Chapter 3
A Brief Overview of the Human Somatosensory System

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Abstract This chapter provides an overview of the human somatosensory system. It is the system that subserves our sense of touch, which is so essential to our awareness of the world and of our own bodies. Without it, we could not hold and manipulate objects dextrously and securely, let alone musical instruments, and we would not have a body that belongs to us. Tactile sensations, conscious or unconscious, arise from the contact of our skin with objects. It follows that the mechanics of the skin and of the hand its interaction with objects is the source of information that our brain uses to dextrously manipulate objects, as in music playing. This information is collected by vast array of mechanoreceptors that are sensitive to the effects of contacting objects, often with the fingers, even far away for the region of contact. This information is processed by neural circuits in numerous regions of the brain to provide us with extraordinary cognitive and manipulative functions that depend so fundamentally on somatosensation.

3.1 Introduction

The overarching purpose of the somatosensory system is to inform the brain of the mechanical state of the body that it inhabits. It shares this function with the vestibular system. But whereas the vestibular system operates in the low-dimensional space of head translations and rotations, the somatosensory system takes its input from almost the entire body. The main sources of information arise in part from the load-bearing structures represented by connective tissues such as tendons and ligaments, in part from the motion-producing tissues, the muscles, and in part from the outer layers of body, that is the skin. As a result, unlike the vestibular system, which is sensitive to the movements of a rigid body—the cranium—the somatosensory system relates to

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S. Papetti and C. Saitis (eds.), *Musical Haptics*, Springer Series on Touch and Haptic Systems, https://doi.org/10.1007/978-3-319-58316-7_3

mechanical domains that are in essence deformable bodies. This explains why, despite the fact that the two systems share the same overall task, they differ fundamentally. The vestibular inputs arise from small, easily identifiable organs in the inner ears, since it is the low-dimensional description of the movements of a rigid body that is of interest. In contrast, the somatosensory system relate to what is essentially an infinite dimensional solid (and liquid) domain and depends on the changes of its internal mechanical state to infer the properties of the objects that are being touched such as their weight, the substance they are made of, or the existence and nature of the relative movement of the body in relation to external objects [35, 74]. In other words, it is a distributed system in the physical sense that its mechanical state is described by (tensor) fields rather than vectorial quantities. This basic fact is of course reflected in its general organisation where very large populations of specific detectors are found in all load-bearing and load-producing tissues. That is not to say that the somatosensory system is unique in its reliance on large populations of sensors. This is also true of all sensory systems, including vision, audition, taste/olfaction and of the vestibular system.

The haptic function depends on several systems of large organs. In an adult person, the skin's mass can reach two kilograms and part of its functions is mechanosensing. However, it must be kept in mind that most of the body's soft and connective tissues are mechanosensitive and associated with abundant innervation. The exact contributions of the different mechanoreceptive channels to the formation of haptic percepts remain today to be established.

Recent research has revealed a number of rather surprising findings. For example, most textbooks teach that the sense of limb's relative position is mediated by mechanoreceptors embedded in the muscles. However, recent research has shown conclusively that the awareness of limb position is also mediated by sensory inputs arising from the skin [20, 21]. Alternatively, it is often assumed that the quality of the surfaces of objects is the exclusive result of cutaneous inputs. Recently, it is been shown that complete abolishment of distal cutaneous input, resulting from trauma or anaesthesia, had negligible effect on participants' ability to discriminate the roughness of surfaces [53], which could be explained by the fact that friction-induced vibrations taking place at the fingertip propagate far inside the anatomy, at least up to the forearm [15], stimulating large populations of mechanoreceptors that might not be located in the skin and that can be quite remote from the locus of mechanical input [69].

These observations demonstrate that the study of the haptic function must be discussed from different perspectives where individual components should not be assigned one-to-one relationships, largely because the sensing organ, as alluded to in the previous paragraph, is by physical necessity distributed in the entire body and not even just at its surface.

3.2 Biomechanics of the Hand

3.2.1 Hand Structural Organisation

David Katz described the hand as a ‘unitary organ’ where the sensory and motor functions take place together [48]. The hand is not the only organ in the body that has this particularity. The foot is in many ways similar to the hand, but configured for locomotion rather than manipulation. Both organs possess an abundantly articulated skeletal structure held together by connective ligaments in the form of joint capsules and tendons that are connected to muscles located remotely in the forearm or the leg. In turn, these muscles insert in the arm and leg bones, and thus, a single tendon path can span up to four joints with the wrist and the three phalangeal joints. To give a sense of scale of the biomechanical complexity of the hand and the foot, it suffices to consider that phalanges receive four tendon insertions except for the distal phalanges that receive only two. Some tendons insert in several bones, and most tendons diverge and converge to form a mechanical network. The hand and the foot also have the so-called intrinsic muscles that insert directly into small bones, notably for the thumb, with some of these intrinsic muscles not inserting in any bones but in tendons only. Thus, if one considers bones, tendons and muscles to be individual elements, all connectivity options (one-to-one, one-to-several, several-to-one) are represented in the biomechanical structure of the hand, foot and limbs to which they are attached.

