Sensation, Perception, Action – An Evolutionary Perspective

Chapter 10

Body Senses: From the control of posture to touch

‘**The Tempi Madonna**’, Raphael, 1508, Alte Pinakothek, Munich

Some of the most personal and most sensuous forms of human communication build on the sense of touch. The tender support and gentle protection offered by the mother’s hands, and the comforting touch of her cheek, leaves the child to look calm into the future.

Overview

The somatic sensory system includes a group of senses that we are usually completely unaware of, because they are not organised around prominent organs like the eye or the ear, and because they are, to a large extent, dealing with information about the internal state of the body (interoception) rather than being exclusively directed at the external world (exteroception). Despite being hidden, somatosensory perception is of great importance for maintaining the physical control and integrity of the body. You might want to know, for instance, where your left foot is at the moment, and whether the chair underneath your back does support your weight. The proprioceptive and the vestibular sense will be introduced as systems to monitor and maintain static and dynamic stability in space. Temperature and pain sensitivity are considered as archetypical alarm systems that keep humans out of danger and prevent or minimise damage. The focus in this chapter will be on touch, with a more obvious exteroceptive, wide-ranging, and everyday significance for navigation in darkness, exploration of objects in the close environment, and social communication. Starting from the physics of 'tactile' stimuli and the biological design of sensors, we will look at the basic and more advanced mechanisms of encoding and higher level processing of tactile information in the nervous system. We will revisit fundamental processing concepts that we know from other sensory modalities concept, such as receptive fields, adaptation, or active exploration. The comparatively low spatial resolution of touch is considered with respect to how it relates to different regions of the body surface. The existence of a somatosensory map, the homunculus, is introduced as another instance of topographic cortical representation, together with the plasticity of re-mapping observed during growth and after loss of parts of the body, leading to 'phantom limbs'.

Body senses – somatosensory information

Whereas all of the sensory systems covered so far are collecting well-defined information about the outside world, and are recognized by a distinct sensory organ such as the eyes or ears, we now turn to a sensory system, which is based on sensors that are widely distributed across the whole body, and which is largely tuned to the internal body states and is used indirectly to control the body relative to the outside world. These somatic senses are monitoring the physical state of the body, based on a variety of information, such as pressure, stress or strain, temperature and pain. Proprioceptors are used to monitor and control the position and posture of body and limbs, further supported by the vestibular system, which indicates movement and acceleration of the body and space; temperature sensors are important to monitor and control body homeostasis, and pain receptors are crucial to detect and avoid noxious stimuli and injury. Finally, the tactile system is based on mechanosensors in the skin, which pick up information about the contact with other objects and thus their location and shape, and the properties of surfaces.

Somatosensory perception is very peculiar, and there are some weird stimuli, such as tickling, which lead to very mysterious responses such as laughter (Blakemore et al 1998). To start with, information about the body is impossible to share with others – you can see the same movie and hear the same song as your classmates and can arrive at a reasonable agreement about your experiences, but you cannot feel their pain. Different from other sensory channels such as hearing or vision, most of the time we are completely unaware of the rich sensory information provided by the somatic senses. And yet this information source is absolutely crucial to live a normal life, and one couldn't even imagine how it would be to survive without this information. You might get a glimpse of this when your vestibular system is malfunctioning during a very bad cold, and you are having difficulties to stay upright and start swaying when you try walk in a straight way, or you are unable to control your speech after visiting the dentist, who gave you local anaesthetics. Now imagine you are losing all the control over your body posture, any sense of movement, and cannot feel anything you touch, like the spoon in your hand or even the clothes on your skin – your whole body would be like a sagging container of water. Partial or complete loss of somatic senses is a very rare event (however, see chapter 3 of Sacks 1998), so luckily it is very unlikely that you will ever experience such a condition. Interestingly, it is the somatosensory sense that is absolutely crucial for four our bodily awareness, linking imagination and the Self (Smith 2006). If there are conflicts between the somatosensory and other information sources, humans can experience very curious state of consciousness, such as the apparent disownment of limbs, or the acquisition of an animated objects as part of their body, as demonstrated in the rubber hand illusion (Tsakiris and Haggard 2005). Somatic senses are crucial to maintain the integrity of the body, both in a direct physical sense, and in a psychological sense of ‘ownership’.

Proprioception and Vestibular system

When you are closing your eyes, how do you know which direction your eyes are looking, where your foot is in space, all whether your thumb is extended or bent? All over your body, in the muscles, in the tendons connecting muscles with bones, and in the joints between bones, there are hundreds of mechanoreceptors that provide the brain with information about position, or angles between parts of the skeleton that define posture, and about changes in the musco-skeletal system, or movement (see chapter 20 of Roberts 2002). These receptors are called ‘proprioceptors’ because they are picking up the body’s own position and movement (from Latin “proprius”, which means “one’s own”), and sometimes are distinguished as inward-looking receptors (‘interoception’) from all major sensory systems that are directed to the outside world (‘exteroception’). Proprioceptors are responsible for getting into an upright position in the morning and maintaining balance for much of the day They control the stretch reflexes (such as the knee-jerk reflex) which clinicians use to test the function of the central nervous system (Sherrington 1907).

Proprioceptors are monitoring the muscle tone that control general tension and relaxation of the body when it is involved in different levels of activities (from lying in the hammock, or exercising Yoga, to lifting weights). By measuring the tension in abdominal connective tissue, they tell you when your stomach has reached capacity limits and you should stop eating. Proprioceptors are instrumental to put the jigsaw fragments, which you capture with your eyes when you look in different directions, together to a uniform coherent image by letting the brain know in which direction gaze has shifted at any time (Wade and Tatler 2005). Although we are completely unaware of the proprioceptive sensory information, the information about the internal states and position relationships of our body parts are fundamental to operating a body, and developing technical systems to provide and process such information is one of the most challenging engineering tasks when designing articulated robots or sophisticated prosthetics (Brooks 2003).

