Summary of the Kinesthetic and Tactile Function of the Human Upper Extremities

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Feasability Study for the Development of a Miniature Hand-Controller with Force and Tactile Feedback Capability : Characterization of the Human Upper Extremities

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1 Introduction

The first part of this study is meant to provide an assessment of the capability of the human upper extremities in view of an optimized design for a bidirectional "hand controller". Such a device serves a dual purpose: it is an input device as well as a display device. In other terms, a hand controller being meant to "simulate" a mechanical task acts as bidirectional signal transducer. A boundary occurs between the handle and the operator's hand. At this boundary, mechanical signals are exchanged. In order to be able to describe this exchange, a causality direction has to be selected. Should the hand controller impress position on the operator hand and read out forces, or impress forces and read out positions? Or conversely, should we specify the acuity of the hand mechanoreceptors in terms of displacements or forces? In fact, this choice will be based on the available actuators and sensors for force and position and their derivatives. Thus, in the discussions, no particular causality direction will be assumed. Nevertheless, before going further, a short discussion on phenomenal causality is made here.

The phenomena of interest are primarily those governed by the relationships between forces and displacements (and their derivatives) at the interface between the controller and the operator's hand. At a detailed level, we might also be concerned with the continuous visco-elastic properties of the hand and finger tissues and their behavior under the influence of a handle, a comparatively ideally rigid object.[1] We might also be concerned by how these mechanical phenomena are transduced into nerve signals and how those are ultimately processed by the central nervous system. A complete analysis of this broad picture is obviously out of question since it would require a complete understanding of all the phenomena involved in the transduction of mechanical signals into conscious sensation. It is however possible to sketch a coarse picture of what might be happening from data gathered in the literature in the anatomical, physiological, and psycho-physical domains. This data is essential to build an understanding of the function of a hand controller.

If we think of vision, it is clear that light "causes" nervous events at the most intrinsic level. The design of a visual display device will follow from that observation.

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[1] In Lagrangian mechanics, there is no need to invoke "forces" to "explain" the observed trajectories, which simply obey Hamilton's principle of least action.

For mechanical senses (tactile and kinesthetic, to be discussed in greater detail), it is not clear whether forces or displacements (or the two) should be thought of as "signals". In a Newtonian framework, the constitutive equations that govern the properties of the physical phenomena of interest do not display *a priori* "natural causality" properties except for the phenomenon of solid friction.

Part of these phenomena can be described by invoking inertial, elastic, viscous, and other friction forces, and how they relate to displacements. These relationships are called constitutive equations. Since we will strive to minimize the effects of friction from our transduction devices, friction is not immediately relevant to the discussion at hand, although it can be easily understood to display a natural causality in the direction of velocity toward force. In other terms, during the occurrence of the friction phenomena, the velocity may be considered as the input because it is easy to modify at will and the displacement-force relationship can be described *robustly* using this causality.[2]

The other sources of natural causality will be the transduction devices at our disposal: actuators and mechanical signal sensors. For example, an electric motor can be advantageously used to approximate a "pure" force source, and a potentiometer a "pure" sink of position. Of course for any sensor or actuator, these models are only approximations. But in any case, the right model will be the robust one and that will decide the "natural" direction of causality.

2   The Human Sensory System

The human sensory system adopts a highly structured organization, the details of which are outside the scope of this report. However some predominant features are recalled here.

Sensory functions at the lowest level are carried out by receptors responding to various stimuli : mechanical, optical, thermal, and so-on. These receptors may be

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[2]Robustly means that an approximate constitutive equation can account for the observed phenomena. For example consider the Coulomb friction model. It states that forces depend on the sign of the velocity. Clearly, this is robust only of the velocity is considered as an input. The other way around infinitesimal changes in force would "cause" infinitely large changes in velocity! Thus we see that the Coulomb model, although it is a crude approximation, is robust.

seen as specialized nervous cells or neurons. Neurons specialized in the transmission of information are collected in fibers, which in turn form pathways which eventually reach the central nervous system. It should be noted that despite specialization, the function of every single cell is multiple: metabolic, computation, and transmission.

Schematically speaking, neurons are the units that transmit electric pulses, the so-called action potential, which propagates along axons, long processes of the cell's body. Axons are connected to shorter processes of other cells called dentrites by means of small gaps called synapses. Most axons are sheathed in insulating material called myelin. Every few millimeters, the sheathes have gaps called the nodes of Ranvier which act as "signal repeaters". It is usually accepted that neural information is mostly coded by means of pulse frequency modulation rather than amplitude. The only way for the brain to identify the source of the information, either a reflex impulse or a sensory input, is to determine which nerve carries the impulse.

2.1 The Spinal Cord Mechanisms

The sensory systems responsible for the kinesthetic and tactile sensations are organized to receive information from the periphery, process it and relay it to higher neural levels [8].

The first neuron of the chain is a receptor neuron which encodes stimuli into neural signals. It only encodes the information coming from a small region which is called its *receptive field*. The receptor neurons converge to second-order neurons in the central nervous system. These may be located in the medulla or in the dorsal horn of the spinal cord (that is, the grey matter of the spinal cord). There are four groups of dorsal horn neurons. The Class 1 dorsal horn neurons are dedicated to the cutaneous mechanoreceptors only. Neurons of Class 2 are excited both by mechanoreceptors and nociceptors. The Class 3 corresponds to the neurons excited by the nociceptors only. In Class 4, the neurons are mainly excited by the thermoreceptors.

Information is then transmitted to third-order neurons in the thalamus via parallel pathways : the dorsal columns-medial lemniscus system, the spinothalamic tract, the spinocervical tract, or the spinoreticular tract (see [14], [8] or [17] for details).

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The dorsal column-medial lemniscus system differs from the cells of the dorsal horn in its discreteness, its lack of convergence between fibers of different specifications and its weakness to descending control. In addition, it transmits only the information from skin contained in a group of large afferent fibers. Conversely, cells of the spinal cord transmit the information from all afferent fibers [20]. The role of the dorsal columns is not clearly outlined and contradictory interpretations are found in the literature. In [20], it is described that the dorsal columns allow to control the analysis of the amount of the information arriving from the other pathways.

The final destination for the sensory inputs is the cerebral cortex [14]. There are two areas of the cortex devoted to somatosensory functions : area S-I and area S-II.

The pathways for conscious perception just described are distinct from the pathways for reflex acts for which the information is transmitted to a motor neuron either directly or via connector neurons, forming a much shorter path in all respects.

Inhibition may occur. It has been classified in three main categories. The *surround inhibition* is observed when the response of a "cortical unit" is reduced in response to a stimulus applied to an area adjacent to the receptive field. The *complementary inhibition* occurs when a stimulus is applied to the contralateral area of the skin. The *cross-modality inhibition* results from the presentation of another kind of stimuli close to the first receptive field. These phenomena are collectively referred to as *masking*.

2.2   The Neurons

A *neuron* is a single nerve cell, it is the structural and functional unit of the nervous system (see figure 1) [6], [21]. The *dendrites* can be viewed as receivers which conduct impulses toward the cell body. The axon and dendrites may or may not have specialized end organs. There is generally only one *axon*. It can be up to 3 ft. long. The cell body is located in the gray matter of the spinal cord and brain or in ganglia located outside the spinal cord.

The *nerve fibers* are intermingled with the body cell or arranged in bundles. In the spinal cord, these bundles are called *tracts, columns or commissures*, although outside of the spinal cord and brain they are known as nerves.

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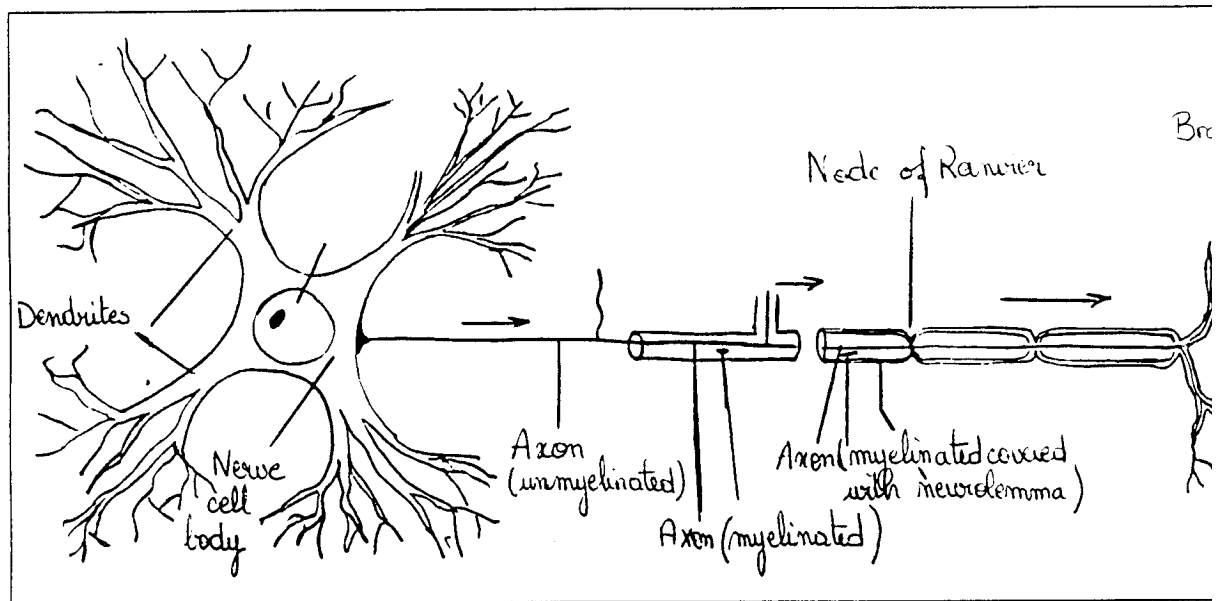
Figure 1: The neuron structure

Neurons within the spinal cord and the brain are *connectors* (internuncial). The peripheral neurons, extending outside the spinal cord and the brain are either afferent neurons (sensory) or efferent neurons (motor).

The neurons operate in an intermittent fashion : excitation is caused when the intensity of a stimulus reaches a threshold value. Nerve pulses then propagate along the axon. For greater intensity, there is no effect on the impulses but the adjacent neurons may become excited.

The *synapse* is the junction between two nerve fibers. Pulse travelling through an axon, propagate across synapses to the dendrites, but never in the reverse direction.

In the brain and the spinal cord, presynaptic neurons have an inhibitory function. They work in the same way as the others but their impulses are inhibitory instead of excitatory.

The figure 2 illustrates the transmission of proprioceptive information to the brain.