3.2.2 Hand Mobility

It is tempting to think of the hand as an articulated system of bodies connected with single-degree-of-freedom joints that guide their relative displacements. This simple picture is quite incorrect on two counts. The first is that skeletal joints are never ‘simple’ in the sense that they allow movements that ideal ‘lower pairs,’ such as simple hinges, would not. In biomechanics, one seldom ventures in quoting a precise number of degrees of freedom which, depending on the authors, can vary from 10 to more than 60 when speaking of the hand only. The biomechanical reality suggests that the kinematic mobility of the hand is simply the number of bones considered six times, but the actual functional mobility suggests that certain joint excursions have a much greater span than others. One could further argue that, save for nails, since the hand interacts with objects through soft tissues, its true mobility is infinite dimensional [35], a problem we shall return to when discussing the sensing capabilities of the hand.

The most productive approach to make sense of this complexity is, counter-intuitively, to augment the complexity of the system analysed and to also include the sensorimotor neural control system in its description. In effect, the mechanics of the hand mean nothing without the considerable amount of neural tissue and attending sophisticated neural control that is associated with it. In this perspective, the concept of ‘synergies’ was put forward long ago by the pioneers of the study of movement production and control (Joseph Babinski 1857–1932, Charles Scott Sherrington 1857–1952, Nikolai Bernstein 1896–1966, and others) and has received much study since.

Loosely speaking, the idea behind this concept is that movements with a purpose—be it sensory, manipulative, locomotive or communicative—are highly organised. Each of these purposes is associated with the coordinated action of groups of muscles through time, but, importantly, the number of these purposes is small compared to the number of all possible movements. The purposes can include reaching, grasping, feeling, drawing, stepping, pressing on keys, sliding on strings or plucking them, bending notes, and, crucially, they can be combined and chained together to yield complex behaviours orchestrated by the central nervous system. The entire sensorimotor system, much of which is dedicated to the hand, is implemented following a hierarchical organisation with nuclei in the dorsal column, the brain stem, the midbrain, the cerebellum and ultimately several cortical regions. The considerable literature on the subject can be approached through recent books and surveys [10, 51, 67].

3.2.3 The Volar Hand

The inside region of the hand is named ‘volar’ by opposition to the ‘dorsal’ region. The volar region is of primary interest since it is the interface where most of the haptic interactions take place. Detecting a small object—say a sewing needle lying on a smooth surface—is absolutely immediate with the fingertip but more difficult with other volar hand regions, and the same object will go undetected by any other part of the body, including the dorsal hand region. It is also evident that the sensitive volar skin is mechanically very different of what is often called the ‘hairy skin’ covering the dorsal region. The most conspicuous feature is the presence of ridges, that is, of a clearly organised micro-geometry that is not seen elsewhere, except in the plantar region of the foot. In fact, the often called the ‘glabrous’ skin differs from the ‘hairy’ skin in four important properties.

Pulp: The glabrous skin is never really close nor very far from a bone. In the fingertip and elsewhere in the hand, it is separated from the bone by a relatively uniform distance of 3 or 4 mm. The space in between is densely filled by a special type of connective tissue called the pulp [33]. This fibrous tissue is crucial to give the volar hand its manipulative and sensorial capabilities since a fingertip can take a load of several hundreds of Newtons without damage and *simultaneously* detect a needle. The pulp gives the skin the ability to conform with the touched object by enlarging the contact surface, which is mainly independent from the load past a certain value [68]. Incidentally, this simple fact makes it evident that the notion of ‘force’ or even of ‘pressure’ must be taken carefully when speaking of tactile sensory performance (see Sect. 4.2).

Ridges: The ridges are peculiarly unique to the volar hand and plantar foot. They long have been believed to have the mechanical purpose to increase friction and indeed are often called ‘friction ridges’. Recent findings have shown that quite the opposite is the case [80]. To understand why that is, one must consider basic notions in contact mechanics evoked in the next paragraph. The main point being that ridges actually diminish the net contact surface of volar surface against an object compared to a non-ridged surface.

Stratum Corneum: The external skin layer, the stratum corneum, is made of keratin, which is a structural material arising from the death of skin cells. This material is mechanically akin to a polymer [61] and is capable of creating complex mechanical effect during sliding, even on optically smooth surfaces [16, 19, 83].

Sweat Glands: While the volar regions of the body cover only 5% of its surface, 25% of all the 2 millions sweat glands are located there with a density reaching 300 per cm^2 [57, 73].

3.2.4 Bulk Mechanics of the Fingertip and the Skin

The glabrous skin covering the volar region of hand is, quite visibly, neither an isotropic nor a homogeneous medium. It is apparent that the ridges introduce preferred directions that facilitate certain types of deformations. The effect of static punch indentation on the human fingertip can be made visible by imaging the shape of finger contact with a flat surface when a small object, such as a guitar string, is trapped at the interface, see Fig. 3.1.

