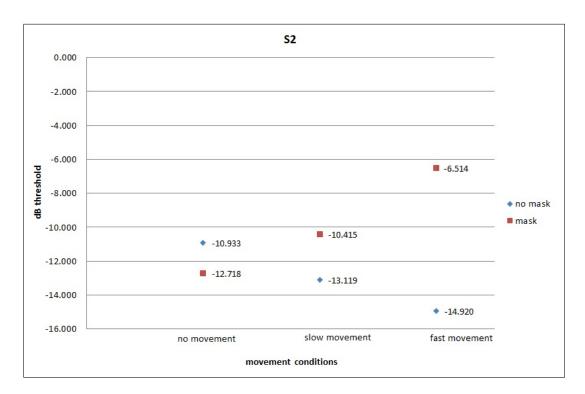


Figure 4.2 Graph of the 2nd subject's data.

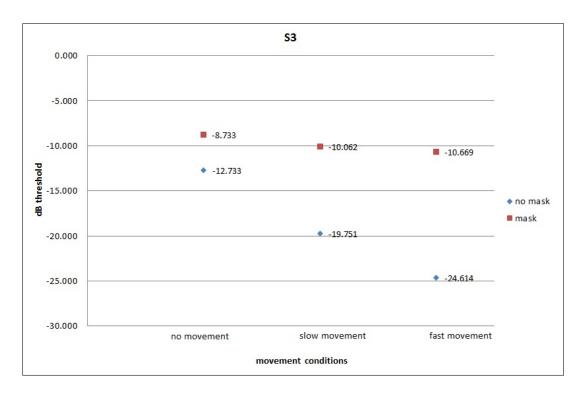


Figure 4.3 Graph of the 3rd subject's data.



Figure 4.4 Graph of the 4th subject's data.

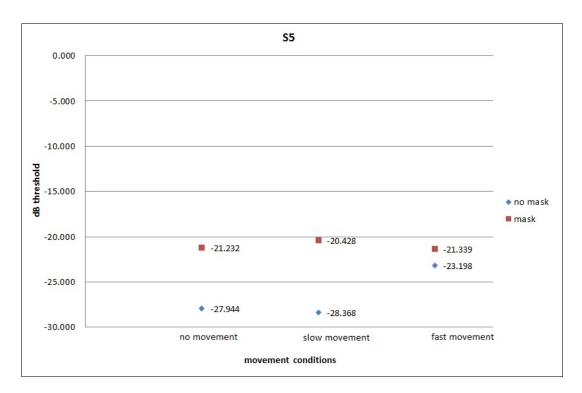


Figure 4.5 Graph of the 5th subject's data.

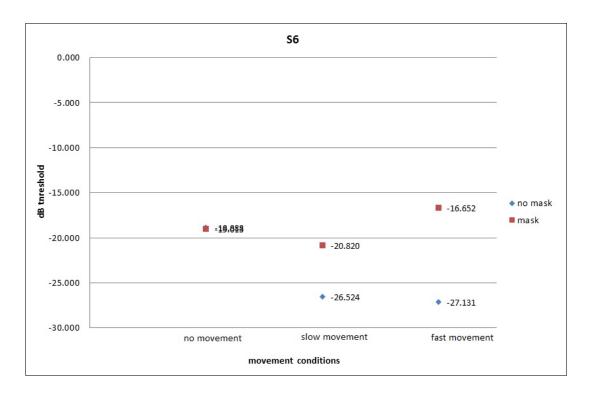


Figure 4.6 Graph of the 6th subject's data.

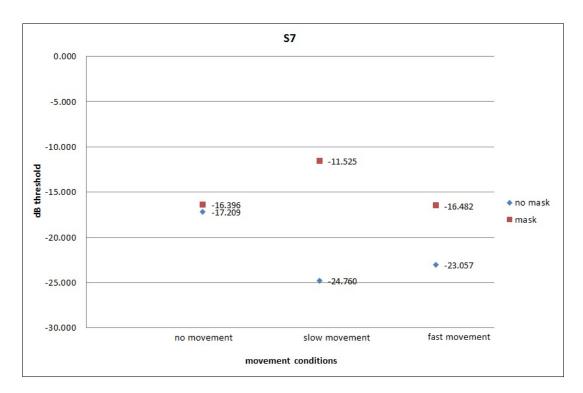


Figure 4.7 Graph of the 7th subject's data.

