CHAPTER 3: THE BODY SENSES

Introduction

The body senses provide information about surfaces in direct contact with the skin (touch), about the position and movement of body parts (proprioception and kinesthesis), and about the position and movement of the body itself relative to the external world (balance). All of this information is supplied by two anatomically separate sensory systems. The somatosensory system deals with touch, proprioception, and kinesthesis, while the vestibular system deals with balance.

The Somatosensory System

Touch mediates our most intimate contact with the external world. We use it to sense the physical properties of a surface, such as its texture, warmth, and softness. The sensitivity of this system is exquisite, particularly at the most sensitive parts of the body such as the fingers and lips. Direct contact with other people is responsible for some of our most intense sensory experiences. Individuals who lack the sense of touch due to a physical disorder are severely disabled, since they lack the sensory information that is essential to avoid tissue damage caused by direct contact with harmful surfaces.

Figure 3.1 (photo of direct contact between two people to be found)

Compared to the sense of touch, proprioception and kinesthesis seem largely invisible. We are not conscious of making use of information about the position and movement of body parts, so it is naturally impossible to imagine being deprived of proprioception. Yet proprioception is vital for normal bodily functioning, and its absence is severely disabling. Some appreciation of its importance can be gained from individuals who have lost their sense of proprioception following illness. Cole and Paillard (1995) describe two such cases, identified by their initials, IW and GL. IW was a 19-year old butcher when he suffered a flu-like viral illness. He became increasingly weak and at one stage fell down in the street. On admission to hospital, he had slurred speech, an absence of sensation in the mouth, no sense of touch on his body, and no awareness of body position. Although he retained an ability to move his body, he had no control over the movement. After recovery from the initial infection, IW spent 18 months in a rehabilitation hospital learning to control his movements, including learning to walk again, following which he was discharged and did not see a doctor for about twelve years. Later investigations established that IW’s illness had destroyed the sensory nerves that supply the brain with information about touch and proprioception, though he could still sense pain and temperature. In the absence of proprioception, IW can only make controlled bodily movements with intense concentration and visual vigilance. Once he had learned to walk, if he sneezed and thus broke his concentration, he would fall over. Even the act of sitting in a chair requires concentration to avoid falling out of it. IW avoids crowded spaces, for fear of being nudged by someone out of view. When navigating an unfamiliar environment he studies it beforehand, much like a mountaineer surveying a difficult climb, to judge the degree of slope in the ground surface, to measure the size of any gaps
through which he must fit, and to estimate the strength of any wind. IW has made use of his acquired skill in assessing environments, and is now used as an advisor by holiday care services, reporting on the suitability of possible holiday locations for disabled visitors.
[On the CD: a short video of IW walking]
The case of IW is a vivid example of the importance of somatosensation.

**Physiology of Somatosensation**
The somatosensory system includes eight different kinds of receptor, a single primary receiving area in the cortex, and two separate pathways linking receptors to the cerebral cortex.

**Somatosensory Receptors**
The table below lists the eight types of receptor, their location, and their primary sensory function.

<table>
<thead>
<tr>
<th>Receptor Type</th>
<th>Location</th>
<th>Sensory Function</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Touch:</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Free nerve endings</td>
<td>All skin, superficial</td>
<td>Pain, temperature, tickle</td>
</tr>
<tr>
<td>Meissner’s Corpuscles</td>
<td>Glabrous skin, superficial</td>
<td>Light, dynamic touch</td>
</tr>
<tr>
<td>Merkel’s disks</td>
<td>All skin, superficial</td>
<td>Static pressure</td>
</tr>
<tr>
<td>Pacinian corpuscles</td>
<td>All skin, deep</td>
<td>Pressure, vibration</td>
</tr>
<tr>
<td>Ruffini’s corpuscles</td>
<td>All skin, deep</td>
<td>Stretching of skin</td>
</tr>
<tr>
<td><strong>Proprioception:</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Muscle spindles</td>
<td>Muscles</td>
<td>Muscle length</td>
</tr>
<tr>
<td>Golgi tendon organs</td>
<td>Tendons</td>
<td>Muscle tension</td>
</tr>
<tr>
<td>Joint receptors</td>
<td>Joints</td>
<td>Joint position</td>
</tr>
</tbody>
</table>