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Figure 2: Transmission of proprioceptive information

2.3 Reflex Actions

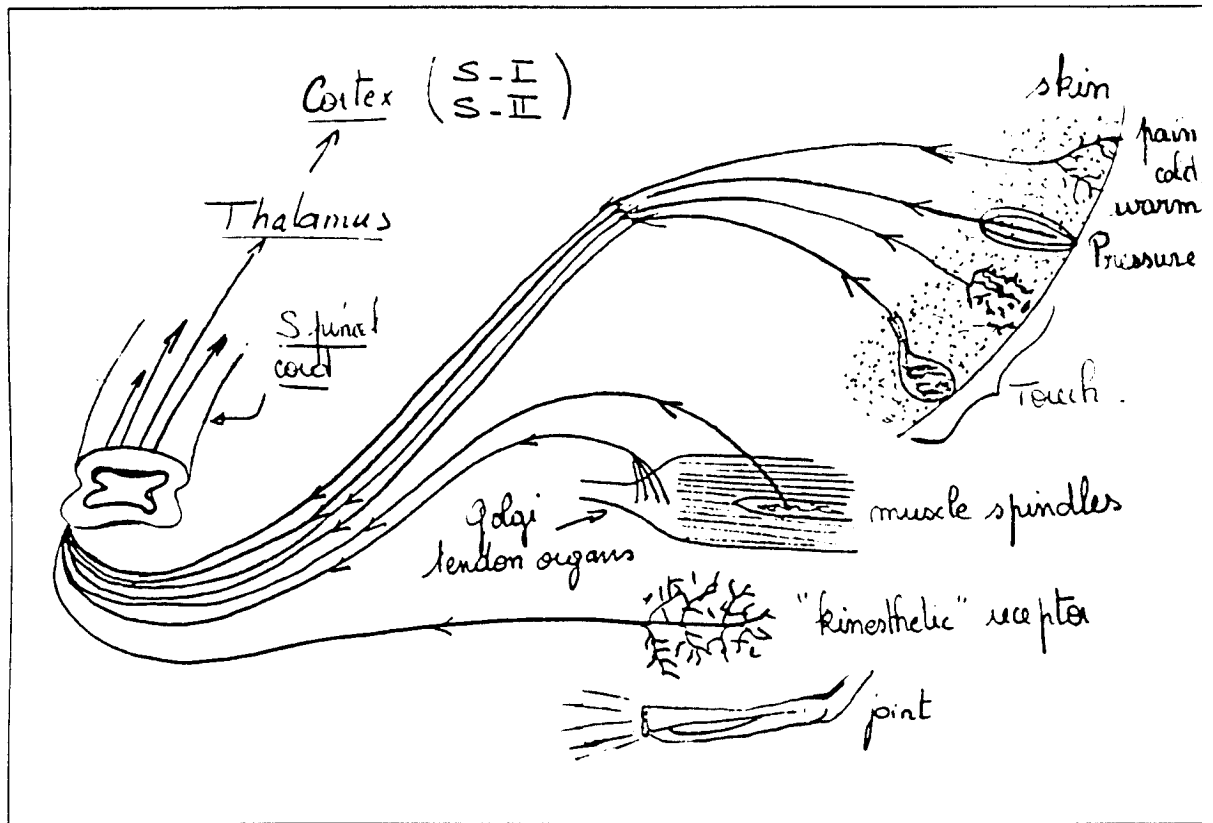A reflex movement is a movement which occurs without volition and without the need of direction from the cerebrum.

The anatomic basis for a reflex act is the reflex arc [6]. An afferent neuron (coming from a receptor organ) enters the spinal cord and makes a synaptic connection either with the dendrites and the cell body of an efferent (motor) neuron (directly), or with one or more connector neurons (indirectly).

2.4 Transduction and Coding

The stimuli are electrically encoded by the receptors. The receptor is activated if the stimulus has reached a threshold value and if it is of the correct type. The electrical potential is dependent on the flow of the cations Na^+ and K^+ through dedicated channels. The stretch of a membrane (by mechanical stimulus) allows or not this flow and thus modifies the potential [14].

The intensity of the stimulus is encoded by the frequency of the code. An increase in intensity acts in two ways, it increases the frequency of the pulses and activates more fibers.

2.5 Kinesthesis and Cutaneous Senses

The tactual perception includes three senses : the cutaneous sense, the kinesthetic sense and the haptic sense. The cutaneous sense refers to the tactile sensations, the thermal sensations as well as to the pain sensations. It is related solely by variations in the cutaneous stimulation. Kinesthesis refers to the sense of movement and forces but often includes a sense of static position of the limbs. It may also be called *Proprioception*. In the haptic perception, both tactile and kinesthetic senses convey the information.

These are distributed senses, their receptors are far-flung missionaries from the central nervous system. They are located in muscular, tendinous, bony and cutaneous tissues. The receptors are generally excited by tissues deformation. There are several parallel channels to carry the impulses : 7 cranial and 31 spinal nerves.

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For hearing and for the vestibular system, which also sense mechanical signals, there is only one nerve. Like vision, they are highly organized and localized systems. Kinesthetic and cutaneous senses are therefore quite different in that they extend over large spatial regions.

In the next paragraphs we will see how the information is processed through the receptors and we will attempt to summarize human performance.

3   The Sense of Touch

3.1   Anatomy

The skin is a system of layers composed of :

- The epidermis.

- The dermis or corium which is below the dermis. This layer contains the nerve endings, encapsulated or free.

- The reticulated dermis. The combined thickness of the epidermis and the dermis is about 1 or 2 mm.

- Beneath begins the subcutaneous tissue which is often fatty.

Various types of mechanoreceptors are located in the skin and they are different in the hairy skin or in the glabrous skin. The structure of the skin is illustrated by the figures 3.

All these mechanoreceptors, except one, are innervated by myelinated, rapidly conducting afferent fibers of group II (diameter 5–12 μm, conduction velocity 30–70 m s^{-1}).

The receptors in hairy skin are :
* the hair follicle receptors are basket endings surrounding the follicles,

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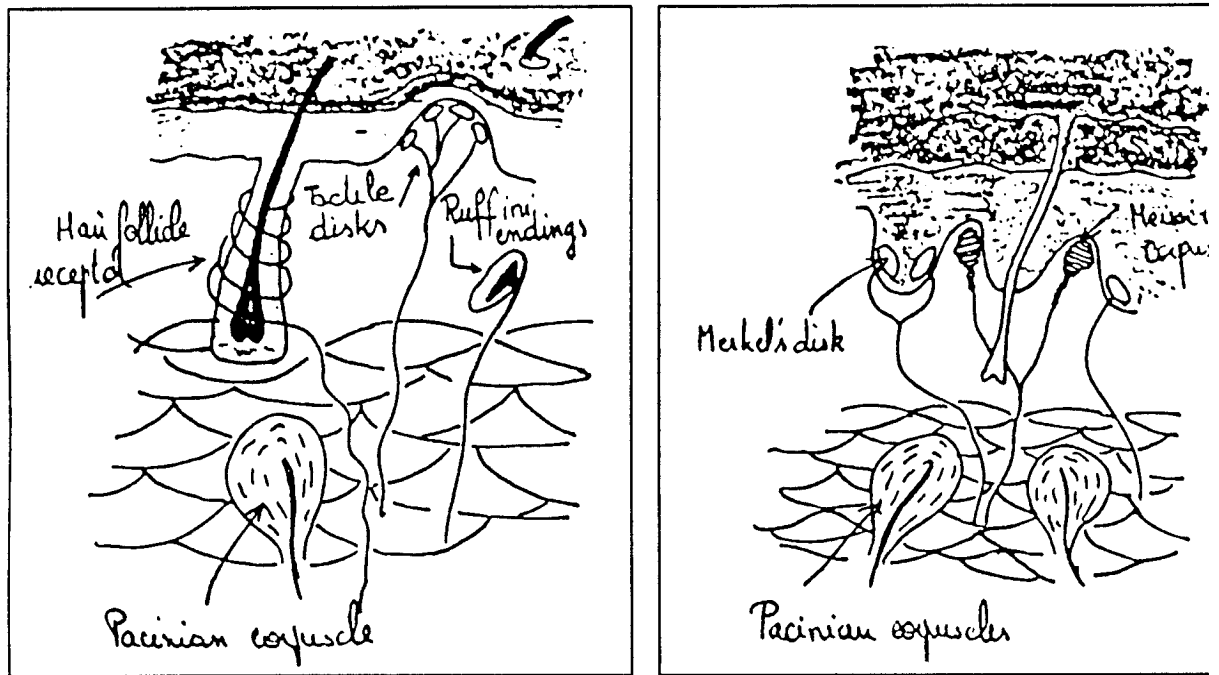
Figure 3: Structure of hairy (left) and glabrous (right) skin

* the Merkel's disks are near the hairs, grouped in tactile discs,
* Ruffini endings are spindle shaped capsules,
* the Pacinian corpuscles,
* and the C-mechanoreceptors (free-nerve endings).

In the glabrous skin, encapsulated receptors are common :
* the Meissner's corpuscles (tiny corpuscles),
* the Merkel receptor complexes,
* the Ruffini endings,
* the Pacinian corpuscles,
* and the free-nerve endings (not encapsulated).
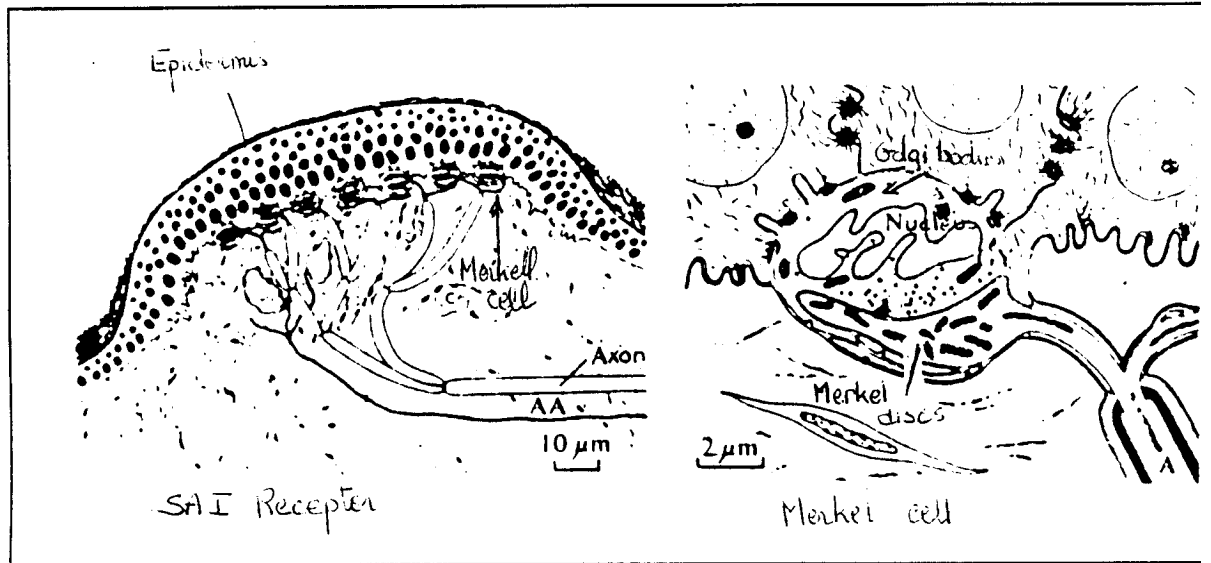
Figure 4: The Merkel's cell

3.1.1 The Merkel's cells

They are located at the base of the epidermis. The Merkel's cell is associated with an expanded terminal of the afferent fiber. This subdivides freely when entering the receptor. There are 50–70 nerve terminal discs in a single spot-like receptor. At the base of each cell, there is a disc-shaped expansion of a branch of a myelinated sensory axon : the Merkell's disc (see figure 4 from [8]).