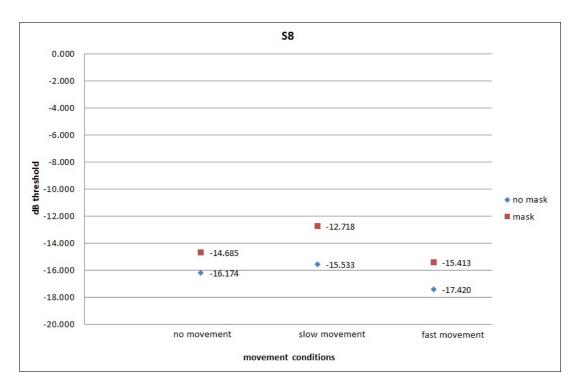


Figure 4.8 Graph of the 8th subject's data.

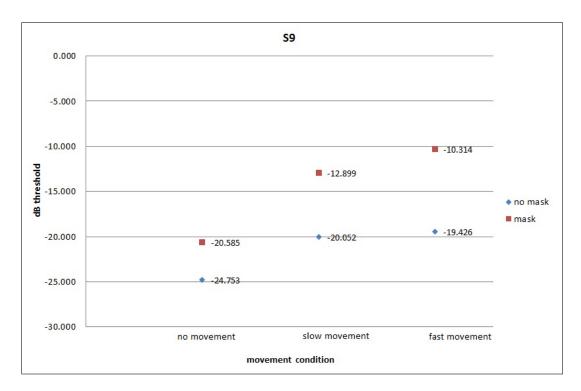


Figure 4.9 Graph of the 9th subject's data.

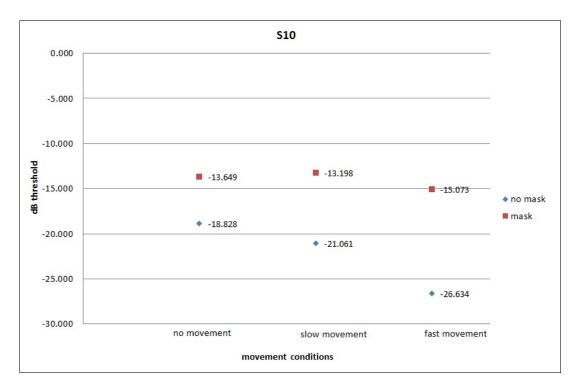


Figure 4.10 Graph of the 10th subject's data.

4.2 Measurement of masked detection thresholds

The entire experimental procedure was repeated by adding a suprathreshold masking stimulus of 250 Hz before the test stimulus (forward masking). Figure 4.1 to Figure 4.10 show the trends of all subjects. The mean thresholds of the subjects are represented with red squares on the graphs. The threshold values are given in dB referenced to 1μ m peak displacement amplitude. The average threshold in passive movement condition was 0.174 μ m, the average threshold in slow movement condition was 0.201 μ m and the average threshold in fast movement condition was 0.225 μ m (Table 4.1). The increasing trend of the detection thresholds is obvious in these data. The averages of the masked detection thresholds for all participants were calculated as -15.204 dB for passive, -13.929 dB for slow movement and -12.937 dB for fast movement conditions. However the increase in the masked thresholds was not statistically significant according to one-tail paired t-tests (p=0.114 for passive vs. slow movement condition, p=0.074 for passive vs. fast condition, and p=0.204 for slow vs. fast movement condition).

One can observe a clear forward masking effect in all subjects. The absolute and masked thresholds were statistically different. Specifically, masked thresholds were elevated (p=0.0261 for passive condition, p<0.001 for slow movement and p<0.001 fast movement conditions). Figure 4.11 and Figure 4.12 show the increase in masked thresholds (see also Table 4.1).

Table 4.1 Mean detection threshold values in μ m for all tested conditions. Standard errors of the mean for each condition were given between parentheses.