The detailed local properties of the ridged skin were investigated in vivo by Wang and Hayward [79] by loading approximately 0.5 mm^2 regions of skin. Unsurprisingly, the measurements revealed great anisotropy according to the ridge orientation when the skin is stimulated in traction, that is, in its natural mode of loading (see Fig. 3.2). On the other hand, the elastic properties of the ridged skin seem to be by-and-large immune of factors such as individuals and thickness of the stratum corneum. Detailed in vivo measurement can also be performed using optical coherence tomography (OCT) or elastography [24, 52], obtaining results similar to those found by direct mechanical stimulation. These findings point out how uncertain it is to predict the properties of tissues across length and timescales. The viscoelastic properties of the ridged skin are dominated by two characteristic times, one very short, of the order of one millisecond, and the other much longer, of the order of several seconds [79], which shows, like the peripheral neural system introduced below, that the mechanical somatosensory system operates at several timescales.

Also of relevance to the design of haptic interfaces is some knowledge of the bulk mechanical properties of the extremities, taken as a whole. Again, this subject is better tackled in terms of specific tasks. When the human finger interacts with a surface, three modes of interaction may be combined: (i) a contact can be made to or released from a surface; (ii) the finger can displace the mutual surface of contact through a rolling motion; (iii) or it can do so through a sliding motion [34, 35]. Each of these

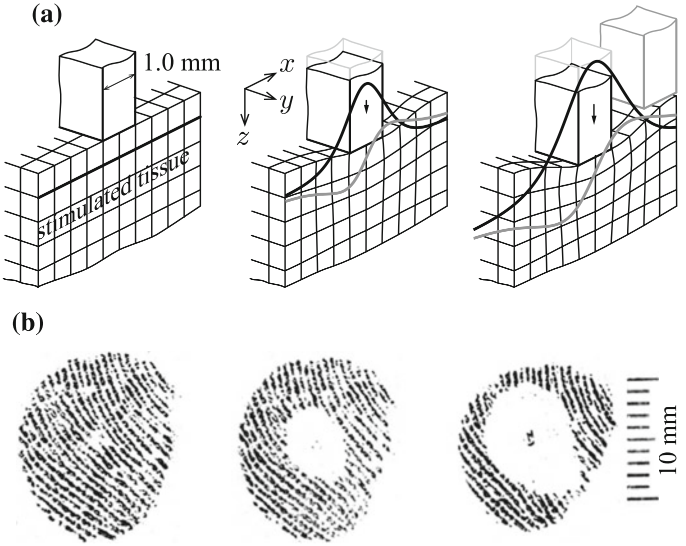

Fig. 3.1 **a** A punch indenting an ideal solid half-space follows the Boussinesq–Flamant's deformation problem, where the elongation follows the pattern indicated by the black line and the shear deformation that of the grey line. **b** Imaging the contact surface indicates that an actual finger grossly follows this pattern. However, a 2 mm indentation made by a 1 mm punch creates a deformation region as large as 6 mm that does not have a circular shape, owing to the anisotropy of the skin introduced by the ridges. Figure from [36]

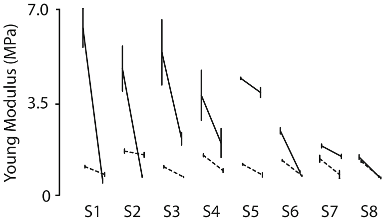

Fig. 3.2 Equivalent material properties of human ridged skin along and across ridge direction (solid lines) for eight different people. For most, the equivalent elasticity in elongation is highly depending on the ridge direction and different people can have very different skins. However, when the deformation is dominated by shear, then it is much less dependent on load orientation and on individuals. Figure from [79]

modes corresponds to specific mechanics. When contact is made, the contact surface grows very fast with normal loading, and normal displacement is accompanied with very steep acceleration of the contact force. To wit, a 1 mm indentation of the fingertip by a flat surface corresponds to a normal load of less than 0.2 N, but at 2 mm the normal load is already 10 times larger at 1.0 N, and it takes only an increment of 0.5 mm to reach the value of 5.0 N [68]; concomitantly, the contact area has reached half of its ultimate value for only 0.5 N of load, and past 1.0 N, it will not increase significantly, regardless of the load [68], suggesting that representing a fingertip by a local convex elastic homogenous solid is far from an being an acceptable model in terms of its ability to conform to the gross shape of touched objects. Moreover, these properties are very much dependent on the speed at which indentation occurs. Pawluk and Howe found that the mechanical response curve under similar conditions varied greatly with speed, a 1.0 mm indentation applied at 0.2 mm/s causes a loading of about 0.2 N, as just mentioned, but the same displacement applied at 80 mm/s causes a contact loading of 1.0 N [63].