3.1.2 The free-nerve endings

The prevalent types are the A-fibers and the C-fibers. Type A has a relatively large diameter and is myelinated, fibers of the second type are more numerous. The C-mechanoreceptors are nerve fibers with free endings located in the outer layer of the skin, the epidermis. They are mostly found in hairy skin [8]. The afferent fibers of the C-mechanoreceptors are non-myelinated fibers, with a small diameter and a conduction speed about 2 m s^{-1} [16], [7], [17].

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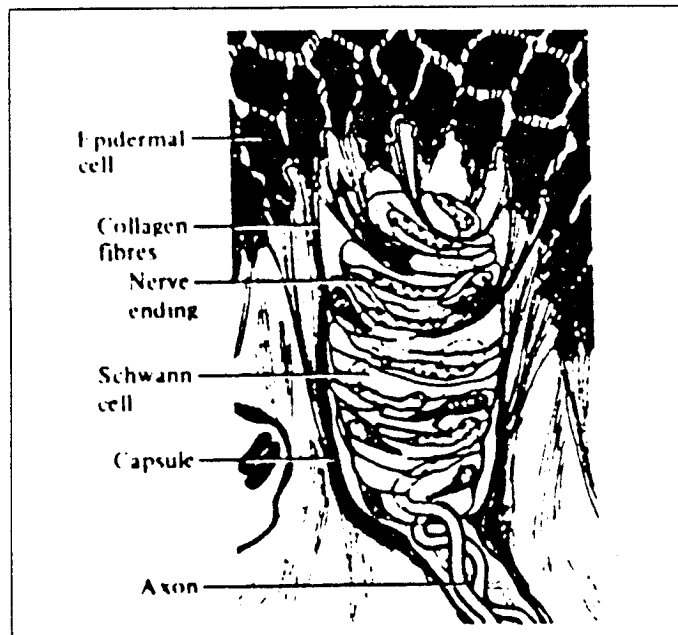
Figure 5: Meissner's corpuscle

3.1.3 The Meissner's corpuscles

They are encapsulated receptors with myelinated afferent fiber present in the dermis of glabrous skin. They are ovoid with the axis perpendicular to the surface of the skin (30×80 μm). They sit 0.5 mm below the skin surface [8].

The capsule is formed by layers of non-nervous tissues. The nerve endings are formed from helical sheets or laminae oriented at right angles to the long axis of the corpuscle and separated by sheets of Schwann cells. Collagen fibers connect the distal half of the receptor to the overlying epidermis (see figure 5, from [8]).

3.1.4 The Hair Follicle Receptors

They are innervated by myelinated efferent fibers which end in a circumferentially arranged complex of endings around the hair root, below the sebaceous gland, sometime called the basket ending [8]. Their nerve terminal are elongated rods running parallel to the hair and the root sheath and spiraling around it. Each ending is sandwiched between or enclosed in Schwann cells (see figure 6, from [8]).
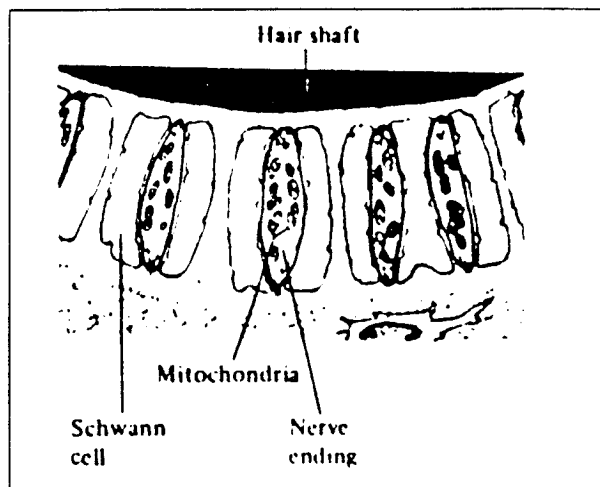
Figure 6: Hair receptor follicle

3.1.5 The Krause End Bulbs

They are found in the glabrous skin of non-primates and exist in two varieties. That's a simple lamellated capsule. The axon ends into the capsule of the receptor either as a single rod-like extension in the cylindrical form or as an intertwined spiral in the globular form [8].

3.1.6 The Ruffini endings

They are encapsulated receptors in the dermis of both hairy and glabrous skin. They lie more deeply than Meissner (and Krause) endings. They can also be found in protective sheath at articular joints. Each corpuscle is an elongated spindle of 0.1 mm on 0.5–2 mm (see figure 7, from [8]).

3.1.7 The Pacinian corpuscles

They are considered as equivocal cutaneous receptors because they are lying 2–3 mm below the surface of the skin (figure 8, from [8]). They can also be found in muscles, joints and mesentery. This is the largest structure to be found in the skin : 1 × 2 mm. For this reason it has been extensively studied [8], [16]. They
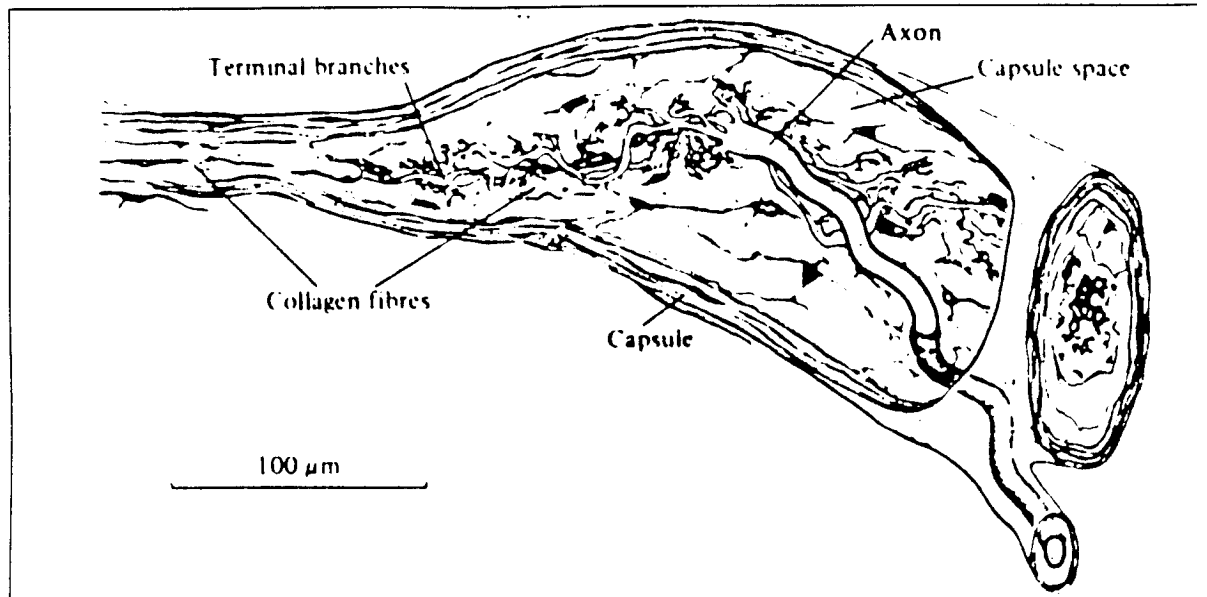
Figure 7: Ruffini endings

are grey pearl-shaped structures. The onion-like lamellar structure is formed of non nervous tissue. The core contains an elongated nerve terminal. The afferent fiber is myelinated and the last node of Ranvier is in the encapsulated receptor.

3.2 Physiology of the Mechanoreceptors in the Skin

The current classification of the receptor systems takes into account their rate of discharge in response to a constant pressure stimulus. The two classes of receptors are the **rapidly adapting** receptors and the **slowly adapting** ones. They may also be described depending on their frequency response, they may be described as displacement-, velocity-, acceleration-, or jerk-sensitive [17]. The relationship between the rate of discharge and the intensity of the stimulus in terms of indentation can be written as follow (equation 1) [8] :

$$R \; = \; a \; S^b \tag{1}$$

Here R stands for the rate of discharge of impulses, a is a constant, S is the depth of indentation as a measure of the stimulus, and b a real exponent.

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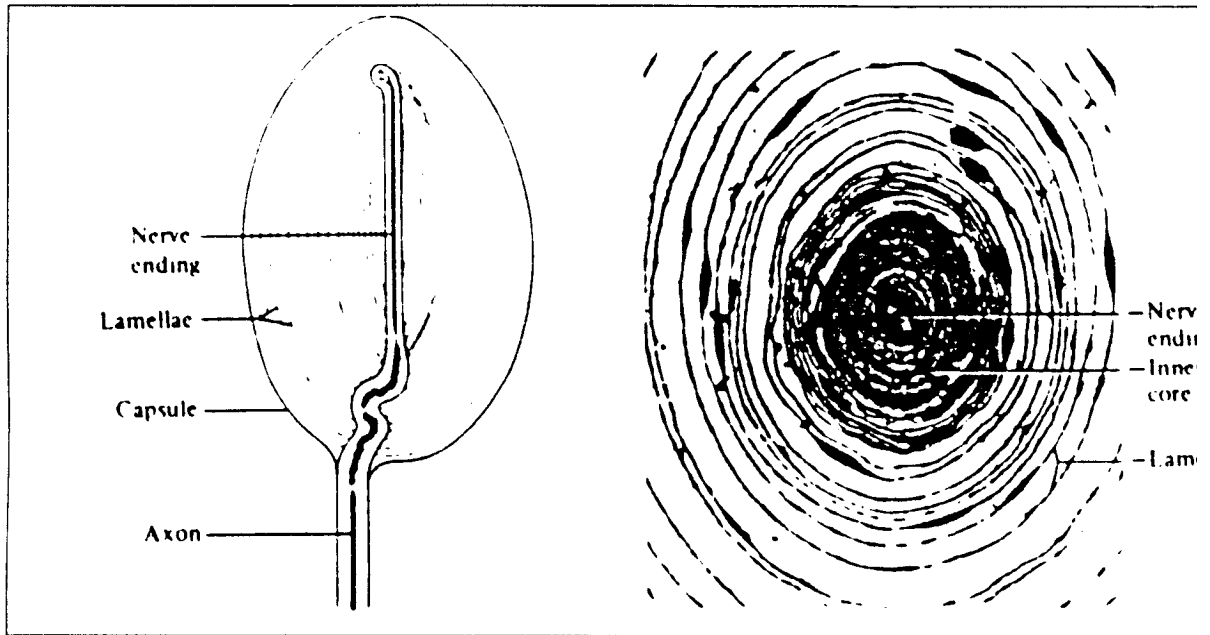
Figure 8: Pacinian corpuscle

Differentiation between nerve fibers depends on their conduction velocities and on the fact they are myelinated or not [17].