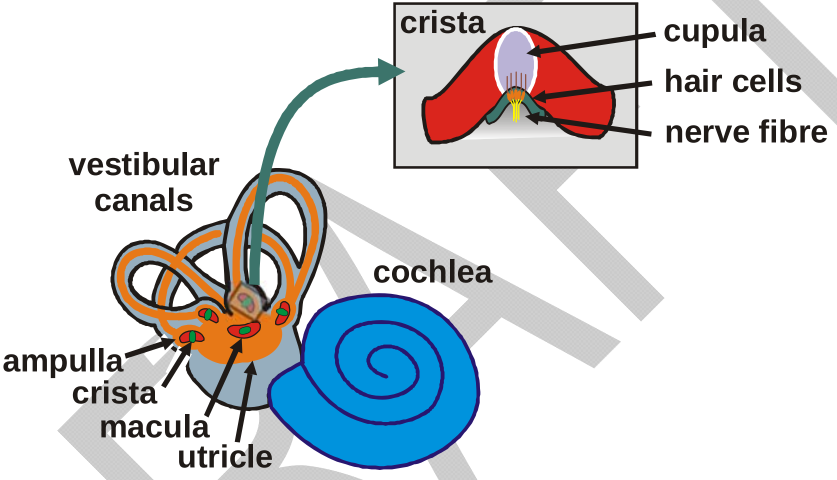

Figure 10.1: The vestibular organ in the inner ear (cf. fig. 7.4). The three ring-shaped ‘vestibular canals’ and the ‘utriculus’ are filled with endolymphe which is accelerated by movement of the head, which consequently leads to stimulation of tiny ‘hair cells’ (mechanoreceptors) attached to a small sensory surface in the ‘macula’ and three ‘cristae’ that are sitting in then ‘ampulla’ at the end of each of the three canals.

The most important somatosensory information that is crucial for maintaining static and dynamic balance, and for sensing self-motion, is captured by the vestibular system. The vestibular system allows us realise being turned on an office chair in the dark, to give one example, and is responsible for noticing that our train starts moving after closing our eyes. Together with the cochlea (see chapter 7), the vestibular system forms the labyrinth, a system of tunnels that are filled with a viscous fluid (endolymph), which constitutes the inner ear (see figure 10.1). There are two parts of the vestibular organ. (i) The two otolithic organs, the utricle and saccule, enable us to detect static position, like being upright, in a horizontal position, or upside down; and linear acceleration, such as experienced when increasing speed in a car or breaking. (ii) The three semicircular canals detect the rotation of the head around any of the three possible axes. Just like the organ of Corti in the cochlea of the hearings system, the physiology of the vestibular system is based on the stimulation of mechanoreceptors, tiny hair cells, by the movement of the endolymph (see chapter 7 in Roberts 2002). It is interesting to note that both the auditory and the vestibular system evolved from the lateral line organ that fish use to detect vibrations and movements in the water surrounding them (Van Bergeijk 1966). This sensory system is essential for motor control, from getting up in the morning, moving around, to laying down in the evening, without swaying, stumbling or falling over, it allows us to walk or run, to jump or ride a bicycle, without getting hurt, and it enables acrobats to do the most amazing tricks in the height of the circus tent. Only when things go wrong, for instance after a middle ear infection, alcohol intoxication, or a stroke, and control over the body is lost, the constant and reliable operation of this highly sophisticated sensory system becomes apparent.

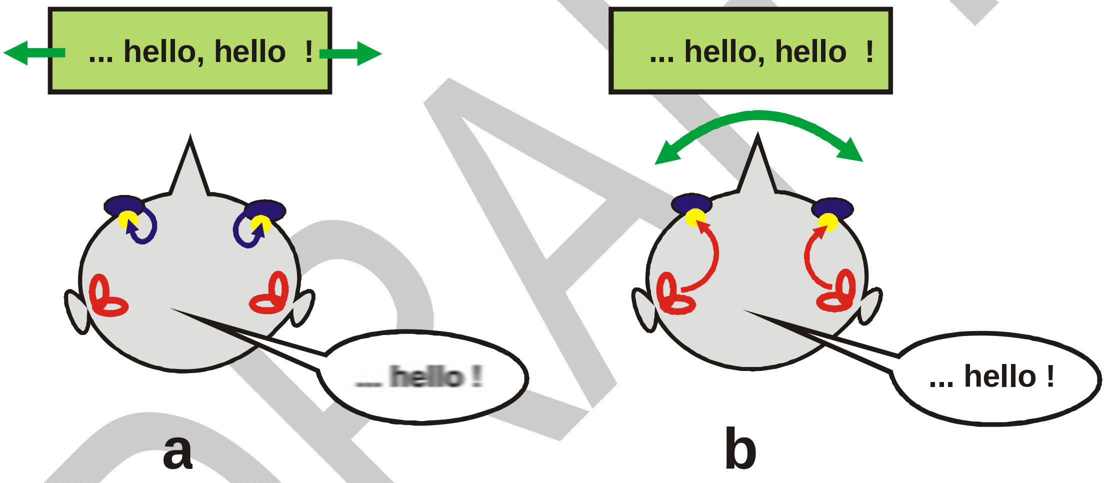

Figure 10.2: Vestibulo-ocular reflex (VOR). (a) When you move a page with text (green rectangle) from side to side (green arrows) in front of you eyes (blue) at fast speed, the text becomes blurred (thought bubble at the back of the head), because the eyes (driven by the retinal motion signals, blue arrows) cannot follow the movement fast enough. (b) When you shake the head at the same speed (green arrow), the text is not blurred, because the vestibular signals (red arrows) can drive compensatory eye movements at higher speeds. (See Colour Plate Plate VII.1)

The information from the vestibular system is transmitted by neurons based in Scarpa's ganglions into the brainstem vestibular nuclei, which connect to other parts of the brainstem including the oculomotor nuclei that connect to the eye muscles. One particularly interesting aspect of the vestibular system is its involvement in the control of eye movements. The information from the inner ear about the movement of the head is used to generate eye movements in the opposite direction, which helps to stabilise the images on the retina (see figure 10.2). This so-called vestibulo-ocular reflex (VOR) can be easily experienced, by moving the book you are reading leftwards and rightwards at such a speed that the letters become blurred from the movement, showing the limits of stabilising the image by tracking the moving book with the eyes. However, when you shake your head in at the same speed, you will notice that the letters will not be blurred. The reason for this sharp image is the fact that the vestibular information about head movement is used by the brain to drive compensatory eye movements, which stabilise the retinal images (Angelaki 2004). There are a number of well-known and rather irritating phenomena such as vertigo or motion sickness, which can be explained by a discrepancy between the visual and the vestibular information driving eye movements.