Most frequently, the finger interacts with a rigid object, which either is oscillating and/or provides the surface on which the finger slides, in all cases generating oscillations in the finger pad. Such occurrences are common during music playing. To model and explain these interactions, it is essential to have a model of the bulk mechanics of fingertip in the small displacements and over the whole range of frequencies relevant to touch, that is DC to about 1 kHz. In the low frequencies, the data can be extracted from studies performed in the condition of slow mechanical loading, transient loading or large displacements [29, 40, 62], but a recent study conducted with the aid of a novel mechanical impedance measurement technique [82] has shown that a fingertip, despite all the complexities of its local mechanics, may be considered as a critically damped mass-spring-damper system with a corner frequency of about 100 Hz and where the contribution of inertia to the interaction force is negligible at all frequencies before elasticity and viscosity [81], see Fig. 3.3. In essence, the fingertip is dominantly elastic below 100 Hz and dominantly viscous above this frequency. In the high frequencies ($\geq$400 Hz), the fingers exhibit structural dynamics that have an uncertain origin. Quite surprisingly, the fingertip bulk elasticity (of the order of 1 N/mm), viscosity (of the order of 1 N s/mm) and equivalent inertia (of the order of 100 mg) are by-and-large independent from a tenfold variation of the normal load. It can be surmised that these properties hold true for all volar regions of the hands and feet.

Friction is arguably the most important aspect of the haptic function since without it we could scarcely feel and manipulate objects. Because the finger is a biological, living object, it has properties which often escape our intuition, especially concerning its frictional properties, that latter having a major impact on the manipulative motor function as well as on its detection and discriminative function [1]. All the aforementioned mechanosensitive sensors in the skin and deep tissues are in fact likely to respond to friction-induced phenomena. A good example of that is any attenuation of the sensitivity of these receptors, for example by a situation as banal as cold hand or dry hands, invariably results in an increase in the grip force as a strategic response of the brain to sensory deficit. This was also documented when fingers are dry since dry skin is more slippery [2]. As another example, recent studies in hedonic touch have established a link between the sensation of pleasantness and the skin's tribological properties that in turn influence the physics of contact [47].

Some key points to keep in mind. First, the notion of coefficient of friction in biotribology must be complemented by the notion of load index, which describes the dependency between net normal load and the net traction, since in most cases of practical importance Amontons' first law, stating that friction is empirically independent from the apparent contact area, does not hold. A second point is the importance of

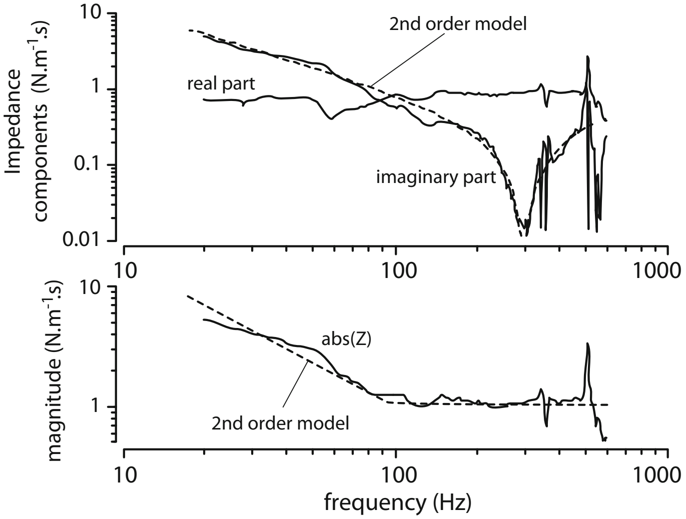

Fig. 3.3 Fingerpad impedance for small displacements. Figure from [81]

the presence of water in the physics of the contact owing to the fact that keratin is the building material of the stratum corneum. Keratin is akin to hydrophobic polymers with the effect that traction increases with the presence of water despite the reduction of the interfacial shear strength. This is true up to a point where, in fact, excess of water hydrodynamically decreases friction in competition with the former effect. A third complicating factor is that the presence of water plasticises the stratum corneum with the consequence of dramatically increasing the effective contact area, which is a phenomenon that occurs at the molecular level [19]. A fourth factor is the very large effect of time on the frictional dynamics. In fact, all these four factors dominate the generation of traction as opposed to the normal gripping load, in direct opposition to the simplistic friction models adopted in the greatest majority of neuroscience and robotic studies [1]. Furthermore, this physics depends completely on the counter surface interacting with the fingers, where the material properties, the roughness of the surface and its structural nature (say wood) interact with the physiology of sudation (perspiration) through an autonomic function performed by the brain [2].