	No movement	Slow movement	Fast movement	
	condition (μm)	condition (μm)	condition (μm)	
No mask	0.128(0.08)	0.091 (0.062)	0.081 (0.047)	
Mask	0.174 (0.096)	0.201 (0.086)	0.225 (0.116)	

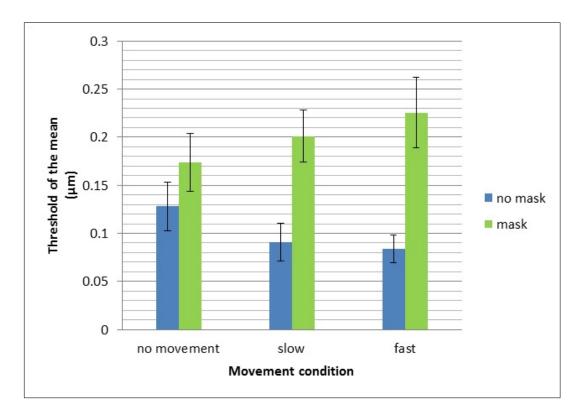


Figure 4.11 Average thresholds in μ m. Error bars are standard error of the mean.

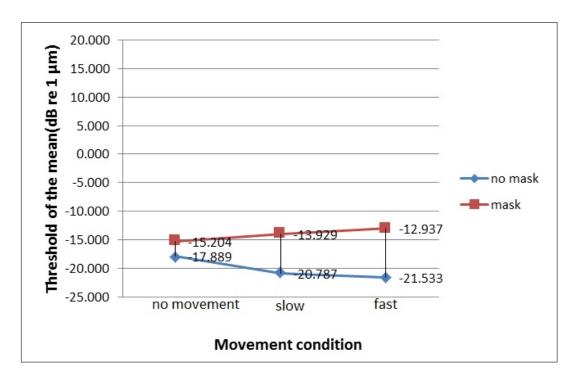


Figure 4.12 Average thresholds in dB.

I also studied the difference in dB thresholds for each condition. Table 4.2 shows those differences in dB values for each subject. On average the difference due to masking was 2.9 dB in passive condition, 7.9 dB in slow movement condition and 9.2 dB for fast movement condition. Figure 4.12 shows an increasing trend of this difference due to movement. Paired t-tests resulted in significant differences between passive and slow conditions (p=0.0040), and between passive and fast movement conditions (p=0.0034). However there was no statistically significant difference between slow and fast movement conditions (p=0.194).

	No movement	Slow movement	Fast movement
S_1	8.349	7.866	12.121
S_2	-1.786	2.704	8.406
S_3	4.000	9.689	13.945
S_4	0.629	13.943	15.604
S_5	6.712	7.940	1.859
S_6	-0.125	5.705	10.480
S_7	0.813	13.236	6.574
S_8	1.489	2.814	2.008
S_9	4.168	7.152	9.112
S_{10}	5.178	7.863	11.561
Average	2.943	7.891	9.167
Standard deviation	3.246	3.748	4.624

4.3 Correlation of temperature and speed with detection threshold

Additional analyses were done to test if there was any correlation between temperature and thresholds. For all tested conditions no significant correlation was found (Table 4.3). Similarly correlation between speed and thresholds was studied and no significant correlation was found (Table 4.4).

 ${\bf Table~4.3}$ Correlation of temperature with threshold for all tested conditions

	No movement		Slow movement		Fast movement	
	R	Pvalue	R	P value	R	P value
No mask	0.247	0.489	0.187	0.603	0.592	0.070
Masked	-0.410	0.238	0.155	0.668	0.609	0.061

 ${\bf Table~4.4}$ Correlation of thresholds with movement speed for no mask and masked conditions

	Slow movement		Fast movement	
	R	Pvalue	R	P value
No mask	0.393	0.260	0.154	0.670
Masked	0.579	0.078	-0.010	0.976

5. DISCUSSION

According to the results of the current experiments, I found that active movement enhances vibrotactile sensation. The hypothesis that movement decreases the detection thresholds of the Pacinian channel was adopted for this work. My aim was to test if active movement has an improvement effect on sensation during voluntary cyclic movements of the hand. According to the results of the experiments which have done to justify the hypothesis I found that active movement enhances the sensation. The study also showed the masking efficiency increased with voluntary movement.