Temperature and Pain

Sensors for temperature were briefly mentioned in chapter 9 in the context of taste, as a means of protecting the body against too hot food or drink. Temperature control, and therefore temperature sensors, have a much wider relevance in protecting the complete body against overheating or temperature loss. Sticking your fingers into the flame of a candle, getting grilled by the relentless sun on some southern beach, or freezing your fingers and toes in ice and snow is far from a healthy lifestyle, although some fire eaters and arctic explorers seem to make a living out of it. Sunburn blisters and frost bites are to be avoided, because they are symptoms of cell death on the body surface, and therefore clear signals of exposure to extreme environmental temperatures. Warm-blooded animals such as humans and other mammals also require thermal homeostasis to maintain a comparatively narrow range of body temperature around 37°. To avoid the pathological consequences of deviating from this required temperature, the whole body is populated with temperature sensors, which not only provide an alarm system for extreme exposure that and immediate threat for the body’s integrity, but are also involved physiological mechanisms to control general body temperature, by adjusting blood flow or breathing, or changing wardrobe. It is clear from these examples that temperature stimuli can either arise from contact with hot or cold objects, or they can be generated by distant sources, like the sun, and transmitted by radiation – in both cases it is the temperature sensors in the skin that picks up the information. Traditionally it has been believed that perception of heat or cold and pain are picked up by separate sensors and transmitted through separate neural pathways, but there is growing evidence that there is a strong overlap between these three types of sensation (Green 2004).

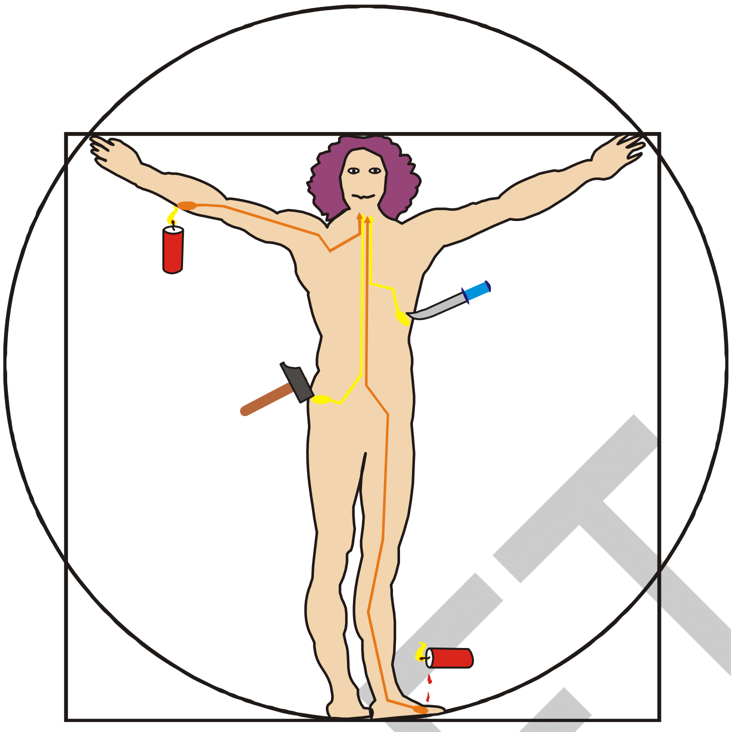

Figure 10.3: The human body (here illustrated with a caricature of Da Vinci’s famous drawing of the ‘Vetruvian man’) contains a dense network of specialised receptors to pick up temperature and pain, which connect through high-speed nerve fibres to the brain, eliciting very fast behavioural responses. Both of these stimuli are key indicators of potential damage of the body (burning, injury), and therefore need to be linked to quick and appropriate action.

Pain sensors, in a natural alliance with temperature and other somato-sensors like those responsible for pressure or stretch, provide input to a second tier alarm system, which detects conditions that pose a serious threat of damage to the body, when the heat is getting too strong, or muscles over-strained – and obviously pain also signals existing tissue damage such as a cut in the skin or a broken bone. The urgency to protect the body against serious or further harm is the reason why pain leads to very strong behavioural responses that often are difficult to control, such as the withdrawal reflex when you burn your fingers (or tears in the eyes). Most importantly, pain is a perception which differs fundamentally in that it can be fully dissociated from the stimulus (see chapter 22 in Roberts 2002). After the initial strong pain following an injury, the sensation of acute pain disappears rapidly, by means of peripheral adaptation and synaptic reorganisation in the central nervous system, and will only recover as part of the healing process. Inversely, patients can complain about – and perceive – chronic pain in the absence of any tissue damage. This reminds us how difficult it is to measure the intensity of pain objectively, a rather tricky issue for the medical profession… Chronic pain affects sufferers in all aspects of their life, and is a problem of outstanding clinical relevance that motivates great research activity about the molecular and neural mechanisms underlying the perception of pain. Sharp and dull pain sensations are originating from fast and slow pain receptors, also called ‘nociceptors’, in two particular types of free nerve endings that can be found in all kinds of tissues (Millan 1999). These signals are transmitted into the spinal chord where they are modulated through descending pathways, and from there into the thalamus and into various parts of the cortex where they further interact with other sensory information. The complexity of the perceptual quality of pain, its interactions with other sensory modalities, and its unusual plasticity makes pain an extremely challenging and exciting, but still puzzling sense to study. With new imaging technologies, we now slowly begin to understand the wide distribution of sensory information about pain in the cortex (Hofbauer et al 2001; Treede et al 2000), and in particular how pain intensity relates to cortical responses (Coghill et al 1999) – could we be on the way to an objective assessment of perceived pain?

Touch: using the body surface as sensory organ

The body sense most people would be immediately aware of is the sense of touch, also known as ‘tactile’ perception. Different from the other somatosensory channels, tactile perception is a dedicated extraneous sense, collecting information about the outside world. This most immediate, physical, interaction with the environment is the reason why the tactile sense is so significant for orientation, exploration and communication. Touch is important for organising behaviour when moving around, in particular for navigating through a cluttered world. Obviously, when trying to find the way around the house in the dark, you use your hands to ‘see’ whether there are any chairs or closed doors in your way, and blind people learn to use the cane to expand their operating range in such exploratory behaviour. But equally you use your touch sensors when sitting down to find out when your back has found support – you don’t need to turn around and look for the chair! Using your fingers to recognise objects and find out about their properties, such as testing the texture and softness (the ‘feel’) of a new jumper or the crispiness of a slice of toast, is an everyday activity, called ‘haptic’ exploration. Often forgotten but rather important, touch can be a major component of communication, in particular in the context of social systems. There is a lot people ‘tell’ each other by physical contact, so there is a lot of information that is being picked up from tactile sensations. Touch even plays a role in the organisation of social system, and there usually are strict rules that the higher ranking individual may touch lower ranking individual, but not the other way around. Figure 10.3 shows the infamous moment in 1992 when the Australian Premier of that time got too close with her majesty (10.3a, earning himself the nickname the 'Lizard of Oz’, and a more recent incidence of political intimacy (10.3b), a meeting between the new American and British foreign secretaries which we still need to make sense of. Rituals at small and large scales, from rubbing shoulders, or exchanging a hug between friends, to the pre-fight war dances of sports teams, are embedded into a culture that needs physical contact as reassurance about personal relationships and group alliances.