3.3 Sensory Organs

3.3.1 Muscles, Tendons and Joints

Muscles are primarily elastic systems that develop a tensional force that depends on several factors among which are at their activation level and their mechanical state, often simplified to just a length. At rest, a muscle behaves passively, like a nonlinear spring that becomes stiffer at the end of its range. When activation is increased from rest to full activation, the active contribution to the passive behaviour is greatest at midrange. As a result, for a given activation level, a muscle looses tonus if it is too short or too long. A muscle that shortens at high speed produces very little tension, while a lengthening muscle gives a greater tension, like a one-way damper. It must be noted that the neuromuscular system takes several hundreds of milliseconds to modulate the activation. Therefore, beyond a few Hertz, the passive portion of the dynamics dominates. Skeletal muscles are in great majority organised in agonist–antagonist systems [84]. These terms describe the fact that separate muscles or muscle groups accelerate or prevent movement by contracting and relaxing in alternation. It is nevertheless a normal occurrence that muscles groups are activated simultaneously, a behaviour termed co-contraction or co-activation. Co-contraction, which result in a set of muscle tensions reaching a quasi-equilibrium around one or more joints, enables new functions, such as stabilisation of unstable tasks [8]. The behaviour of an articulation operating purely in an agonist or antagonist mode is nevertheless very different from that of the same articulation undergoing co-contraction.

A consequence of co-contraction which is relevant to our subject is to stiffen the entire biomechanical system. This can be made evident when grasping an object. Take for instance a ruler between the thumb and the index finger, grip it loosely and note the frequency of the pendulum oscillation. Tightening the grip results in a net increase of this frequency as a consequence of the stiffening of all the tissues involved, including the muscles that are co-contracting: a tighter grip resists better to a perturbation. This also means that the musculoskeletal system can modulate stiffness at a fixed position, for instance when grasping. This observation requires to consider any linear model of the musculoskeletal system with much circumspection.

We can now see how this system can contribute to the sensation of the weight of objects since in one of the strategies employed by people in the performance of this perceptual task is to aim at reaching a static equilibrium where velocity tends towards zero, a condition that must be detected by the central nervous system. For instance, when it comes to heaviness, it has been noticed many times that subjects tend also to adopt a second strategy where rapid oscillations are performed around a point of equilibrium. In the latter case, it is possible to suppose that it is the variation of effort as a function of movement and of its derivative that provides information about the mass (and not about the weight). Muscles are connected to the skeleton by tendons which also have mechanoreceptors called the Golgi organs. These respond to the stress to which they are subjected and report it to the central nervous system, which is thus informed of the effort applied by the muscles needed to reach a static or dynamic equilibrium.

The joints themselves include mechanoreceptors. They are located in the joint capsule, which is a type of sleeve made of a dense network of connective tissues wrapping around a joint and containing the synovial fluid. These receptors—the so-called Ruffini corpuscle—respond to the deformation of the capsule and appear to play a key role when the joint approaches the end of its useful range of movement, in which case some fibres of the capsule begin stretching [28].

The sensory organs of the musculoskeletal system give us the opportunity to introduce a great categorisation within the fauna of mechanoreceptors, namely rapidly adapting (RA) and slowly adapting (SA) receptors. The distinction is made on a simple basis. When a RA receptor is stimulated by undergoing a deformation, it responds by a volley of action potentials for a duration and a density that is driven directly by the rate of change of the stimulus, just like a high-pass filter would (but direct analogies with linear filters should be avoided). When a SA-type receptor is deformed, it responds for the whole duration of the stimulus but is rather insensitive to the transient portion and in that resembles a low-pass filter including the zero frequency component.

This distinction is universal and is as valid for the receptors embedded in ligaments and capsules (SA) as for those located in muscles and in the skin (SA and RA). To pursue the analysis of the perception of object properties, such as shape, we can realise that the joints too are involved in this task, since any muscular output and any resulting skeletal movement have an effect on the joints in the form of extra loading, relative sliding of structures and connective tissue deformation. These observation illustrates the conceptual difficulties associated with the study of the haptic system, namely that it is practically impossible to associate a single stimulus to an anatomical classification of the sources of information.

3.3.2 Glabrous, Hairy and Mucosal Skin

The body surface is covered with skin. As mentioned above, it is crucial to distinguish three main types of skin having very different attributes and functions. The mucosal skin covers the ‘internal’ surfaces of the body and are in general humid. The gums and the tongue are capable of vitally important sensorimotor functions [7, 39, 75]. The tongue’s capabilities are astonishing: it can detect a large number of objects’ attributes including their size, their shape, very small curvature radii, hardness and others. Briefly, one may speculate that the sensorimotor abilities of the tongue are sufficient to instantly detect any object likely to cause mechanical injury in case of ingestion (grains of sand, fish bones).

The glabrous skin has a rather thick superficial layer made of keratin (like hairs) which is not innervated. The epidermis, right under it, is living and has a special geometry such that the papillae of the epidermal–dermal junction are twice as frequent as the print ridges. The folds of the papillae house receptors called Meissner corpuscles, which are roughly as frequent in the direction transversal to the ridges as in the longitudinal direction. The Merkel complexes (which comprise a large number of projecting arborescent neurites) terminate on the apex of the papillae matching the corresponding ridge, called the papillary peg. The hairy skin does not have such a deeply sculptured organisation. In addition, each hair is associated with muscular and sensory fibres that innerve an organ called the hair follicle.