3.2.1 The Rapidly Adapting receptors

The Pacinian Corpuscles. These are very rapidly adapting units, they send one or two impulses per stimulus. They will be denoted PC. They are vibration receptors, acceleration-sensitive. They are quite sensitive to pressure but not to direction and respond primarily to vibration. Between 30 and 200 Hz, there is a sharp decrease in the threshold (-2 slope) approached by the equation (2) :

$$S_0 = C f^{-2} \qquad (2)$$

Here S_0 stands for the amplitude threshold, C is a constant, f the frequency, the stimulus here.

The minimum threshold occurs at 250–300 Hz. Above these frequencies, the threshold increases and at very high frequencies, the 1:1 response is no longer obtainable.

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The Meissner's Corpuscles. They are moderately rapidly adapting units with a discharge ceasing after 50–500 ms. They are denoted RA. They discharge only during movements of the skin and they are velocity-sensitive mechanoreceptors. Their effective frequency range is from 10 to 200 Hz. They respond to light touch. They are high frequency transducers.

In hairy skin, the hair follicle receptors seem to play a similar role. The Krause end bulbs are RA receptors, they are more sensitive in the range 10–100 Hz, they do not give any response to steadily maintained indentation of the skin.

3.2.2   The Slowly Adapting receptors

They continue to discharge stimulus-induced action potential even when the pressure is maintained for a long time.

The two varieties of slowly adapting mechanoreceptors are type I (SA I) and type II (SA II).

The SA I receptors are normally silent in the absence of applied stimulus whereas the SA II units often carry a resting discharge (2–20 s^{-1}). SA I units respond at high frequencies and SA II are easily excited by stretching the skin. The SA I units fire impulses at an irregular rate whereas the SA II discharge their impulses in a regular stream. The response of SA receptors for steadily maintained deformations are enhanced by cooling the skin.

Merkel's Cells. These are receptors for SA I afferent units. With a large bandwidth, they can respond to compression and shear stimuli.

Tactile discs. They have the same behavior as the Merkel cells (we remind there that in hairy skin, the Merkel discs are located in special tactile discs).

Ruffini Endings. They can provide a continuous indication of the intensity of steady pressure or tension within the skin. They are receptors for SA II afferent units.

C-mechanoreceptors. These fire slowly-adapting discharge for skin indentation or hair movements (in hairy skin) but they do not respond to a repetitive excitation after 20–30 s. As the same stimulus may give rise to different responses, they cannot signal changes in intensity accurately. They respond to a variety of stimuli, such as pain and temperature.

3.2.3 The receptive field characteristics

RA and SA I. These receptive fields are characterized by several zones of maximal sensitivity distributed over an area covering 5-9 epidermal ridges. The receptive field is small with distinct borders [10].

For RA and SA I units, the receptive fields overlap as a function of the indentation amplitude, when the amplitude increases, the receptive field is enlarged. Even for small amplitudes, a large number of RA and SA I units are involved. The sensitivity of the growth of the fields varies from one unit to the other. It also can be noted that the density of innervation of the skin differs from one site of the body to the other.

PC and SA II. These receptive fields have only one zone of maximal sensitivity as opposed to the two previous ones. The fields are not sharply delimited [10].

Table 1 presents the innervation density of the skin expressed in units per cm^2, it is extracted from [10]. Note that the nail units are excluded although they may play a central role in haptic processes.

The table 2 illustrates the classes of receptors as described above, in relation with the size of the receptive field [9], [10], [17].

The figure 9, extracted from [14] p 297, represents the receptive fields for (a) : the Meissner's corpuscles, (b) : the Pacinian corpuscles, (c) : the Merkel's receptors and (c) : the Ruffini endings. The arrows refer to the direction in which the rates of response to stretch are higher, this characteristic will be developed in a further subsection.

Region of the hand	RA	SA I	PC	SA II	Relative density
Finger tip	140.5	70.2	21.4	9.2*	4.2
Rest of the finger	37.1	29.7	9.5	13.8	1.6
Palm	24.5	8.0	9.3	15.7	1

Table 1: Innervation density of the skin in units per cm^2
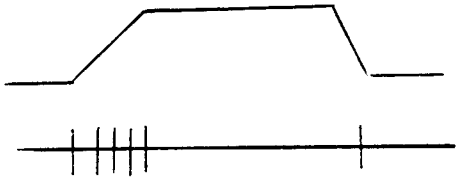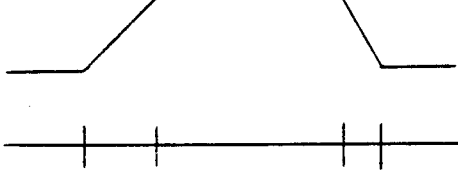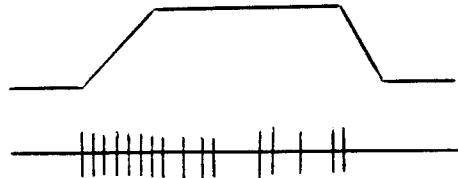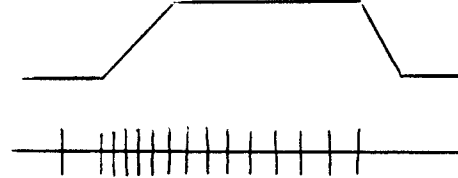
Adaptation	Receptive field characteristics	
	Distinct borders Small size	Indistinct borders Large size
Rapidly Adapting	RA (Meissner corpuscles)	PC (Pacinian corpuscles)
Slowly Adapting	SA I (Merkel cell)	SA II (Ruffini ending)

Table 2: Relationship Rate of adaptation/Field Size

Rapidly Adapting Mechanoreceptors
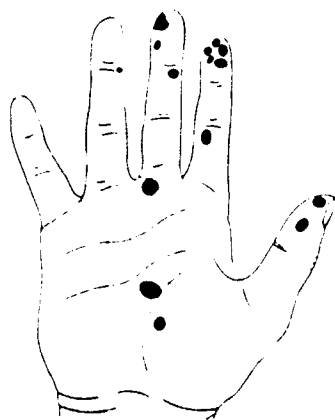
(a) : Meissner's corpuscles
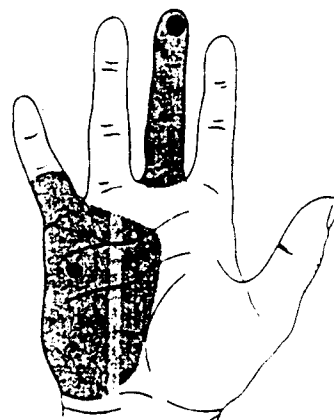
(b) : Pacinian corpuscles

Slowly Adapting Mechanoreceptors
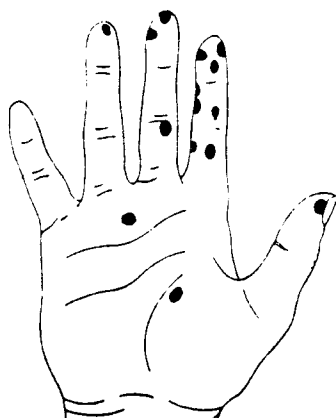
(c) : Merkell's receptors
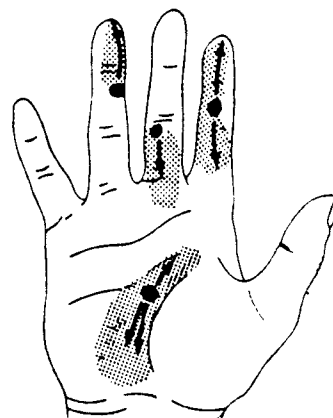
(d) : Ruffini endings

Figure 9: Receptive fields in the inner surface of the hand

3.2.4 Classification by function

As it is generally admitted, the mechanoreceptors are tuned to be more sensitive to some kind of excitation. We will now attempt to clarify their role even though they all are involved in every sensation [16].

Pressure receptors :   Intensity detectors.
The SA receptors are best suited for this function. They also signal the duration of the pressure signal. In glabrous skin the Merkel's discs play this role, in hairy skin they are replaced by the Ruffini endings but they also may be found there, located in special tactile discs (about 30–50 Merkel's discs in one tactile disc). The peak response of the Merkel's discs is at about 10 Hz [1].

Stretch receptors :   The Ruffini endings.
The stretch receptors are intensity detectors as well. The Ruffini endings are supposed to be most responsible for the skin stretch sensitivity. They respond at low frequencies.

Touch receptors :   Velocity detectors.
The hair follicles of hairy skin detect the hair movement and maybe the velocity of movement. In glabrous skin, Meissner's corpuscles detect velocity (with a peak response at about 30 Hz).

Vibration receptors :   Acceleration detectors.
In hairy and glabrous skin, this function is fulfilled by the very rapidly adapting mechanoreceptors, in other words, by the Pacinian corpuscles (with the best performance at 250–300 Hz).

Special case, the free nerve endings :   Temperature and pain.
As opposed to the other mechanoreceptors, they are not in corpuscular structures. Some of them are thermoreceptors, many are pain receptors (nociceptors), and a few are sensitive to low intensity touch stimuli. Observations show that two intensity levels can be discriminated so that they would be threshold detectors.

finger tips	6–8 μm
midsection of the fingers	10–14 μm
finger top	10–18 μm
between thumd and index	20 μm
palm	15–24 μm

Table 3: Amplitude thresholds for the inner surface of the hand

3.3 Psychophysical Observations

The psychophysical experiments intend to provide curves correlating the values of thresholds to those of frequencies, amplitude or time.

3.3.1 Thresholds for Touch

Several experiments have been carried out in order to determine the threshold for sensation of a mechanical stimulus of the skin. Expressed in terms of depth of indentation necessary to produce a just detectable sensation of touch, the results for the inner surface of the hand are listed in table 3 (from [16]).

The velocity of indentation is related to threshold touch sensations [12]. If done slowly enough (about 0.05 mm s^{-1}), the skin may be indented as much as 1.5–2 mm without any sensation.