Figure 10.4: Touch in social communication. (a) How inappropriate was it of the Australian Premier, Paul Keating, to touch the Queen (1992, BBC News 27/03/2000)? The tabloids called him the 'Lizard of Oz'! (b) A meeting of minds: the foreign secretaries of the UK and the US are reinvigorating the special relationship between their countries. What are David Miliband and Hilary Clinton up to (Getty Images 2009)? Note that in these images we use our perception to construct narratives from the (limited) visual information given about the use of tactile information in social communication.

The adequate stimuli for the tactile sensory system are simple physical events such as pressure, deformation, or stress of the skin. To measure such forces, humans have a large number of mechanoreceptors embedded in their skin tissue, distributed all over the body. The main four different types of mechanoreceptors (see figure 10.4 for a schematic representation) respond to different physical conditions (see chapter 18 of Roberts 2002): (i) Merkel discs, embedded in the top layers of the skin, are comparatively slow and respond to light touch, i.e. slow changes of the pressure on the skin (best response at approximately 1 Hz frequency). (ii) Meissner corpuscles are activated by light touch and vibration (flutter) at medium frequencies (approximately 10 Hz). (iii) Ruffini cylinders are embedded in the deeper layers of the skin and are mainly activated by fast stretch (approximately 100 Hz). (iv) Pacinian corpuscles are found in the neighbourhood of tendons and muscles (Adrian and Umrath 1929), as well as in the deeper layers of the skin, where they are preferentially activated by heavy pressure, and fast vibrations (approximately 400 Hz). It should be noted that each of these receptor types is specifically tuned to the physical quality and a temporal frequency of a stimulus. They also have spatial receptive fields as will be discussed in the next section, and they have specific profiles of adaptation effects (Johansson et al 1982). All of these aspects are standard elements of neural encoding of sensory information, which we know from other sensory modalities. The combination of information from these different mechanoreceptors can be used to create more abstract representations of force patterns such as the direction of a force on the fingertip (Birznieks et al 2001), and it creates the unitary perception of touch, which can be used in a wide range of behavioural contexts.

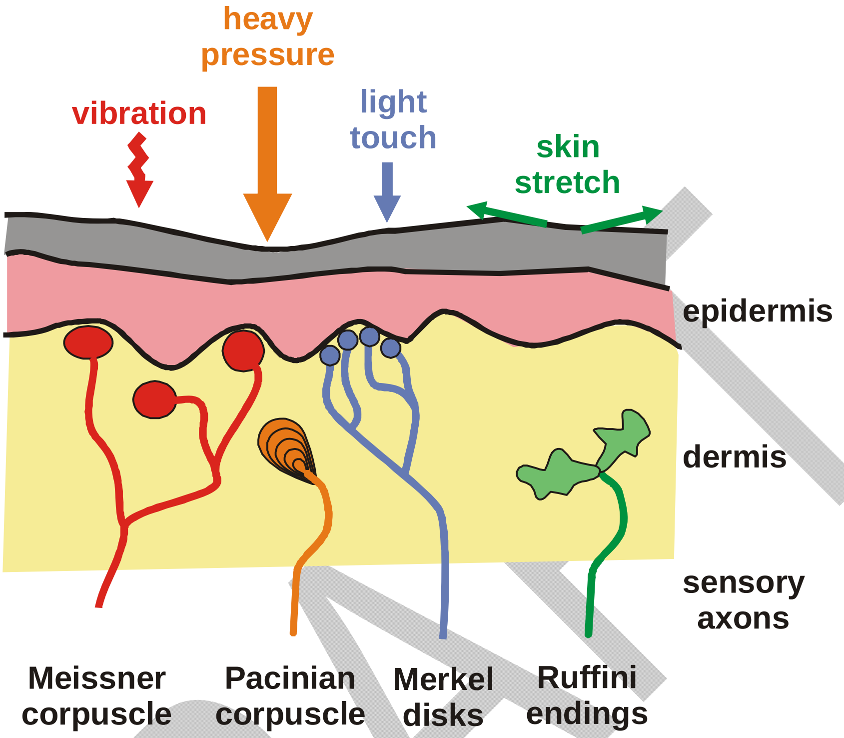

Figure 10.5: Four types of touch sensors that are embedded in the lower layers of the human skin (bottom, indicated by different shades of grey: Meissner corpuscle, Paccinian corpuscle, Merkel disks, and Ruffini endings) that are responding to different types of tactile sensation (top), thus monitoring the status of the body surface.

Tactile space

Each of the mechanoreceptors in the skin is characterised by its location, optimum temporal frequency, and its spatial receptive fields. Tactile receptive fields can be studied by applying two pressure points (for instance the two tips of a compass tool separated by a small distance), which can only be perceived as separate if they are stimulating the receptive fields of different mechanoreceptors (see figure 10.5a) – if they are positioned within a single receptive field they cannot be discriminated from a single pressure point (Johnson and Phillips 1981). Conversely, the receptive field size determines the spatial resolution in a particular region of the skin, which is the number of pressure points that can be detected in a given skin area, and corresponds to the tactile grating resolution. By applying such stimuli with different separation the tactile resolution, corresponding to receptive field size, can be shown to vary considerable for different areas of the body surface (see figure 10.5b): resolution on the finger tips is better than palm of the hand, which is better than that on the arm, which is better than on the shoulder, and so forth. Two-point resolution of touch is in the range of millimeters on the fingertips and amounts to several centimeters on the back (Weinstein 1968). This resolution can change with age and experience, for instance it appears to be much higher in blind individuals (Stevens et al 1996). Similar regional patterns are described for the absolute sensitivity to tactile stimuli, such as the minimum pressure that can be detected (Sekuler et al 1973). The highest sensitivity and resolution is found for the finger tips and lips, which could be interpreted in the context of our evolutionary history as an indication of how important it is to manipulate food between fingers and lips. Equally, one might speculate whether the growing significance of manual handling and speech production for humans led to optimisation of tactile resolution for these critical regions of the body surface, although this would not explain why other animals have similar specialisations.