Researchers who are interested in the effect of movement on sensation came to different conclusions depending on the factors like receptive field, type of stimulation or frequency of the stimulus. We have chosen 250 Hz specifically knowing the optimum sensitivity of the PC. The effect of movement on suprathreshold level was indirectly studied by forward masking. It was thought that movement would increase the effect of the masking stimulus, in other words, change the masking efficiency. Enhancement during forward masking would imply more masking, therefore an increase in masking efficiency.

Verrillo (1971) measured detection thresholds on finger pad and thenar eminence of the hand by using different sized contactors at several frequencies [35]. Mean detection threshold of the finger pad in Verrillo's experiments was found to be between -7 to -9 dB (re to 1 μ m peak) when the contactor with the area of 0.005 cm^2 was used. The contactor area used in my experiments was 1.47 cm^2 (radius=0.685 cm) and average of thresholds was -15 dB when no mask was applied in passive condition. The underlying reason for this difference is probably the contactor size and spatial summation. Besides, when a contactor almost equal size to our contactor was used on thenar eminence in Verrillo's work, absolute threshold was found around -22 dB to -24dB.

5.1 Components of active touch

Hartmann (2009) suggested that a movement can be called as active when it includes intent (a psychological variable) besides the activation of receptors (a physiological variable) [26]. In daily life it is hard to determine the intent behind a specific movement. Most of the movements include both sensation and displacement goals. For example when we hold the wheel during driving we both feel the fabric, ovality and size of the wheel, and also turn it when needed by the displacement of our limbs. Figure 5.1 shows various types of active somatosensation ranging from a pure displacement goal to a pure sensory goal. The principal definition of active touch is moving directly to an external object aiming a sensory goal. Our work does not satisfy this definition entirely because of difficulties controlling stimulus during an active touch experiment. The movement was not directed to a sensory goal in our experiments per se. The voluntary movement here was just concurrent with sensation. This is as close as we could get to active touch.

Active Somatosensation in a Moving Sensory Surface Displacement Sensory Goal Goal Locomotion Exploration ACTIVE TOUCH Limb Movements To Explore Manipulation ' **Directed Towards** an External Object Non-Directed To Effect Action

Figure 5.1 Components of active touch by Hartmann (2009)[26]

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5.2 Sensory gating or enhancement

Chapman and her colleagues (1987) stated that in the presence of voluntary motor activity the ability to detect near threshold electrical stimuli applied to skin decreases whereas perception of suprathreshold stimuli is not affected [31].

They based their hypothesis on previous work conducted by several researchers [36, 37]. These researches asserted that transmission of sensory information to the thalamus and somatosensory cortex is diminished when associated with movement. Reduction of amplitude of evoked potentials in the lemniscal system during and prior to voluntary limb movements in cats is an evidence for this idea.

Chapman and colleagues applied electrical stimulation to mid-ventral aspect of the forearm. The electrical stimulus is a very artificial way to stimulate mechanoreceptors and not sensitive enough to give information about vibrotactile sensation. In daily life we do not face electrical stimulation. We are imposed to mechanical forces that come from different sources and directions. Additionally, electrical stimulation excites other fibers, temperature and pain receptors which are processed by different systems in the brain. As a matter of fact the excitation of these superior fibers may be the reason for the gating effect.

Because we applied well controlled vibrotactile (mechanical) stimuli particularly targeting the PC, we support the idea that tactile sensation improves at a small scale (3 dB for passive to slow movement, 1 dB for slow to fast movement) near threshold with voluntary movement. This improvement is probably effective at suprathreshold levels as well because we obtained more masking during movement. Therefore, our work can be explained as enhancement, not gating. However the exact source of this enhancement cannot be identified in this thesis because self-movement contains both proprioceptive and motor signals.

5.3 Whisker studies

Active touch literature stepped up with whisker studies that rely on experiments conducted on rat vibrissae. Rat vibrissal system is recognized to be a good model for active sensing. For active sensing, invasive manipulations can be done on rats.