3.3.2 Thresholds for vibration

The experiments showed that to different sizes of contactors correspond different thresholds in terms of amplitude of the skin indentation but the curve remains a U-shaped curve with a minimum value at about 250–300 Hz [19]. At low frequencies in the range of 20 to 40 Hz, the threshold has been found independent of the contactor size. The absolute threshold varies inversely to the contactor area for higher frequencies. For very small contactors (0.005 cm^2, 0.02 cm^2), the threshold becomes
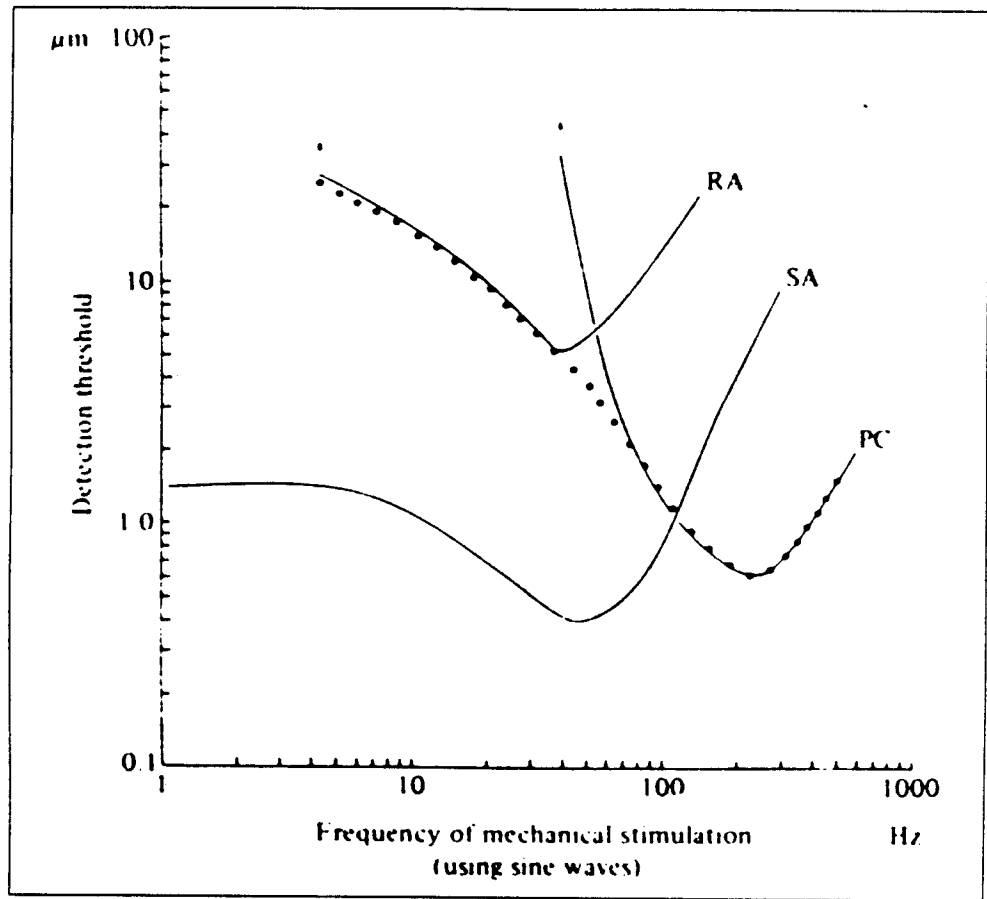
Figure 10: Thresholds/Frequency relationship for RAs, PCs, SAs units and human

independent of the frequency of the stimulus.

The dotted line on figure 10 illustrates these remarks (from [8]).

The lower limit to the sensation of vibration (i.e. the pulses fuse into one continuous sensation : vibration) is rather subjective but should be considered in the range from 10 to 80 Hz. The upper limit revealed by experiments and cited in [12] is 8,192 Hz. In [1], Brooks reports that the sensation of mechanical vibration has been measured at 10,000 Hz but the ability to discriminate one signal from the other declines above 320 Hz.

The use of static surround may lead to somewhat different results also dependent of the size of the gap between the contactor and the surround [12], [17]. Experiments

showed that the threshold can be increased by the surround at high frequencies although it is lowered for the low frequencies.

The temperature of the skin has a great influence on the threshold value. Warming the skin 4° above the neutral temperature enhances its sensitivity and the threshold for a 100 Hz vibration is at a minimum.

The effect of the contactor area on the response is referred as the *spatial summation*. For low frequencies, we already said that the threshold is not dependent of the size of the contactor : there is no spatial summation there. Conversely, for higher frequencies, the spatial summation can be observed. When the area of the contactor is up to 2.9 cm^2, with a double-size contactor, the threshold is divided by two : there is a complete summation in this case.

The activity at low frequencies is referred to as the non Pacinian system and for the higher frequencies it is said to be the Pacinian system. The characteristic curve of the Pacinian Corpuscles neural thresholds fits well with the U-shaped part of the curve for the psychophysical measurements [19], [12]. The characteristics of the rapidly adapting receptors are correlated to the flat part of the curve where no spatial nor temporal summation occur.

The difference limen expressed in terms of frequency measures the minimum rate difference necessary for evoking sensations of different frequency vibrations. In the range of 20–300 Hz, the Weber fraction $\frac{\Delta f}{f}$ lies between 20 % and 25 %. The just noticeable difference at 20 Hz is then about 4 Hz and increases to 60–75 Hz at 300 Hz [17]. (The auditory Weber fraction is 1 %.)

The curves of figure 10 represent the detection threshold of RA and PC units to mechanical stimuli. The dotted curve represents the human sensory threshold, from [7] and [14].

3.3.3 Perception of the Orientation of the Direction of Movement of Tactile Stimuli

In active or passive touch, our ability to detect slip is related to the cutaneous mechanoreceptors innervating the contact area [3], [18]. The spatio-temporal period of a moving stimulus is well matched by the responses of the different fibers. It

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has been shown that human observers are able to detect 1-3 μm dot (550 μm in diameter) when it is stroked on the finger pad, although it can not be detected with a stationary contact. With or without slip, the stretch of the skin is well perceived by the observers (in [18], the experiments are realized for the transversal direction).

When a blank plate is presented, none of the subjects are able to detect the slip motion but any minimal feature enables the detection of the relative motion. It has been observed that RAs and PCs afferent fibers both discharge only during the skin stretching phase at the beginning of the stroke, with no discrimination in the direction. The SAs fibers responses were maintained during the stroke, they presented a clearly directional activity : the discharge rates were ten times higher in one direction than in the reverse (which one is not reported in the paper). The conclusion is that only the SAs fibers are responsible of the coding of the skin stretch direction [18]. There is no clear distinction between the role of the SA I and SA II fibers.

When there is a single dot on the plate, the slip is detected for a 1-3 μm high, 550 μm diameter dot and only the RAs fibers have thresholds low enough to perceive it. This leads to the conclusion that the RAs fibers are solely responsible for the perception of the relative motion for such surface.

When a texture plate (a regular matrix of dots with height lower than thresholds) is presented and slipped, the SAs fibers have biased responses to the direction but there is no difference between the response for the blank plate and the texture plate. RAs fibers responded only to the initial skin stretch, with no distinction between the blank and the texture plate. Conversely, the PCs afferents were only excited by the slip of the texture plate. The response of these fibers is related to the vibrations produced by the slip of the texture on the contact area. In this experiment, the response was the same in any direction [18], but Darian [3] found that the response was better in the transversal direction than in the longitudinal direction.

For higher dots, all the fibers are activated, providing redundant cues (the threshold for the dots are RA : 1-3 μm, SA : ≥ 8 μm, PC : ≥ 21 μm). This is very important in our ability to grip objects : the intermittent "stick-slip" permits to adjust the force to grip a fragile object.

In conclusion, the SA afferents detect the direction of the stretch (see figure 9)

and then the slip, whereas RA & PC afferents signal the slip with spatio-temporal (local feature) or intensive codes (smooth background distributed on the surface).

Various experiments have been carried out to determine the sensitivity to the detection of the direction of a movement on the skin. If a line is impressed on the skin of the forearm, either in the longitudinal or in the transverse direction, the minimum length to discriminate this direction is about 16.8 mm according to Gould et al. [5]. The authors think that the skin, in this part of the body, is frequently subjected to stimuli that move across the surface of the skin. It could be that orientation detection is greatly enhanced when sequential cues are present.

In another experiment, the detection of orientation is subjected to two points which are presented either simultaneously, or successively but in longitudinal or transverse direction. The sequential application gave the best results, 8.7 mm instead of 13.1 mm for the simultaneous one. When a plastic arc is rolled over the surface of the skin, causing a continuous stimuli, the threshold is lower (10.5 mm) than for the lines. If the direction is presented by the stroke of a probe on the skin, the improvement is terrific. If four excursions are permitted : distal or proximal, medial or lateral, the threshold for the average excursion necessary to discriminate the direction is 4.3 mm.

Various experiments were carried out in order to appreciate the contribution of skin stretch in the direction detection sensitivity. A probe is glued on the skin of the forearm, without any noticeable indentation of the skin. With 1 mm excursions in the four directions, the subjects were able to determine the orientation of the stretch in about 95 % of the trials. An experiment with an air jet (with air in the thermoneutral temperature zone) was performed (moving indentation without component of friction) on the skin of the forearm, for four orientations. The result is 11.3 mm which is close to the threshold for a line impressed on the skin for the same subjects (14.0 mm). The same persons answered well for 2 mm excursions of a glued probe.

The skin stretch provides the most salient cue for the discrimination of the direction of objects across the surface of the skin [5], [23].

The table 4 from [5] presents the thresholds for various experiments in order to discriminate the direction or the orientation of the stimulus on the skin with or

Stimulus	Discrimination task	N° of subjects	Thresholds in mm
Line	orientation Lo/Tr	14	16.8
Rolled arc	orientation Lo/Tr	14	10.5
2-points simultaneously	orientation Lo/Tr	14	13.1
2-points sequentially	orientation Lo/Tr	14	8.7
5 g stroke	orientation Lo/Tr	10	4.3
stretch	direction M-L vs P-D	10	< 1
0.7 g stroke	direction M-L	4	14.0
0.7 g air stream	direction M-L	4	11.3
stretch	direction M-L	4	< 2

Table 4: Thresholds for the discrimination of the direction or orientation for various stimuli

with	Lo	: longitudinal	M	: medial	D	: distal
	Tr	: transversal	L	: lateral	P	: proximal

without stretch.

The thresholds to determine the skin stretch direction are dependent on the velocity of the movement:

at 1 cm s^{-1}, the mean threshold is 0.6 mm

at 1 mm s^{-1}, the mean threshold is ≥ 2 mm.

Experiments on monkeys showed that an interruption in the spinal cord column caused a deficit in the sensitivity to the direction. It suggested that the dorsal columns are adapted to code spatio-temporal stimulus sequences [5].

In conclusion, some authors [5] assert that the skin stretch is an important source of information for the somatosensory system. The SA II receptors (or Ruffini corpuscles) are most likely sensitive to skin stretch. However these last results are

in conflict with the characteristics of the afferent fibers of those receptors. However, the enhancement of the performance is not necessarily related to stretch but to the forces generated between the superficial layers of the skin and underlying tissues [5].

In an experiment described in [13], two gratings are presented successively, the subject has to decide whether or not they have the same orientation. An additional variable is the depth of indentation. The best results are listed below :

| Spatial period | 2.25 mm | 1.84 mm | 1.68 mm |
| Indentation | 500 μm | 900 μm | 1200 μm |

In [23], the response of S-I neurons (in the postcentral gyrus of the cerebral cortex, area S-I) is studied. The receptive fields of these neurons are located in the body half contralateral to the recording site. The rate of discharge for stimulus across the skin appears to be higher than for a stimulus perpendicular to the surface of the skin (skin indentation). According to Whitsel et al., the majority of the S-I neurons do not respond differentially to different direction stimulus but some of them process a preferential response in one direction (directionally selective). This response is dependent on the velocity and on the traverse length. These results are contradictory with those obtained previously by Werner and Whitsel [22]. They reported that there was an uniformity over the family of the S-I neurons in that way they presented a directional polarization for response to moving stimuli.

The neurons of the somatosensory area S-II (S-II neurons) have a more complicated behavior. Many of them have a receptive field at symmetrical sites on the ipsi- and contralateral half of the body. Three types of S-II neurons can be differentiated. Type A neurons are independent of the direction of the stimulus. For types B & C, there is a difference between one direction and the reverse one.