This geometry can be better appreciated if considered at several length scales and under different angles. A fingerprint shows that the effective contact area is much smaller than the touched surface. The distribution of receptors is highly related with the geometry of the fingerprint. In particular, the spatial frequency of the Meissner corpuscles is twice that of the ridges. On the other hand, the spatial frequency of the arborescent terminations of the Merkel complexes is the same as that of the ridges. This geometry explains why the density of Meissner corpuscles is roughly five times greater than that of the Merkel complexes [37, 45, 55, 59]. Merkel complexes, however, come in two types. The other type forms long chains that run on the apex of the papillae [60]. The distinctive tree-like structure of this organ terminates precisely at the dermal–epidermal interface.

It is useful to perform simple experiments to realise the differences in sensory capabilities between glabrous and hairy skin. It suffices to get hold of rough surfaces, such as a painted wall or even sand paper, and to compare the experience when touching it with the fingertip or with the back of the hand. Try also to get hold of a Braille text and to try to read it with the wrist. The types of receptors seem to be similar in both kinds of skin, but their distribution and the organisation and biomechanical properties of the respective skins vary enormously. One can guess that the receptor densities are greatest in the fingertips. There, we can have an idea of their density when considering that the distance between the ridges of the glabrous skin is 0.3–0.5 mm.

The largest receptor is the Pacini corpuscle. It is found in the deeper regions of the subcutaneous tissues (several mm) but also near the skin, and its density is moderate, approximately 300 in the whole hand [11, 71]. It is large enough to be seen with the naked eye, and its distribution seems to be opportunistic and correlated with the presence of main nervous trunks rather than functional skin surfaces [32]. Receptors of this type have been found in a great variety of tissues, including the mesentery, but near the skin they seem to have a very specific role, that of vibration detection. The Pacinian corpuscle allows to introduce a key notion in physiology, that of specificity or ‘tuning’. It is a common occurence in all sensory receptors (be it chemoreceptors, photoreceptors cells, thermoreceptors or mechanorectors) that they are tuned to respond to certain classes of stimuli. The Pacinian corpuscle does not escape this rule since it is specific to vibrations, maximising its sensitivity for a stimulation frequency of about 250 Hz but continuing with decreasing sensitivity to 1000 Hz. It is so sensitive that, under passive touch conditions, it can detect vibrations of 0.1 micrometer present at the skin surface [78]. Even higher sensitivity was measured for active touch: results addressing a finger-pressing task are reported in Sect. 4.2.

The Meissner corpuscle, being found in great numbers in the glabrous skin, plays a fundamental role in touch. In the glabrous skin, it is tucked inside the ‘dermal papillae’, and thus in the superficial regions of the dermis, but nevertheless mechanically connected to the epidermis via a dense network of connective fibres. Therefore, it is the most intimate witness of the most minute skin deformations [72]. One may have some insight into its size by considering that its ‘territory’ is often bounded by sweat pores [55, 60].

Merkel complexes, in turn, rather than being sensitive axons tightly packed inside a capsule, have tree-like ramifications that terminate near discoidal cell, the so-called Merkel cells. In the hairy skin, these structures are associated with each hair. They also very present in mucoscal membranes. In the glabrous skin, they have up to 50 terminations for a single main axon [30]. The physiology of Merkel cells is not well understood [54]. They would participate in mechanotransduction together with the afferent terminals to provide these with a unique firing pattern. In any case, Merkel complexes are associated with slowly adaptive responses, but their functional significance is still obscure since some studies show that they can provide a Pacinian-type synchronised response up to 1500 Hz [27].

The Ruffini corpuscle, which we already encountered while commenting on joint capsules, has the propensity to associate itself with connective tissues. Recently, it has been suggested that its role in skin-mediated touch is minor, if not inexistent, since glabrous skin seems to contain very few of them [58]. This finding was indirectly supported by a recent study implicating the Ruffini corpuscle not in mechanical stimulation due to direct contact with the skin, but rather in the connective tissues around the nail [5]. Generally speaking, the Ruffini corpuscle is very hard to identify and direct observations are rare, even in glabrous skin [12, 31].

Finally the so-called C fibres, without any apparent structure, innervate not only the skin, but also all the organs in the body and are associated with pain, irritation and also tickling. These non-myelinated, slow fibres (about 1 m/s) are also implicated in conscious and unconscious touch [76]. It is however doubtful that the information that they provide participates in the conscious perception of objects and surfaces (shape, size, or weight for instance). This properties invite the conclusion that the information of the slow fibres participates in affective touch and to the development of conscious self-awareness [56].

From this brief description of the peripheral equipment, we can now consider the receptors that are susceptible to play a role in the perception of external mechanical loading. As far as the Ruffini corpuscles are concerned, several studies have shown that the joints, and hence the receptor located there, provide proprioceptive information, that is estimation of the mechanical state of the body (relative limb position, speed, loading). It is also possible that they are implicated in the perception of the deformation of deep tissues which occurs when manipulating a heavy object. It might be surprising, but the central nervous system becomes aware of limb movements not only by the musculoskeletal system and the joints, but also by the skin and subcutaneous tissues [22].