Carvell and Simons (1995) examined whisker movements of rats by using videobased motion analysis [38]. Before several weeks of the beginning of the testing period, removable blindfolds were custom-fitted to the adult female rats. A forced two choice discrimination method was used as the detection task in behavioral tests. An elevated platform was designed for the animals to stand on. Two other platforms which have textured surfaces attached to them were stretched to the previous one. The animals were responsible for palpating these textured surfaces via their whiskers and jumping on the appropriate stand to take the reward. Discriminanda, which are plastic cylinders, were mounted to front sides of the two platforms. These cylinders were made by opening grooves using a lathe. The animals were divided into two groups. One group of rats was named as rough-smooth (RS) and other group was named as rough-rough (RR). RS group was trained on the cylinder that had fine continuous grooves with $15\mu m$ width and $5\mu m$ depth and also had a second set of grooves with spacing of $500, 250, 200, 150, 100, 75, 50\mu m$. This task was named as "microgeometric". RR was trained to discriminate a discriminandum which had grooves 1 mm deep. The spacings were 3.0, 2.0, 1.75, 1.5, 1.25, 1.125, and 1.06 mm. RR task was named as "macrogeometric" because it had widely spaced features. Measurements were taken from four vibrissae (two right, two left). According to the results of the two groups in terms of performance, whisker hairs were less bent on better performers because there was probably more force exerted during whisking. They also used more time for palpating the discriminanda. The two groups differed in of protraction velocity. RR group showed a good performance on higher velocities whereas RS group performed better at lower velocities. Performance mostly depended on spatial domain for RR group while it depended on temporal components of the whisking patterns for RS group. Without considering the palpating surface, the study mentioned that good discrimination ability was related to features of whisking behavior. Additionally, sensory discrimination

performance and motor patterns were both factors that distinguish the animals individually. Therefore, the study stated that central representation of tactile periphery has both integrative and dynamic components.

Another study based on neural recordings was conducted by Szwed and colleagues [24]. The aim of the work was to investigate the encoding principles of active touch by rat whiskers. Artificial whisking method was used by stimulating the facial motor nerve. Records were taken extracellularly from 80 NV (trigeminal ganglion) neurons in urethane anesthetized rats. These neurons were classified according to their response properties. "Touch cells" (n=30) only produced a response when the whisker contacts with an object. "Whisking cells" (n=14) only produced a response to whisking itself. "Whisking/Touch cells" (n = 15) produced a response when the whisker contacts with an object and whisking itself. "High threshold cells" (n=21) produced only a response to passive stimulation. As a comparison between active and passive sensation 62 of 80 neurons were stimulated with passive computer controlled forward backward deflections. 60% cells were found as RA and 40% as SA. Interestingly, all four classes of cells included analogous proportions of RA and SA cells. In active touch, a rich repertoire of responses were presented whereas the same result could not be seen with passive deflection stimuli. Four events were encoded by individual neurons: whisking, contact with object, pressure against object and detachment from object. Whisking and touch responsive neurons serve two specific decoding schemes. The neurons responsible from whisking fired at specific deflection angles to show the precise position of the whiskers. The neurons responsible for touch encoded the horizontal coordinate of object's status by spike timing. It would be interesting if similar classes of neurons can be found in monkeys during active exploration of tactile objects. For simplicity such an experiment may be designed by controlling movement and vibrotactile stimulus at the same time as in this thesis.

5.4 Limitations of the study

Although some researchers argue that attention may have a detrimental effect on detection [30], the experimental design used in this thesis produces results not depending on attentional processes. The tracking algorithm adopted with the forced choice task does not converge if the subject does not pay attention to the task. Therefore, no result is obtained in such trials, preventing the use of confounded data. I only use trials which converged to 75% probability of detection.

The major limitation of my experiments is how the speed of voluntary movement was controlled. The speed was not specified on a trial by trial bases. I only made sure the average of the cyclic speed was within the range throughout each measurement session. Therefore, during some trials the instantaneous speed was higher or lower than this average. However, since speed change was periodic, on average there would be approximately equal number of high and low instantaneous speed values during an experiment. This probably reduced a systematic bias in the measurement of thresholds. It is rather difficult to design a repetitive and controlled movement during a psychophysical detection task.

Experimental set-up and procedure are influential in the results that have controversy with the references given before. I could not find any study which incorporated movement in a vibrotactile detection task. Whisker studies and animal experiments will help to provide better insight for the mechanisms of active touch. Specifically, similar psychophysical experiments can be performed on monkeys while recording directly from cortical neurons. Further experiments and parallel studies will promote this work.