3.3.4 Spatial factors

Point Localization. In this experiment, the skin of the subject is touched while she or he is asked to identify the point. The results are dependent of the site of the body tested. Another factor of error is the time elapsed between the identification

of the point and its localization by the subject. Another version of this experiment is to present the subject two stimuli successively.

The *tau phenomenon* is described as the decrease in distance that separate two tactile stimuli judged to be two as the time interval between their presentation increase.

The Two-Point Limen. The *difference limen* (DL) or *difference threshold* or *just noticeable difference* is the smallest distance between two points allowing the subject to feel two distinct sensations of touch. This is also called the differential sensitivity [17]. For smaller separations, the sensations merge into a single one. The difference with the experiments of point localization is that the point were referenced successively and they are now touched simultaneously.

The two-point limen refers to the spatial resolution of the skin. For the finger tips, the tongue and the lips this value is low : in the range of 1–3 mm.

Spatial Summation. It refers to the ability of correlate the area of the skin excited and the response processed by the receptors. It has been already discussed in the subsection devoted to the threshold for vibration. This phenomenon occurs for high frequencies but is not observed for the low frequencies (see figure 10).

3.3.5 Temporal factors

Temporal summation has been observed for low intensities at about 100–250 Hz.

3.3.6 Time and space interactions

The Tau Phenomenon. Three equally loud stimuli are successively presented at different places with unequal delay times. The space between the two stimuli with the lowest time interval is judged to be smaller.

The Phi Phenomenon. It is a tactile apparent movement. If two vibrators are 10 cm apart, one with a frequency of 40 Hz and the other with 500 Hz and a phase shifted sinusoid. Then there is a shift in localization from one source to the other. Similarly, with equal frequencies, there is a single "phantom" sensation of touch [12], [17]. A similar phenomenon can be observed for the auditory sense.

Saltation. The cutaneous saltation is related (but different) to the Phi phenomenon. It gives a discontinuous sensation as superficial as light touch.

Temporal Acuity. It is the minimum time interval that must separate two tactile stimuli (at the same locus) for they being perceived as different. It is about 5.5 ms for stimuli of 1 ms. For ear, 10 μs stimuli must be separated by 10 μs.

Masking. In the subsection on the spinal cord mechanisms, we already gave some idea of what is a masking effect. This inhibition phenomenon can have three different sources. They are referred as the surround inhibition, the complementary inhibition and the cross-modality inhibition and result from the presentation of a second stimulus respectively to an area adjacent to the first one, contralateral to it or of a different kind of stimulus.

3.4 Conclusions

As we have seen in this first section, a large literature is available on the subject of tactile perception. A great many experiments have been carried out in order to evaluate the performance of our sense of touch. Relationships between the thresholds and variables like the depth of indentation, the frequency of a stimulus or the delay between two successive events have been proposed. But there are only few results dealing with the human ability to perceive the direction of a stretch. Some results on this topic are reported above but they are not sufficient for our purpose. Moreover, nothing has been reported, to our knowledge, on the ability to guess the direction of a vibration applied to the skin. In every experiment on vibration, there is an indentation of the skin perpendicular to its surface.

These remarks give rise to the following evidence. Although crucial figures can be extracted from the literature for the design of a high-fidelity display device, we must come up with another source of experiments to fill the existing gap, even if the results summarized in subsection 3.3.3 contribute to partial answer to our questions.

We also noticed the work of Moore [15] whose purpose is to find a relationship between the visco-elastic characteristics of the skin and tissues and the vibration applied. These characteristics are related to the impedance of the surface of the body. The resistance per unit area remains relatively constant over a range of frequencies. The reactance is frequency-dependent, it is determined by the elasticity and the mass of the tissues. At low frequencies, the elasticity prevails but for high frequencies the mass component becomes the more influent.

4 The Kinesthetic Sense

The term kinesthesis refers to the sensation of movement, but in this section it will take its broadest meaning which also includes the sensation of static position of a limb as well as the sensations arising from the contractions of the muscles.

4.1 Psychophysics

Two classes of experiments are usually carried out. In the first one, passive positioning or passive movements are caused on a subject, and in the second, the positioning or movement is active.

For a given velocity, the proximal joints appear to be capable of a smaller minimal detectable angle for the passive movements than the distal ones. A displacement too small to be perceived at one rate may become apparent at a higher velocity. In terms of linear velocity and displacement, the proprioceptive performance is superior at more distal joints. At any angular velocity, the fingers show a poor acuity, they need a large excursion to detect movement. However, in terms of percentage change in muscle length, the performance is similar for proximal and distal joints.

Experiments showed that tensing muscles improve the movement sensation, enhancing the response of the receptors in the muscle but no explanation can be offered

at this point.

The phenomenon of *postural persistence* is a kind of after-effect : prior movements or postures can influence the perception of position, leading to an offset error.

The accuracy of positioning a limb also varies with the angle. The acuity seems to reach a maximum at mid-range.

Our sense of effort and the muscle force are related to our ability to gauge the forces produced by the contraction of our muscles. This is because the biomechanics of limbs lead to extremely low residual friction forces. As a consequence, any external force applied to a limb (including gravity, inertial forces, and so-on) must be counteracted by muscle forces. The sense of effort results from a number of muscle tension forces, usually acting in the agonist and the antagonist configurations. Effort and tension are two distinct notions, our ability to gauge the tension in the muscles is used for the estimate of the effort but the CNS also plays its role. The sense of effort can be altered by disorders of the CNS : disorders may produce movements without any sense of effort, repeated contractions or vibrations can influence our judgment of weight for example [2].

There are two mechanisms for obtaining information about position or movements of the limbs. The central nervous system receives sensory inputs from tension receptors in the muscle (the Golgi tendon organs). The CNS also monitors its own commands. The *corollary discharges* influence our perception, they are the signals that get fed back to the perceptual portion of the brain.

4.2 Physiology

4.2.1 Overview

There are two broad classes of inputs from the mechanoreceptors :

Position or displacement signals : The information about joint angles are continuously available during a maintained position of a limb.

Movement or transient signals : these signals are available only during the movement of the limb.

The signals may include information about :
- the rate at which the limb changes its position,
- the acceleration of the movement,
- higher-order derivatives.

The motor nerve fibers that innervate the muscles are :

A-alpha fibers : conducting impulses at 70–120 m s^{-1}, they innervate the skeletal muscle cells and signal them to contract.

A-gamma fibers : conducting impulses at 15–40 m s^{-1}, they carry control signals to the muscle spindles receptors (*the muscle spindles receptors* are the muscle length receptors).

Three groups of sensory fibers are related to the muscles :

Group Ia : they innervate the muscle spindle primary endings,

Group Ib : they innervate the Golgi tendon organs,

Group II : they innervate the muscle spindle secondary endings.

4.2.2   Coding Position and Movement

Each class of receptor has its preferred stimulus, the so-called adequate stimulus. This is equivalent to a high degree of specificity. This specificity and the particular neural channels carrying the information form a dedicated channel or a labeled line. The type of activity of a receptor defines its pattern code. The kinesthetic receptors probably use both dedicated channels and pattern codes. Observers may detect the occurrence of a movement without sensing its direction or velocity. This leads to the conclusion that the sense of movement is coded independently of its direction or speed. A lot of receptors are available for the detection of the movement but

their role in the process if any, is till an open field of investigation. The sense of the position of a limb seems to be easier to understand. Two major theories are based on the response of the SAs afferent fibers in one hand and on an opponent system in the other hand [2].

Three possible sources of kinesthetic sensory information are :
- mechanoreceptors in the skin,
- mechanoreceptors in the joints,
- mechanoreceptors in the muscles.

In [6], Gregor enumerates at least ten receptors that may contribute to kinesthesis :

1. Free, unencapsulated nerve endings sensitive to pain.

2. Meissner's corpuscles, sensitive to touch.

3. Flower-spray endings (Ruffini endings), responding to changes in the joint position. These receptors in the skin are excited by stretch.

4. Pacinian-like receptors, responding to change in the capsule pressure during movement.

5. Pacinian corpuscles, sensitive to deep pressure.

6. Labyrinthine receptors.

7. Visual receptors.

8. Auditory receptors.

9. Golgi tendon organs.

10. Muscle spindles.

4.2.3 Mechanoreceptors in the Skin

They have been extensively described in the first section of this report. However, there is no candidate to report kinesthetic sensations or even play a minor role. In the digits, the skin receptors enhance the kinesthetic sensations elicited from other sources. The same results are observed for the tongue and the lips, we have some difficulties for speaking when the skin is anaesthezied there. The behavior of the foot skin is quite similar. These results are likely to be related to the high degree of innervation in the hands. But anaesthesia of the skin around the knee does not influence the perception of position or movement.

4.2.4 Mechanoreceptors in the Joints

In the ligaments and in the capsule of the joints there are numerous slowly adapting mechanoreceptors presenting almost non adapting response to stretch [21], [2]. The low compliance of the ligaments leads to think that the tension seems to be more relevant than stretch.

The Golgi tendon organs : some of them have been found in the capsule where they respond to its compression but most of them are located at the junction of muscle fibers and their tendinous attachments at both ends so they are said to be in series with the muscle.

The Ruffini types endings (flower spray or FS organs) : in the joint capsule, they respond to the stretch of the capsule, they provide a slowly adapting response similar to the SA II units. They do not seem to have a great influence on the joint position detection.

Some receptors respond in the midposition of the limb but in this case they do not respond to flexion or extension of the limb, so they can not provide any real information on the position. Their poor activity on a wide range of the joint position strengthens the conclusion that the receptors in the joints are not the source of our knowledge of the limb position. However, the controversy is open as some have found responses over the whole range of the joint.

4.2.5 Mechanoreceptors in the Muscles

The CNS commands the muscle fibers to contract. The result on the muscle (shorten, lengthen or remain the same length) depends on the external forces. The force of contraction is related to the number of fibers involved (this is called the *recruitment*) and the rate of firing (from a brief twitch to tetany).

These receptors are slowly adapting receptors : the Golgi tendon organs and the muscle spindles.

The Golgi Tendon Organs.   They are in series with the main muscle fibers and thereby are in a position to measure the tension in a muscle. They receive innervation from large diameter fibers and rapidly conducting axons. They are sensible both to stretch and contraction of the muscle, without any distinction between the two. They respond to the very extreme positions of the joints. They inhibit the action of their own muscle and by the way act as a safety valve but they are incapable of coding position [6]. Each one is associated with 10–20 muscle fibers having different motor units, so that they provide to the CNS a sample of the tension in the muscle.

It has been reported that hormonal discharge, in case of perceived danger for example, can block this inhibition, thus endangering the integrity of the muscle or of the tendons given that the full power of muscle is usually larger than the strength of the supporting tendons.

The Muscle Spindles.   They lie in parallel with the main muscle fibers [6], [2]. They measure the length and the rate of change of length of the muscle fibers. The muscle spindles are long, slender bundles of 2–12 modified muscle fibers (*the intrafusal fibers* in opposition to the extrafusal or regular fibers) encased in a fluid-filled capsule. Each spindle is about 1 mm long.

Two types of intrafusal fibers can be distinguished, the nuclear bag fibers for which the nuclei are in cluster and the nuclear chain fibers with the nuclei lying in chain. Figure 11 illustrates these structures.