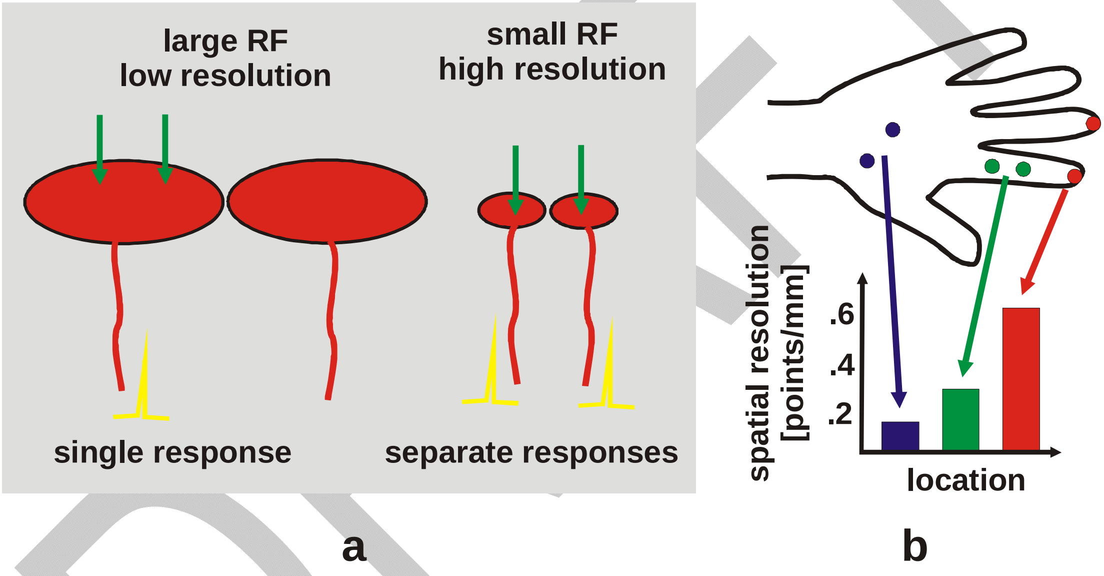

Figure 10.6: Tactile receptive fields and spatial resolution for touch. (a) The size of receptive fields can be tested in a 2-point-resolution task: two pressure points can only be discriminated if they stimulate separate (i.e., small) receptive fields; left: two close stimuli (green arrows) stimulate the same receptive field (red ellipse) and therefore elicit only a single response (yellow spike), as if there were only a single stimulus; right: two separate receptive fields are stimulated, leading to separate responses (spikes). (b) The spatial resolution (number points that can be discriminated per millimeter) for such tactile stimuli varies for different regions of the hand – it is highest at the tip of the index finger.

The psychophysical approach to test the spatial limits of touch perception (Loomis 1981) can go beyond the question of how many tactile stimulus points can be resolved on the skin, by studying the smallest distance of two objects touching the skin that can be discriminated (see figure 10.6a). This performance limit can be compared to the limit of how well the position of an object touching the skin can be detected relative to others (see figure 10.6b). Indeed, localisation acuity is by about an order of magnitude better than the spatial resolution limit. The assessment of tactile perception in terms of spatial resolution with two-point stimuli and gratings (Johnson and Phillips 1981), and comparing this with localisation acuity by using position shift stimuli (Loomis 1981), or sensitivity for movement, resembles very much the procedures to describe the spatial performance of the visual system (cf. chapters 3, 6), and suggests that there are commonalities in the underlying encoding strategies. This analogy goes even further, as demonstrated by experiments with multiple pressure points which suggest that lateral inhibition mechanism operate in the tactile system as well (von Békésy 1967). Furthermore, there are similar strategies to expand the sensitivity limits of touch and of vision by moving the fingertips, similar to moving the eyes. This element of active exploration is crucial for the detection of tactile texture, for which humans can reach outstanding sensitivity, using basic qualities like smooth/rough, soft/hard or sticky/slippery (Hollins et al 2000). Patterns of pressure changes can be detected when moving the fingertips across different materials, like glass, silk, or sandpaper (see figure 10.6.c) which correspond to depth variations reflecting the texture of a surface. If these variation of depth span as little as a few tens of micrometers, textures can be detected and discriminated as long as the fingertips are moving across them (Bensmaia and Hollins 2005)! The latest research in this area suggests that the tiny ridges on the skin that generate fingerprints and improve grip by increasing friction are crucial to achieve such a performance, by amplifying the vibrations generated when brushing the surface with the fingertips (Scheibert et al 2009).

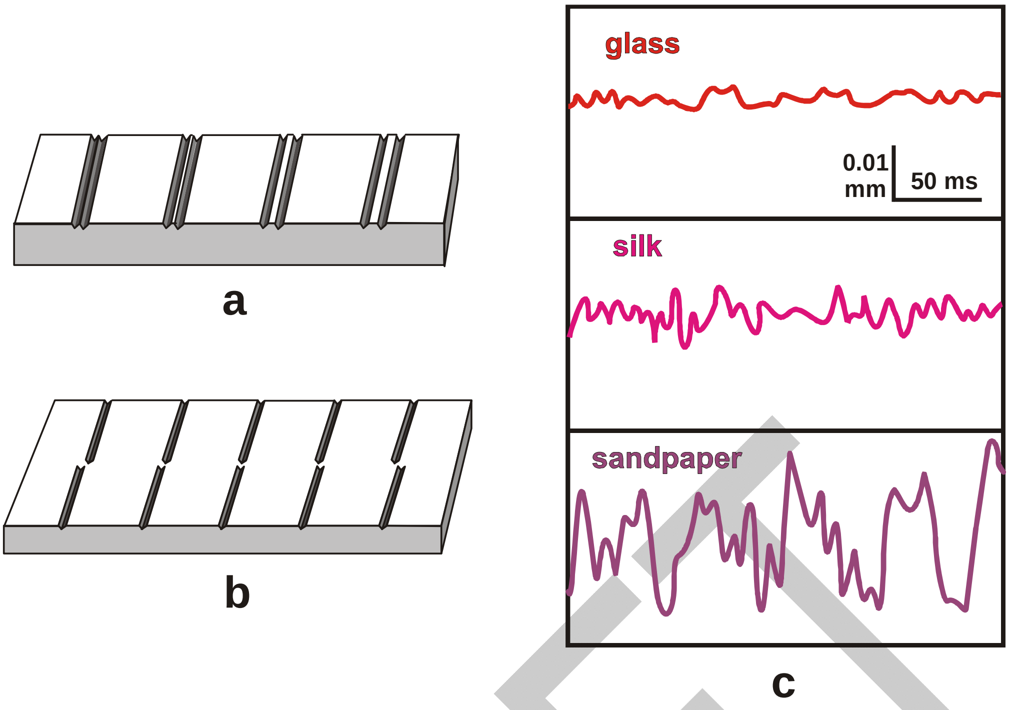

Figure 10.7: Limits for tactile resolution and localisation acuity can be tested by means of two-point stimuli (a) and relative position stimuli (b), respectively. (c) Moving the fingertips across different materials, minute variations of the surface texture can be detected and discriminated.