5.5 Future work

In addition to basic scientific information which can be obtained from active touch experiments, robotics and neuroprosthetics applications will directly benefit from this research. Currently neuroprosthetic limbs generate movement by decoding spike patterns in the motor cortex. They do not have tactile sensation which has recently become a hot topic. From what we know about active touch, the artificial tactile sensation incorporated into these devices should consider the movement component. As a matter of fact embodiment of the artificial limb can only be possible if tactile sensation compliments voluntary movement.

There is also a specific experiment which can follow the work in this thesis. When the subjects performed voluntary movement motor neurons were activated in addition to proprioceptors. The enhancement by self-movement may be due to proprioceptors, motor signals or both. In order to separate these two contributions an experiment can be designed in which the movement was generated artificially, devoid of voluntary motor signals. If the enhancement stays at the same level, one can conclude that it is mostly due to activity originating from proprioceptors. Additional studies can be done to model these systems computationally.

REFERENCES

- 1. Moller, A. R., Sensory systems, anatomy and physiology, San Diego: Academic Press, 2003.
- 2. Bolanowski, S., Somatosensory coding in D. Roberts (Ed.), Signals and perception: The fundamentals of human sensation, The Open University, Palgrave, MacMillan, 2002.
- 3. Kandel, E. R., J. H. Schwartz, and T. M. Jessell, *Principles of Neural Science*, McGraw Hill, 4th ed., 2000.
- 4. Proksch, E., J. M. Brander, and J. M. Jensen, "The skin: An indispensable barrier," *Experimental Dermatology*, Vol. 17, pp. 1063–1072, July 2008.
- 5. Greenspan, J. D., and S. J. Bolanowski, *The psychophysics of tactile perception and its peripheral physiological basis*, pp. 25–103. Handbook of perception and cognition 7: Pain and Touch, USA: San Diego:Academic Press, l. kruger ed., 1996.
- 6. Lederman, S. J., and R. A. Browse, "The physiology and psychophysics of touch," NATO ASI Series: Sensors and sensory systems for advanced robots, Vol. F43, 1988.
- 7. McGrath, J. A., and J. Uitto, *Anatomy and organization of human skin*. Rook's textbook of dermatology, West Sussex, UK: Wiley-Blackwell, 2010.
- 8. Johansson, R. S., and A. B. Vallbo, "Tactile sensory coding in the glabrous skin of the human hand," *Trends in Neuroscience*, Vol. 6, pp. 27–32, 1983.
- 9. Bolanowski, S. J., G. A. Gescheider, R. T. Verrillo, and C. M. Checkosky, "Four channels mediate the mechanical aspects of touch," *Journal of Acoustic Society*, Vol. 84, pp. 1680–1694, November 1988.
- 10. Johansson, R. S., and A. B. Vallbo, "Tactile sensibility in the human hand: relative and absolute densities of four types of mechanoreceptive units in glabrous skin," *Journal of Physiology*, Vol. 286, pp. 283–300, 1979.
- Squire, L. R., F. E. Bloom, S. K. McConnell, J. L. Roberts, N. C. Spitzer, and M. J. Zigmond, Fundamentals of sensory systems. Fundamental Neoroscience, San Diego: Academic Press, 2003.
- 12. Bell, P. B., and B. Safiejko-Mroczka, "Pacinian corpuscle," 2013. https://casweb.ou.edu/pbell/histology/Captions/Integument/42.pacinian.10x.htm.
- 13. Loewenstein, W. R., and R. Skalak, "Mechanical transmission in a pacinian corpuscle," *Journal of Physiology*, Vol. 182, pp. 346–378, 1966.
- 14. Johnson, K. O., "The roles and functions of cutaneous mechanoreceptors," *Currents Opinion in Neurobiology*, Vol. 11, pp. 455–461, 2001.
- 15. Forta, N. G., Vibration intensity difference thresholds. PhD thesis, University of Southampton. Faculty of Engineering, Science and Mathematics. Institute of Sound and Vibration Research, UK, 2009.
- 16. Gescheider, G. A., *Psychophysics: The Fundamentals*, Lawrence Erlbaum Associates, Publishers, 1997.