Both of them have a central non contractile area where the nuclei are situated and polar ends that are contractile, responding to action potential from the CNS
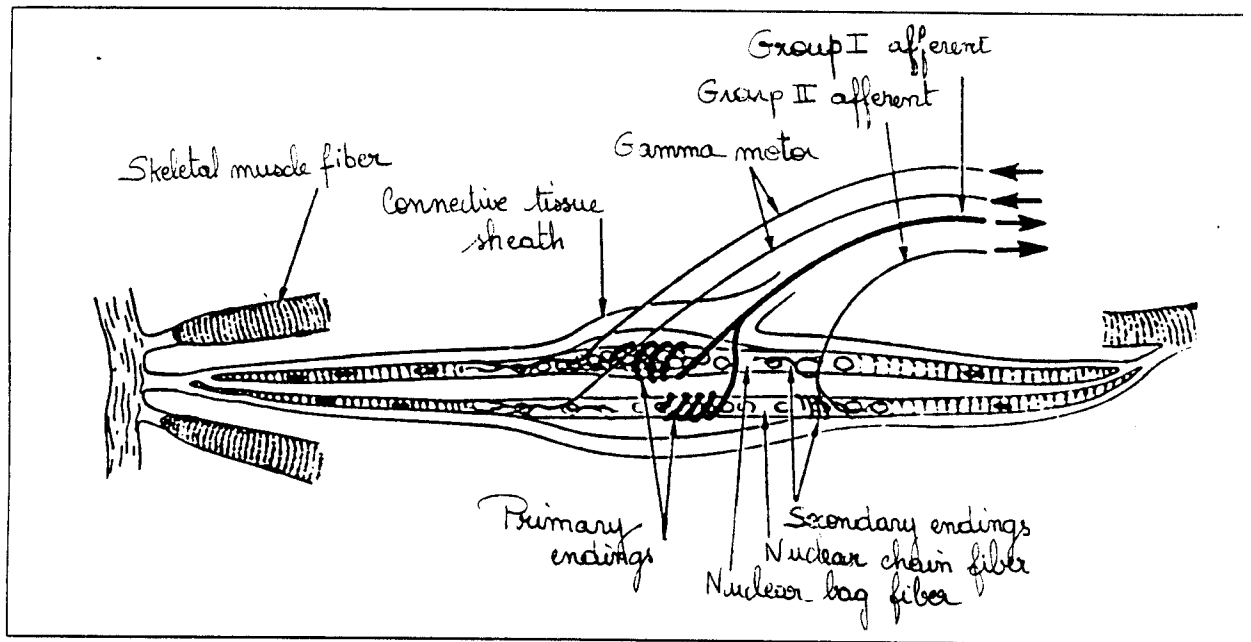
Figure 11: The muscle spindles

via the gamma efferents. Each spindle is supplied with one large fiber -afferent neuron- (but 1-5 intermediate sized sensory fibers). This neuron has a characteristic annulospiral ending AS divided in as many branches as there are intrafusal fibers. Each branch (primary ending) is coiled around the non contractile midsection of the intrafusal fiber. The afferent fibers leading from the AS endings are large (8-12 μm diameter), belong to group Ia , and have high conduction rate. Sensitive to the fiber changes of length, their discharges produce a contraction known as the stretch reflex.

Most of the spindles also have 1-5 sensory endings (secondary endings) : the flower-spray endings SP. Each SP has its own sensory fiber. They are found at the either end of the non-contractile midsection of the intrafusal fibers. The afferent fibers are relatively small (6-9 μm diameter) and belong to group II. They have a lower conduction rate than the fibers from group I. They are believed to register the static muscular length but their precise function is yet to be determined. They might inhibit further contraction if the spindles are overstretched. They may be responsible for a flexor reflex with inhibition of the extensors.

The spindles are also supplied with their own (6–12 fibers) small efferent fibers. They are called the gamma fibers or gamma efferents in order to differentiate them from the regular motor neuron named alpha efferents. The gamma system is responsible of an increase in the sensitivity of the intrafusal muscle fibers afferents. A non negligible part of the CNS motor flow is dedicated to the control of this sensitivity.

4.3   Central Integration

No single receptors type can be responsible of the whole amount of information processed to determine the position or the movement of a limb. Conversely, they all play their role in this mechanism and even if the way it works is not always very clearly apparent, their absence causes lower performance. The Golgi tendon organs as well as the muscle spindles are able to discharge responses at very high rates, up to 300 Hz [1]. It is however clear that proprioception does not occur at such a rate. It is likely that the CNS integrates all the impulses over time to determine more accurate lumped values. The scheme of figure 12 represents the central processing procedure for the proprioceptive sensations.

During movement, the commands destined for the muscles are also routed to the perceptual portion of the brain, entirely within the central nervous system. There they may produce sensations. These signals are called the *corollary discharges* or the *efference copy*. These terms are sometimes used in the same meaning but they are in fact quite different. The corollary discharges perform a feed forward function that affects the sensations in the perceptual center of the brain provided by the sensory receptors. The efference copy is related to a more complex system. The signal of the command is not directly routed to the perceptual center. It is directed into a "comparator" which provides the result of the difference between the command and the response from the receptors. A correction may then be returned to the command center (see figure 13 from [2] p 13-57).

4.4   Operator Response

The movements of the wrist (that may interest us) occur around two axes (figure 14) :
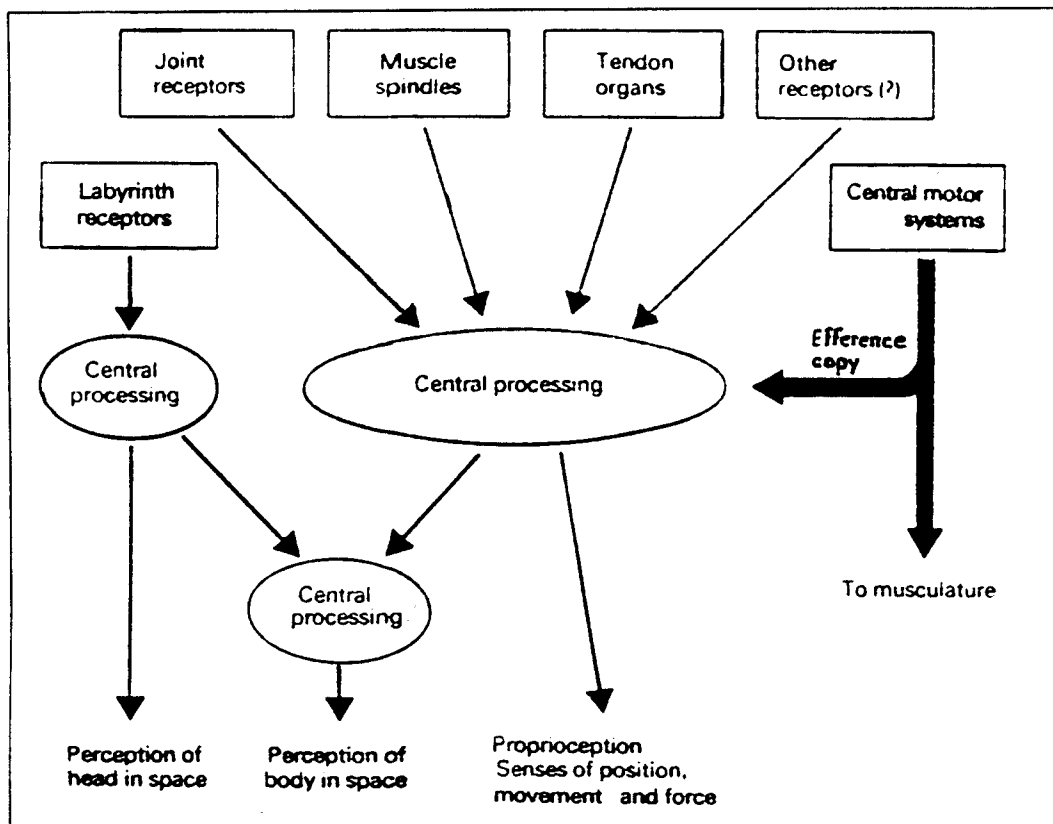- a transverse axis for the flexion/extension movement,
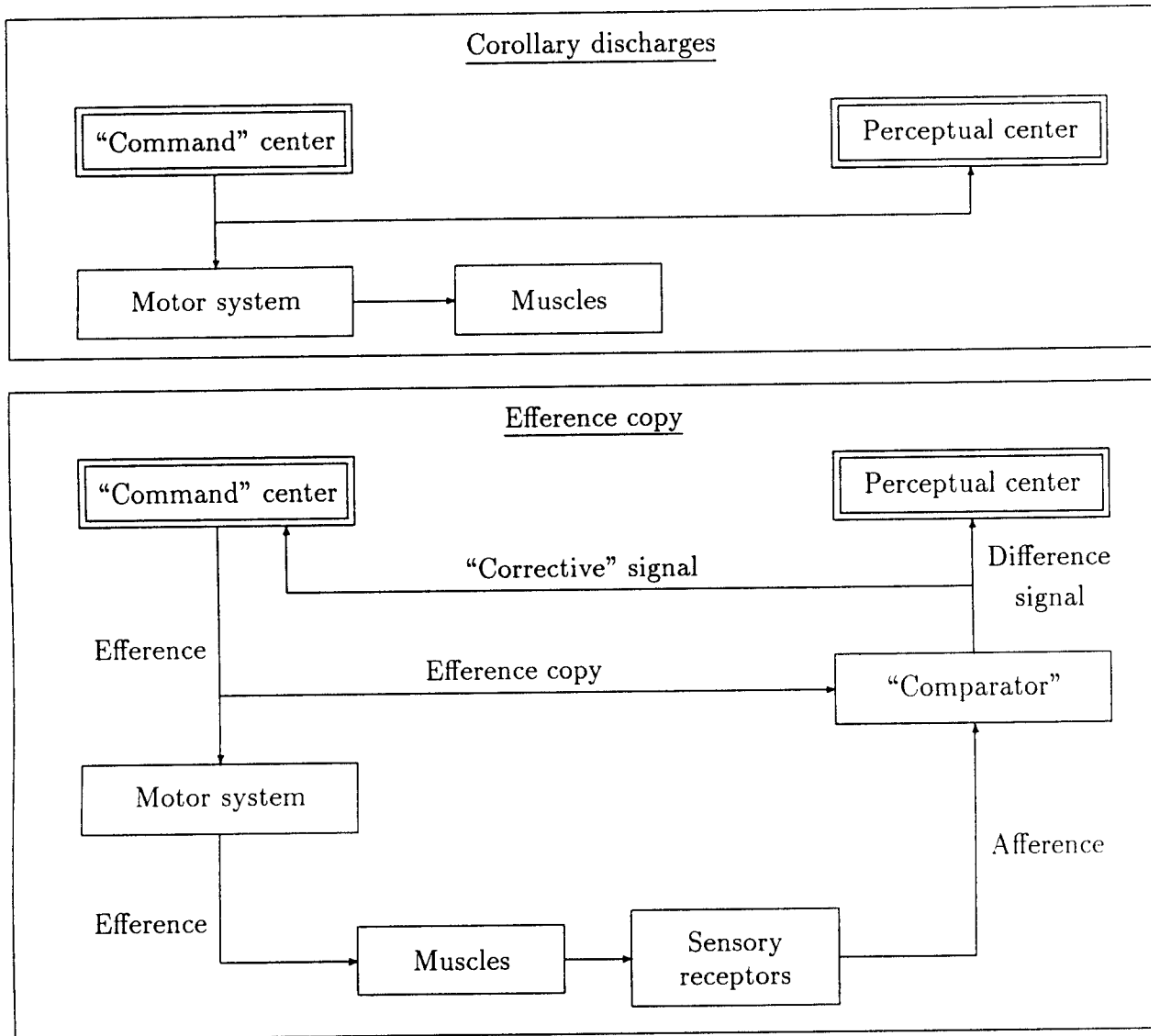
Figure 12: Central integration scheme