Cortical representation

How is the local somatosensory information, for instance the pressure distribution arising from the fingertips brushing a surface represented in the cortex ? Tactile information from all over the body is transmitted through the spinal chord (and the trigeminal nerves for face regions) into the brainstem and thalamus, and finally into the somatosensory cortex (see figure 10.7a) where all the information needed for tactile perception is further processed and joined together (chapter 18 ad 19 in Roberts 2002), to create a representation of the complete body surface. Similar to what we know it from the functional architecture of cortical representations of other sensory domains (cf. chapter 2), a map is formed on the cortical surface such that the neighbourhood relations in the brain correspond to those on the sensory surface. This ‘somatotopic’ representation means that a map of the body surface itself is created – and a little person can be outlined on the cortical surface (see figure 10.7b), representing the sensory input from the body, which is called the ‘homunculus’ (Penfield and Rasmussen 1950). Interestingly, there is a second homunculus, on the other side of the central sulcus in the primary motor cortex. This motor map in the cortex represents locations of motor outputs in the body, and is involved in motor control, which obviously can benefit greatly from the close neighbourhood of sensory information.

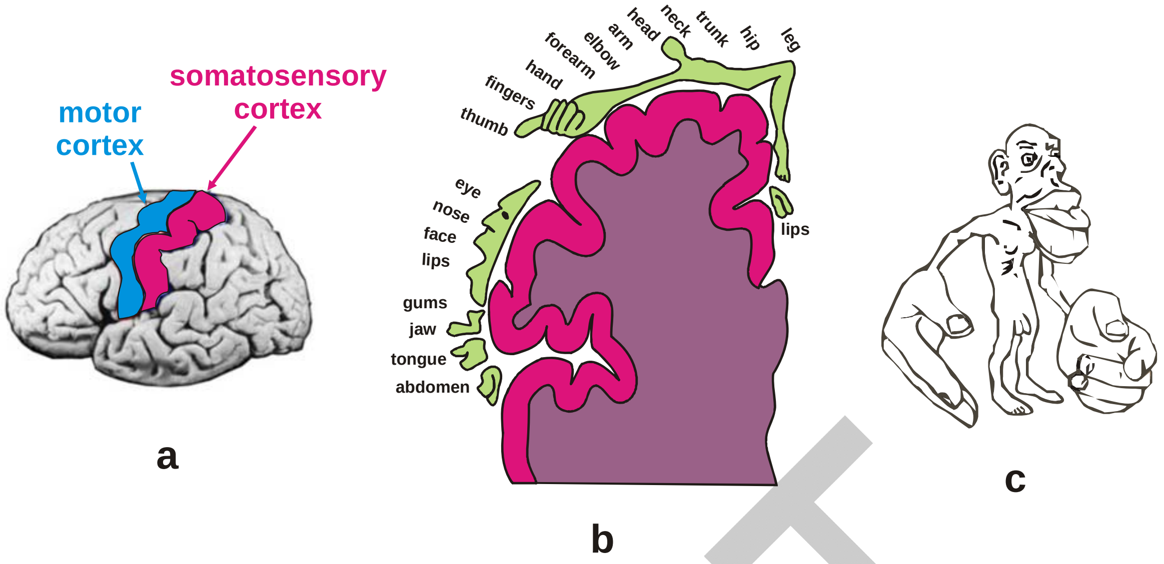

Figure 10.8: The homunculus. (a) The somatosensory cortex sits in close proximity to the primary motor cortex, and both are organised in terms of somatotopic maps. (b) In somatosensory maps neighbouring body regions are projecting to neighbouring regions on the cortical surface, scaled with the spatial resolution of the somatosensory sampling at that location. (c) The reconstruction of a resolution-scaled homunculus demonstrates the relative importance of particular body parts to somatosensory perception.

The amount of space on the cortex surface, or cortical volume, in the somatotopic map dedicated to a particular region of the body surface differs widely between different body areas in such a way that the scale of the map reflects the somatosensory resolution in these areas. Wherever the density of separable touch points (number of points per skin area) is large, a large cortical area is dedicated to this somatosensory information (see large fingertips and lips ion the homunculus shown in figure 10.7b). This scaling of the cortical representation area according to the number of sensory sampling points dedicated to the various body parts (see figure 10.7c) gives 3D models of the homunculus a very curious appearance (such a model can be seen in the Science Museum in London).

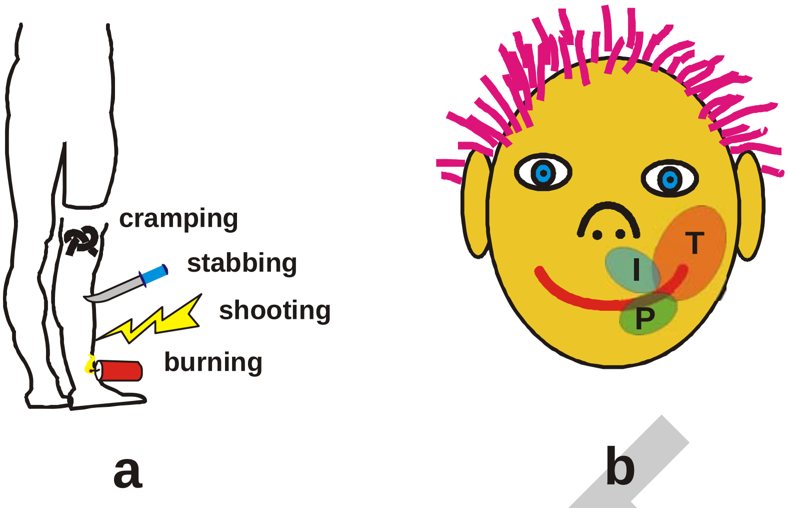

Figure 10.9: Re-wiring the brain. (a) After amputations, many patients suffer from vivid somatosensory sensations, phantom experiences, such as pain, itching, or burning. (b) By touching specific regions of the face, tactile sensations can be triggered in the phantom hand, which are localised to particular fingers (t = thumb. I = index finger, P = pinky) and specific to the type of sensation (the phantom hand can be tickled!).