It is clear that the receptors that innerve the muscles also have a contribution to make, since at the very least the nervous system must either control velocity to zero, or else estimate it during oscillatory movements. Muscles must transmit an effort able to oppose the effects of both gravity and acceleration in the inertial frame. Certainly, Golgi organs—which are located precisely on the load path—would provide information, but only if the load to be gauged is significantly larger than that of the moving limb. Lastly, the gauged object in contact with the hand would deform the skin. From this deformation, hundreds of mechanoreceptors would discharge, some transitorily when contact is made, some in a persisting fashion.

At this point, it should be clear that the experience of the properties of an object, such as its lack of mobility, is really a 'perceptual outcome' arising from complex processing in the nervous system and relying on many different cues, none of which alone would be sufficient to provide a direct and complete measurement about any particular property. This phenomenon is all the more remarkable, since, say a saxophone, seems to have the same weight when is held with the arms stretched out, squeezed between two hands, held by the handle with a dangling arm, held in two arms—among other possibilities—each of these configurations involving distinct muscle groups and providing the nervous system with completely different sets of cues!

3.3.3 Electrophysiological Response

3.3.3.1 Categories of Responses

The idea behind the study of the electrophysiological response is to measure directly the signals transmitted by the neurons, the so-called action potentials. This measurement can be done by inserting electrodes in peripheral nerves, something that can be done in people without measurable consequences for health. It is when making such measurements that it was realised that there existed the two types of responses already mentioned (SA & FA). It is nevertheless important to distinguish the capacity that has a given receptor to respond to fast stimuli from the type of responses.

For the receptors located in the skeletomuscular system, it is relatively easy to determine their response mode from the anatomy, but in the skin this is not possible. Mechanoreceptors, with the exception of the Pacinian corpuscle, are very small and very dense, and recording is only possible at some distance (wrist, arm, leg). The consensus is that the Ruffini corpuscles (not observed in the glabrous skin) are of the SA type and so are the Merkel complexes. On the other hand, the Meissner corpuscle is of the FA type.

Some of these inferences are made by stimulating the skin with *von Frey filaments*, from Max von Frey who introduced them at the end of the nineteenth century as a calibrated method to stimulate touch. Using this method, it is possible to determine that certain afferent nerve fibres respond from stimulating a tightly limited territory, say of a size of 2 mm (type I), while some others respond to stimulation applied within a much wider territory, up to one centimetre in size, or more (type II). This physiological distinction—yet not anatomical—gives rise to four possibilities: FA-I, FA-II, SA-I, SA-II. The receptive fields are very varied in shape and sizes throughout the surface of the body, frequently overlapping, and often, they do have clear borders [42, 43, 46, 77].

Most mechanical phenomena at play, however, are nonlocal; detecting a one mm^2 crumb with the finger has mechanical consequences that spread up to 100 mm^2 of skin tissue; sliding the finger on a surface with $10\,\mu\text{m}$ asperities has easily measurable consequences up the forearm [15, 69]. In that sense, it is highly probable that most motor and perceptual behaviours simultaneously engage all mechanoreptors' populations [66].

3.3.3.2 Coding Options

It stands to reason that the flow of the action potentials must be able to encode information arising from peripheral stimulation. Before proceeding further, it is important to recall that information ascending from the periphery is not the only source that determines the conscious experience, far from it. In fact, self-generated movement [13], intention [85], and learning [17], not counting stimuli coming from other sensory modalities [18, 34], all modify the conscious percept arising from a same stimulation.

A number of codes have been discovered that represent information arising from touch and kinaesthesia neurally. It is likely that many more will be discovered in the future. As far as kinaesthetic information is concerned, it was found that the specific recruitment of nerve fibres encodes spatially the position of a joint [9]. With regard to the direction of movement, it seems plain that the agonist–antagonist organisation of the motor system encodes it automatically. The muscle spindles respond specifically to velocity by a frequency code: the larger is the amount of change of length per unit of time (that is speed), the higher is the number of nerve impulses (or action potentials) per unit of time. This code has the property to be resistant to noise and perturbations: an action potential missed or fired accidentally does not make a great difference over a long period of time. On the downside, this code is by construction not temporally precise because it takes a minimum number of action potentials to encode a rate.

As far as touch is concerned, codes are still mysterious but a few have been found. For low intensity stimulation, certain FA receptors behave like oscillators synchronised with the waveform [65], which corresponds to a temporal code. In touch, it is also clear that spatial coding is fundamental. For instance, when reading Braille each dot specifically stimulates a small population of receptors which convey the presence of the dot [26]. The shape of a touched object can be directly coded by the contact surface [49]. Other codes, however, are likely to be at play. When a fingertip is mechanically loaded ramping from rest to a maximal value in the tangential direction—an event that occurs each time we pick up an object—it was shown that this event is represented by a correlation code [41]. This means that is the temporal coincidence of two or more action potentials that convey the nature of the mechanical interaction between the finger and the object. It has also been shown that when a finger slips on a surface with a single asperity, action potentials are synchronised with encounter of this asperity with each ridge of the print, which corresponds to an extremely fine spatiotemporal code [50].