- 17. Craig, J. C., Vibrotactile pattern recognition and masking, pp. 229–242. Active touch—The mechanism of recognition of objects by manipulation: A multidisciplinary approach, Oxford: Pergamon Press, g. gordon ed., 1978.
- 18. Zion, L. C., "Making sense," Kinesthesia. et Cetera, Vol. 53, p. 300, 1996.
- 19. Broadmann, K., "Vergleichende lokalisationslehre der grosshirnrinde," *Leipzig: Johann Ambrosius Barth*, 1909.
- 20. Smith, C. U. M., Biology of sensory systems, John Wiley and Sons Ltd., 2008.
- 21. Gibson, J. J., "Observations on active touch," *Psychological Review*, Vol. 69, pp. 477–490, 1962.
- 22. Craig, J. C., "Vibrotactile spatial summation," Perception and Psychophysics, Vol. 4, no. 6, 1968.
- 23. Welker, W. I., "Analysis of sniffing of the albino rat," *Behaviour*, Vol. 22, pp. 223–244, 1964.
- 24. Szwed, M., K. Bagdasarian, and E. Ahissar, "Encoding of vibrissal active touch," *Neuron*, Vol. 40, pp. 621–630, October 2003.
- 25. Kleinfeld, D., E. Ahissar, and M. E. Diamond, "Active sensation: insights from the rodent vibrissa sensorimotor system," *Current Opinion in Neurobiology*, Vol. 16, pp. 435–444, 2006.
- 26. Hartmann, M. J. Z., "Active touch, exploratory movements, and sensory prediction," *Integrative and Comparative Biology*, Vol. 49, no. 6, pp. 681–690, 2009.
- 27. Magee, L. E., and J. M. Kennedy, "Exploring pictures tactually," *Nature*, Vol. 283, pp. 287–288, 1980.
- Brisben, A. J., S. S. Hsiao, and K. O. Johnson, "Detection of vibration transmitted through and object grasped in the hand," *Journal of Neurophysiology*, Vol. 81, pp. 1548– 1558, 1999.
- 29. Güçlü, B., and A. Murat, "Active touch does not improve sequential processing in a counting task," *Acta Neurobiol. Exp.*, Vol. 67, pp. 165–169, 2007.
- 30. Post, L. J., I. C. Zompa, and C. E. Chapman, "Perception of vibrotactile stimuli during motor activity in human subjects," *Exp. Brain Res.*, Vol. 100, pp. 107–120, 1994.
- 31. Chapman, C. E., D. Bushnell, D. Miron, G. H. Duncan, and J. P. Lund, "Sensory perception during movement in man," *Exp. Brain Res.*, Vol. 68, pp. 516–524, 1987.
- 32. Güçlü, B., and Öztek. Ç, "Tactile sensitivity of children: Effects of frequency, masking, and the non-pacinian i psychophysical channel," *Journal of Experimental Child Psychology*, Vol. 98, pp. 113–130, 2007.
- 33. Zwislocki, J. J., and E. M. Relkin, "On a psychophysical transformed-rule up and down method converging on a 75% level of correct responses," *Proceedings of the National Academy of Sciences of the USA*, Vol. 98, pp. 4811–4814, 2001.
- 34. Montag, E. D., "Psychometric function," 2013. http://www.cis.rit.edu/people/faculty/montag.

- 35. Verrillo, R. T., "Vibrotactile thresholds measured at finger," *Perception and Psychophysics*, Vol. 9, no. 4, pp. 329–330, 1971.
- 36. Ghez, C., and G. L. Lenzi, "Modulation of sensory transmission in cat lemniscal system during voluntary movement," *Pflügers Arch*, Vol. 323, pp. 273–278, 1971.
- 37. Coulter, J. D., "Sensory transmission through lemniscal pathway during voluntary movement in cat," J. Neurophysiology, Vol. 37, pp. 831–845, 1974.
- 38. Carvell, G. E., and D. J. Simons, "Task and subject related differences in sensorimotor behaviour during active touch," *Somatosensory and Motor Research*, Vol. 12, pp. 1–9, 1995.