Knowing about the cortical organisation of somatosensory perception, we can make an attempt to explain a very puzzling phenomenon, the experience of phantom sensations the loss of limbs or other body parts after surgical removal. After amputation, the majority of patients report a range of sensations including pain, warmth, cold, itching, squeezing, tightness or tingling. These sensations are impossible to control because they arise from a part of the body that physically no longer exists, hence the name 'phantom' (see figure 10.8a). They can be best understood as cortical plasticity, resulting from the reorganisation of somatosensory maps that connects the orphaned projection regions to neighbouring sensory input fibres. Such plasticity in mapping the sensory surface onto the cortex (see figure 10.8c) following amputation has been demonstrated in animal models (Merzenich et al 1984), which can lead to stable novel maps in the long term (Manger et al 1996). In humans, rapid cortical reorganisation was observed together with sensitivity changes for touch as consequence of cutaneous anaesthesia (Björkman et al 2009). In all of these cases, brain regions originally dedicated to the severed body region seem to be connected to other peripheral regions – through such re-wiring tactile information is no longer going to the correct destination and can be misinterpreted, as phantom sensations! A particularly stunning example has been described by Ramachandran and Rogers-Ramachandran (2000) of a patient who localizes individual fingers of his amputated hands on particular regions of the face, such that a map of the phantom hand can be drawn on his face (see figure 10.8b). It is tempting to speculate that the absence of sensory input from the amputation stump which originally represented the hand results in invasion of input connections from the neighbouring somatosensory regions representing the face (these neighbourhood relationships can be seen in figure 10.7b), which then can be perceived as stimuli to the phantom limb.

Haptics: active exploration

It was mentioned in the context of tactile texture recognition above that tactile exploration improves performance tremendously. The active deployment of the sensory organ in fingers, haptic exploration, is a very powerful, and constantly used behavioural strategy to collect information – we talk about ‘handling’ objects. Lateral motion across a surface to scrutinise its texture, increase of contact surface to sample object temperature, following contours or enclosing an object to assess its overall shape, applying pressure to feel its softness, or just picking and holding it up to estimate its weight, are just a few examples how the interaction between the main somatosensor array – the hand – and the environment is used to maximise the information that is collected. Precise coordination between the sensory and the motor processes is needed to make reliable information available, and it is no surprise that we experience illusions when using the sense of touch, like the haptic Müller-Lyer illusion, very similar to some phenomena known from the visual system (Heller et al 2002).

Haptic exploration has a very special relevance, because it is the basis of reading Braille by using the fingertips (Foulke 1982). Braille letters are specifically designed symbols for stimulating the fingertips by punching them into the paper. They are better to identify at the low spatial resolution that limits the tactile sense (Loomis 1981) than embossed conventional characters. By using a raster of well spaced points to define a set of spatial relationships that carry the information to be read, rather than conventional letters such as Roman characters, a system is developed that is less susceptible to blur. This is demonstrated in figure 10.9b, where two lines of Roman (lines A) and Braille (lines B) characters are blurred in order to simulate low spatial resolution of the sensory system picking up such information. It is clear that blurred Roman characters (lines C) are amorphous blobs that barely can be discriminated from each other, whereas blurred Braille (lines D) retains characteristic patterns that can be easily identified and discriminated. But why would it not simpler just to use larger Roman characters, in order to cope with the low spatial resolution of touch? Whereas such a technique indeed could overcome the problem with discriminability, now the overall size of each character would much larger, and a new problem would be created. Because of the restricted size of fingertips, which acts like a restricted field of view for tactile information, very few characters could be touched at the same time, and more hand movement, and more coordination between the motor and the sensory system would be necessary to read a text – which would make it much more difficult to learn to read by touch. Just imagine if you were to read a book through a mask which only allows you to read one letter at a time! It can be concluded that the design of the communication technology, the Braille characters in this case, needs to take into account the sensitivities and the limitations of the sensory processing mechanisms, in this case the spatial resolution of the tactile system, to make communication reliable, efficient, and reasonably easy to learn.

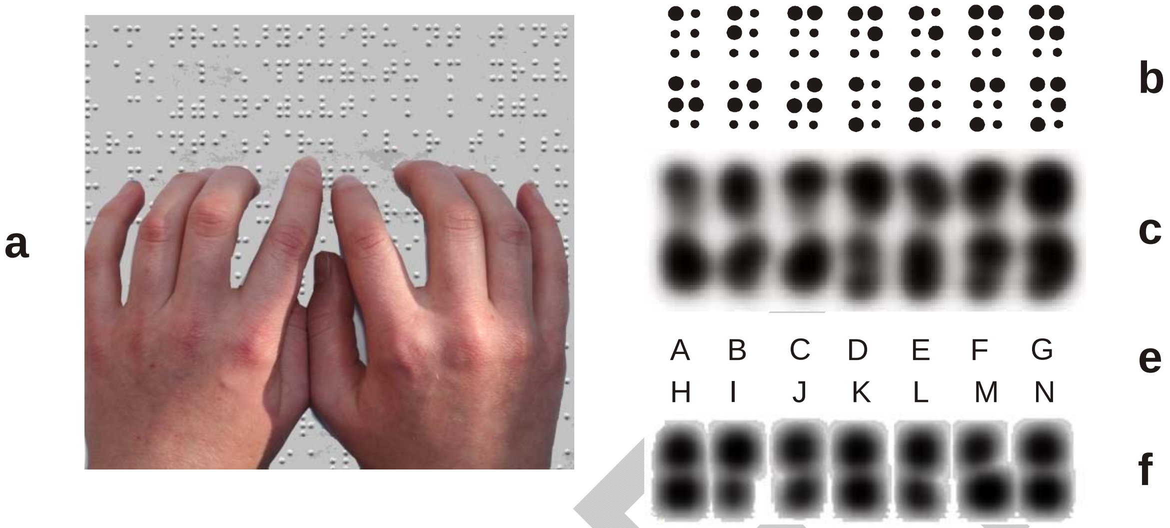

Figure 10.10: (a) Reading Braille code is based on tactile recognition of patterns of dots punched into the paper, and therefore needs to be resistant against blurring from low spatial resolution. A set of six dots in a cell define the letters of the Braille alphabet, as shown in 2 lines for the first 14 letters (b), just as the characters in (e) compose the Roman alphabet; when blurred, the Roman characters turn into blobs that are difficult to discriminate (f), whereas the Braille characters retain their distinct patterns (c).