During gripping, the recruitment code has also been documented as coding directly in skin coordinates [26]. A similar observation can also be made of curvature, since the ratio between the contact surface and the normal load depends on it [25]. It is highly probable that sliding and sticking and transitions between these two states are coded by the relative response of RA and SA populations, which is another form of correlation [70]. Another important attribute of a contact detected by touch is simply the average load—namely its direction and magnitude in the normal and tangential directions [4]—which leads to believe that generally information is coded by receptor populations and not by individual ones. It is also probable that the elastic properties of the touched object are coded peripherally and specifically by composite populations in space and time. Last but not least, the coding of texture, or rather of the micro-geometry of surfaces that interact with the glabrous skin, was the subject of a considerable number of studies [38]. Despite these works, it is likely that most of the codes employed by primates remain to be discovered.

The question of codes can also be considered from the viewpoint of the physiological response of receptors. Unfortunately, this approach is fraught with numerous difficulties. It is very rare when one can stimulate specifically one particular receptor and to measure its response. Since stimulation can only be effected from the surface of the skin, even the most concentrated indentations have consequences far away from the contact site: deformation propagates several millimetres around the zone of stimulation [14]. As a result, it is generally impossible to associate a physiological response to a particular anatomical characteristic.

Due to its size, the Pacinian corpuscle is nevertheless an exception because it is possible to study its response in vitro [3, 6]. It has interesting characteristics some of which are shared with Merkel complexes [27]. The first peculiarity is a frequency-dependent sensitivity: the deformation needed to trigger a single action potential is smallest at 250 Hz. In this condition, the discharge of action potentials is synchronous with the stimulation, giving a direct temporal code. If amplitude is reduced, the corpuscle looses this synchronicity property but still responds over several cycles to truly microscopic deformations. This feature translates into transfer function with a strong, obvious nonlinear jumping behaviour. For a given frequency, the response does not change with amplitude over a range, but once a threshold is reached, a frequency doubling is observed.

Taking the example of the perception of the weight of an instrument, it should become increasingly clear that such perception does not result from a single or simple family of neural signals, but from a veritable jungle of motor and sensorial signals whose conscious perception is that of a unitary percept attributed to the held object. This could contribute to explain why the motor system and the perceptual seem to operate independently from each other, at least when it comes to the conscious knowledge of either action or perception [23, 64].

3.4 Central Organs

It is not easy to paint a concise and logical picture of the central nervous organisation of the haptic system. Besides, it would be misleading to believe that it can be confined to a small number of functionally and anatomically well-delimited cortical areas, ganglions and pathways. The discovery of this organisation is a work in progress. Originally discovered due to the random consequences of war, accidents, diseases, surgical innovations, and today with electrophysiology (in humans, but mostly in monkeys and rats) and brain imaging techniques (pet, fMRI, and very recently optical imaging), it can be said that the representation that is made of this organisation constantly changes with the introduction of new techniques.

Nevertheless, it is useful to have a general idea of the great structures [44]. Sensory pathways ascend through the spine and first project on dorsal column nuclei which in turn project onto the ventral posterior nucleus of the thalamus, located at the apex of the spine, right at the centre of the cranium. Many functions are ascribed to the thalamus, but one of them is to transmit all sensory afferent information (with the exception of olfaction and vestibular inputs) to the cortical regions. This organ seems to be able to process peripheral information into a form that is suitable for cortical processing.

The somatosensory cortex is located on both sides of the great parietal circumvolution, and a huge number of fibres project onto it. The cortex is divided into two main areas, SI (primary) and SII (secondary), on each side of the central parietal sulcus. According to Brodman's nomenclature [86], SI is divided into four areas: 1, 2, 3a and 3b, based on their neuronal architectures. Thalamic fibres terminate for the most part in 3a and 3b which are, in turn, connected to areas 1 and 2, portraying a hierarchical organisation where, like in the other sensory modalities, increasingly abstract representations are successively formed. One believes, for instance, that area 1 is implicated in the representation of textures, that area 2 encodes size and shape, and that areas 3a and 3b are dedicated to lower-level processing. It has been discovered that two other areas of the parietal posterior region, 5 and 7, are also involved in haptic processing. In any case, the somatotopic organisation progressively reduces with the distance from peripheral inputs.

3.5 Conclusions

The somatosensory system is distributed throughout the entire body with mechanical, anatomical and physiological attributes that vary greatly with the regions considered. These variations can be explained by the mechanical function of each organ: the fingertip is very different from, say, the elbow, the lips or the tongue. It is therefore tempting to relate these attributes to common motor functions, such as gripping, throwing objects, eating or playing musical instruments.

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