Figure 13: Corollary discharges vs Efference copy
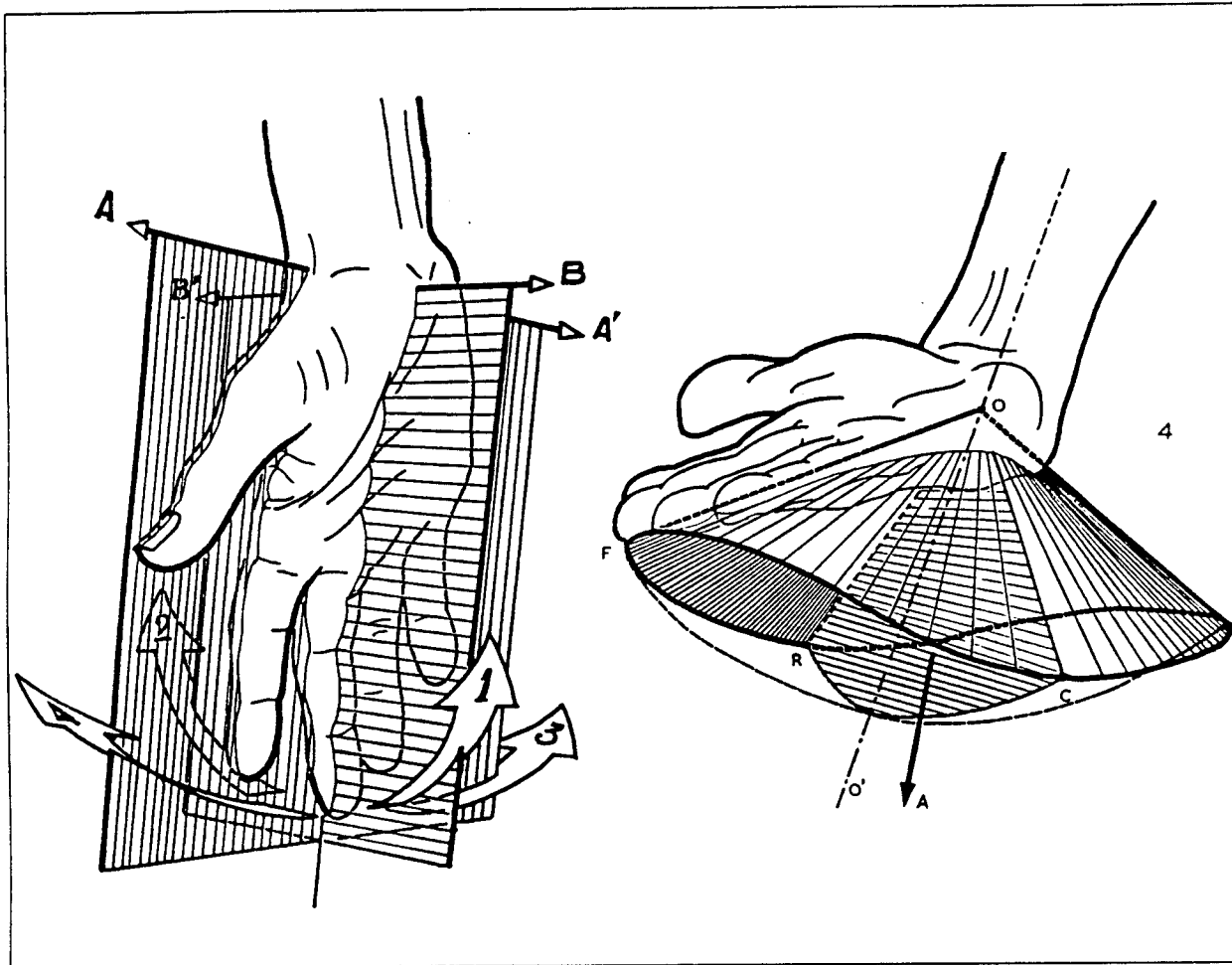
Figure 14: Movements of the wrist, cone of circumduction

- an antero-posterior axis for the adduction/abduction movement.

The range of movement in abduction is about 15°, for adduction it is between 45° and 55°, depending on the reference axis. The range of adduction or abduction is minimal when the wrist is fully flexed or extended. The range for extension and flexion are about the same, 85°. The range is maximal when the hand is neither adducted nor abducted. The combination of these movements is called *circumduction* and occur around both of the axes. A cone of circumduction can be defined to represent the path covered by the middle finger [11].

In the robotics literature, various attempts to define the requirements of teleoperation devices can be found referring to the human capabilities. One main point of interest is related to the output bandwidth of the human operator. It is commonly admitted that the forward bandwidth (from the operator to the slave) is around 10 Hz [4].

If the human operator is considered to give a sinusoidal signal, with an amplitude of 1 inch, the velocity would be 31.4 in/sec. An estimate of the acceleration on the same scheme would lead to approximatively 6gs'. The flexion of the elbow has been measured : 5gs' [1]. Obviously, the acceleration for the digits and the hand are lower than for the elbow but actually, we do not have any estimation of this value at this point.

Brooks reports that moving a loaded joystick, pilots can reach the rates of 75 in/sec when the load does not exceed 35 lbs. This value decreases to 50 in/sec for a 35 lbs. resistance and 10 in/sec for a 100 lbs. load. The velocity of the human arm has been measured at 168 in/sec unloaded.

In the determination of the bandwidth of a system, there is one important parameter, the kind of task to perform. Weither the task is isometric, isotonic or intermediary, the results will differ. An *isometric* task is performed with a stationary environment and a sinewave force command. The *isotonic* case refers to a sinusoidal position command and a free space. In the third configuration, a constant force command is applied with a sinewave moving environment.

In a report on the requirements for teleoperators [1], Brooks studied the response characteristics of the operator. From experiments and studies he concludes that the "human operator can generate trajectories and responses with up to 5 Hz components".

The neuromuscular response of the muscles shows that for a single muscle fiber, the lowest level of response, named *twitch motion* presents the following characteristics :
- a latent period prior to movement, 10 ms,
- a shortening period, the fiber reaches its shortest length, 40 ms,
- a relaxation time, 40 ms,
- a recovery period, 40 ms.

When twitches are initiated shortly one after the other (10–30 Hz), there is a summation motion with a staircase effect resulting in a physiological tremor. Stimulating the muscle more than 30 times per second leads to tetany, that is a maintained contraction of the muscle [1]. Clark and Horch [2] reports that few voluntary movements exceed rates of a few hertz (though, involuntary tremors may have frequency components exceeding 10 Hz).

Only a two-third of the muscle fibers are voluntarily contracted simultaneously. Generally, the change of length for a muscle from its maximum to its minimum length is about 20 % but very often only a part of this range is used. In the case of reflexive isometric control, the operator is capable of responses up to 10 Hz components.

4.5   Comments and Conclusions

Even though non-kinesthetic cues are available to determine the position of a limb, the kinesthetic system provides fundamental informations coming from the receptors located in the joints, the skin, and the muscles. Our sense of position and movement are independent. The muscle spindles are responsible of our knowledge of the position of the limbs. In association with the skin receptors they provide our sense of movement.

Kinesthesis of the finger differs from that of the other limbs. For example, anaesthesia of the skin around the knee does not affect our perception of its position. If the skin of the hand is anaesthezied, our performance are considerably reduced.

Our sense of tension in the muscle certainly comes from the Golgi tendon organs found in the muscles. We also have a sense of effort which is not directly dependent of the sense of tension.

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5 Summary

As was discussed in this report, there is multiple evidence that both tactile and kinesthetic senses are combined to provide for haptic perception. This perception is obtained through a variety of cues coming from extraordinarily numerous mechanoreceptors distributed throughout the structure of the system (joints, muscles, tendons, derma, skin). Using these cues, a subject experiences the simultaneous sensation of position of, and forces applied to, an object held in the hand. As for any human perceptual channel, it is generally accepted that a stable representation in the central nervous system of the motion of a held object results from a combination of several channels, in particular position and force.

There are various cutaneous mechanoreceptors located in the outer layers of the skin. The free nerve endings are the most numerous and may play an active role in the perception of pain, cold and warmth. Most of the receptors are encapsulated. They differ in the hairy and glabrous skin. We are more concerned by the glabrous skin since hand/fingers perception is central to this study. There, we find Meissner's corpuscles, Merkel's discs and Pacinian corpuscules. Ruffini endings may as well be present. Each kind of receptor is tuned to respond to a certain category of stimuli above a given threshold. The central nervous system integrates all the cues to provide a tactual information.

The mechanoreceptors are classified in three categories according to their rates of discharge in response to a constant pressure stimulus. The Pacinian corpuscles (PC) are very rapidly adapting receptors which discharge one or two impulses per stimulus and may be considered as acceleration or vibration detectors. The rapidly adapting receptors (RA), the Meissner's corpuscles, can be seen as velocity detectors, and discharge only during movements of the skin. The slowly adapting receptors, or intensity detectors, continue to discharge in response to a maintained pressure. Two units are involved: the Merkel's cells (SA I) and the Ruffini endings (SA II).

Each class of mechanoreceptor respond preferentially over a frequency range : the minimum threshold (highest sensitivity) for the PC units is around 250–300 Hz but they respond from 30 Hz to very high frequencies. The RA units effective frequency range is between 10 and 200 Hz, with more sensitivity below 100 Hz. The SA units respond at low frequencies. The sensitivity threshold for touch is about 6–20 μm

for the depth of indentation on the hand. A relationship between the threshold value and the frequency reveals that RA's units are likely to be responsible of the perception under 40–50 Hz and the PCs units are responsible of the detection for higher frequencies. The receptive fields characteristics are larger for the PC receptors (their density is lower). This, related to the previous remark leads us to conclude that when the frequency increases, our ability to detect the **localization and the direction** of a vibration decreases. The experiments intending to characterize the detection of the direction of a movement on the skin showed that the SA's units are responsible for the detection of stretch and they present a directional activity (for a 20 g indentation force, the stretch is well detected). The PCs and RAs units are more likely to detect the relative motion of slip. The stretch enhances the ability to detect movement on the surface of the skin, at 1 cm s^{-1}, the threshold is 0.6 mm.

The frequencies of interest for kinesthesis are much lower than for the tactual perception.

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