Take home messages

- The somatosensory system provides information about the internal physical state of the body and collects information about the external world through the body surface
- Pain and temperature contribute to homeostatic and alarm systems that are responsible fro the physical integrity of the body
- The proprioceptive and the vestibular system provide information about body posture and motion that is crucial for various stabilisation reflexes
- Touch is a spatial sense with a range of biological functions; in many aspects tactile perception makes use of very similar neural encoding mechanisms and data collection strategies as we know from other sensory systems
- Active exploration is crucial to overcome the low spatial resolution of touch perception; haptics is a powerful tool to explore the outside world and communicate

Discussion Questions

- Describe briefly the design and function of the vestibular system
- How can we measure the spatial resolution of the tactile sensory system?
- What is meant by somatosensory map?
- Discuss in what ways Braille code for blind reading is well adapted to the limitations of the tactile sense.

References

Adrian E D, Umrath K, 1929 "The impulse discharge from the pacinian corpuscle" *J Physiol* **68** 139-154

Angelaki D E, 2004 "Eyes on Target: What Neurons Must do for the Vestibuloocular Reflex During Linear Motion" *J Neurophysiol* **92** 20-35

Bensmaia S, Hollins M, 2005 "Pacinian representations of fine surface texture" *Perception & Psychophysics* **67** 842-854

Birznieks I, Jenmalm P, Goodwin A W, Johansson R S, 2001 "Encoding of Direction of Fingertip Forces by Human Tactile Afferents" *J. Neurosci.* **21** 8222-8237

Björkman A, Weibull A, Rosén B, Svensson J, Lundborg G, 2009 "Rapid cortical reorganisation and improved sensitivity of the hand following cutaneous anaesthesia of the forearm" *European Journal of Neuroscience* **29** 837-844

Blakemore S-J, Wolpert D M, Frith C D, 1998 "Central cancellation of self-produced tickle sensation" *Nat Neurosci* **1** 635-640

Brooks R A, 2003 *Robot: The future of flesh and machines* (Penguin)

Coghill R C, Sang C N, Maisog J M, Iadarola M J, 1999 "Pain intensity processing within the human brain: a bilateral, distributed mechanism" *Journal of neurophysiology* **82** 1934-1943

Foulke E, 1982 "Reading braille", in *Tactual perception: A sourcebook* Eds W Schiff and E Foulke (Cambridge: Cambridge) pp 168

Green B G, 2004 "Temperature perception and nociception" *Journal of neurobiology* **61**

Heller M A, Brackett D D, Wilson K, Yoneyama K, Boyer A, Steffen H, 2002 "The haptic Muller-Lyer illusion in sighted and blind people" *Perception* **31** 1263-1274

Hofbauer R K, Rainville P, Duncan G H, Bushnell M C, 2001 "Cortical representation of the sensory dimension of pain" *Journal of Neurophysiology* **86** 402-411

Hollins M, Bensmaia S, Karlof K, Young F, 2000 "Individual differences in perceptual space for tactile textures: Evidence from multidimensional scaling" *Perception and Psychophysics* **62** 1534-1544

Johansson R S, Landstrom U, Lundstrom R, 1982 "Responses of mechanoreceptive afferent units in the glabrous skin of the human hand to sinusoidal skin displacements" *Brain Res* **244** 17-25

Johnson K O, Phillips J R, 1981 "Tactile spatial resolution. I. Two-point discrimination, gap detection, grating resolution, and letter recognition" *Journal of Neurophysiology* **46** 1177

Loomis J M, 1981 "Tactile pattern perception" *Perception* **10** 5-27

Manger P R, Woods T M, Jones E G, 1996 "Plasticity of the Somatosensory Cortical Map in Macaque Monkeys after Chronic Partial Amputation of a Digit" *Proceedings: Biological Sciences* **263** 933-939

Merzenich M M, J. N R, Stryker M P, Cynader M S, Schoppmann A, Zook J M, 1984 "Somatosensory cortical map changes following digit amputation in adult monkeys" *The Journal of Comparative Neurology* **224** 591-605

Millan M J, 1999 "The induction of pain: an integrative review" *Progress in Neurobiology* **57** 1-164

Penfield W, Rasmussen T, 1950 *The cerebral cortex of man: a clinical study of localization of function* (Macmillan)

Ramachandran V S, Rogers-Ramachandran D, 2000 "Phantom Limbs and Neural Plasticity" *Archives of Neurology* **57** 317-320

Roberts D R, 2002 *Signals and Perception: The Fundamentals of Human Sensation* (Palgrave Macmillan)

Sacks O W, 1998 *The Man Who Mistook His Wife For A Hat* (Touchstone)

Scheibert J, Leurent S, Prevost A, Debregeas G, 2009 "The Role of Fingerprints in the Coding of Tactile Information Probed with a Biomimetic Sensor" *Science* 1166467

Sekuler R, Nash D, Armstrong R, 1973 "Sensitive, objective procedure for evaluating response to light touch" *Neurology* **23** 1282

Sherrington C S, 1907 "On the proprio-ceptive system, especially in its reflex aspect" *Brain* **29** 467-482

Smith J, 2006 "Bodily Awareness, Imagination and the Self" *European Journal of Philosophy* **14** 49-68

Stevens J C, Foulke E, Patterson M Q, 1996 "Tactile acuity, aging, and braille reading in long-term blindness" *Journal of experimental psychology: applied* **2** 91-106

Treede R D, Apkarian A V, Bromm B, Greenspan J D, Lenz F A, 2000 "Cortical representation of pain: functional characterization of nociceptive areas near the lateral sulcus" *Pain* **87** 113-119

Tsakiris M, Haggard P, 2005 "The Rubber Hand Illusion Revisited: Visuotactile Integration and Self-Attribution" *Journal of Experimental Psychology: Human Perception and Performance* **31** 80-91

Van Bergeijk W A, 1966 "Evolution of the Sense of Hearing in Vertebrates" *Amer. Zool.* **6** 371-377

von Békésy G, 1967 *Sensory Inhibition* (Princeton NJ Princeton University Press)

Wade N J, Tatler B W, 2005 *The moving tablet of the eye: The origins of modern eye movement research* (Oxford University Press, USA)