Figure 3.2 illustrates the location of the five different touch receptors below the surface of the skin. As indicated in the table, some lie near the surface of the skin whereas others lie deeper below the surface. Free nerve endings do not have any structural specializations for transducing stimuli, and it is not possible to determine their preferred stimulus on the basis of morphology. The mechanism of transduction is not well understood (Delcomyn, 1998). However, they are known to mediate perception of pain from tissue damage, and perception of hot and cold. In the remaining four types of touch receptor the nerve ending is encapsulated within a specialized structure that governs the receptor’s response to mechanical stimulation. Pacinian corpuscles, for example, have an onion-like capsule in which layers of membrane lamellae are separated by fluid. Mechanical stimulation deforms the structure and leads to a response from the receptor. Pacinian corpuscles are able to vary their activity at a very high rate (250-350Hz) in response to dynamic stimulation, allowing them to respond to high-frequency vibration of the skin, such as that produced by the movement of a fine-textured surface across the skin. Merkel’s disks
and Ruffini’s corpuscles, on the other hand, have a very sluggish temporal response, making them best-suited to signal relatively stable, unchanging mechanical stimulation. Meissner’s corpuscles have an intermediate temporal response (30-50Hz), able to detect moderate dynamic stimulation. It would be misleading to assume too neat a division in sensory function between different receptor types. Skin contact with an external surface produces a complex pattern of activation across all receptor types. One’s perception of the properties of the surface depends jointly on the information provided by all of them.

**Figure 3.2 (re-draw)**

Receptors for proprioception are found in and around the limbs, either in the muscles themselves, in the tendons that attach the muscles to bone, or in the joints. Muscle spindles are relatively well understood, whereas little is known about joint receptors. Muscle spindles consist of between four and eight specialized muscle fibres surrounded by a capsule of connective tissue. The axons of sensory nerves encircle the fibres within the capsule to provide information on muscle length. Large muscles that generate fairly coarse movements possess relatively few muscle spindles, while muscles used for very fine and accurate movements, such as those in the hand and surrounding the eyes, are well supplied with muscle spindles.

**Somatosensory pathways**

The mechanoreceptors mediating somatosensation are modified sensory neurons. Their cell bodies are located in the dorsal root ganglia, which lie just outside the spinal column. Their peripheral axons end in various sensory specializations below the surface of the skin, while their central axons project toward the brain. Mechanical stimulation of a particular sensory neuron provokes a graded change in receptor potential. When the receptor potential exceeds a certain minimum value, an action potential will be triggered, which travels along the cell’s axon. The action potential will be transmitted along one of two routes, known as the spinothalamic pathway and the lemniscal pathway. The flowchart in figure 3.3 summarises these two routes to the brain.

**Figure 3.3 (as-is)**

In the spinothalamic pathway (right-hand route in the flowchart), central axons carrying responses from free nerve endings (mediating pain and temperature sensation) terminate in the spinal cord in areas called Rexel’s laminae I and II (Purves et al., 2001). Responses are then relayed to cells in laminae IV to VI, whose axons project all the way up the spinal cord to the thalamus. In the lemniscal pathway, central axons carrying responses from mechanoreceptors ascend the spinal cord as far as the brain stem. They terminate in the dorsal column nuclei of the medulla. Projections from the medulla terminate in the thalamus. In both the spinothalamic pathway and the lemniscal pathway, neurons in the thalamus send axons to the primary somatosensory cortex. Both pathways also contain branching projections in the spinal cord that are responsible for reflexes, such as withdrawal from painful stimuli, and the “knee-jerk” reflex (horizontal arrows in the flowchart).

Axons associated with mechanoreceptors in the lemniscal pathway are myelinated (covered in a laminated wrapping) and as a result have relatively fast conduction velocities of about 20 m/sec. Axons in the spinothalamic pathway are only lightly myelinated or unmyelinated, and have relatively slow conduction velocities of about 2
m/sec. This difference in conduction velocity can be sensed when a drop of hot water falls on the hand. The contact of the water drop on the hand can be sensed about half a second before its temperature (Delcomyn, 1998).
[Incidentally – In the case of IW described earlier, all myelinated fibres were destroyed by the disease, depriving him of all sensory information from mechanoreceptors]

**Cortical representation of somatosensation**

The primary somatosensory cortex occupies a long thin strip of cortical surface running from ear to ear across the head (the grey area in the side view of the cortex shown in the top-left of figure 3.4). The axons of thalamic neurons project to an area known as Brodmann’s area 3 (subdivided into a and b), but the adjacent areas 1 and 2 also represent somatosensation. The cross-section in figure 3.4 (middle-left) is taken along the line labeled A – A’ in the top-left, and shows the locations of the three areas. Close inspection of the properties of neurons in area 3 reveals a very high degree of selectivity and organization.

**Figure 3.4 (re-draw)**

**Receptive field properties** Mountcastle (1957) found that each cell in primary somatosensory cortex receives input from only one type of receptor. For example, one cell may be connected to Merkel disks, while another cell may receive inputs only from Meissner corpuscles. All of the receptors projecting to an individual cortical neuron are located in a small area of the body. As a result, each cortical neuron responds to stimulation only in that area, which defines the cell’s **receptive field**. Figure 3.5 illustrates the receptive field of a typical somatosensory cortical neuron (the middle neuron on the right of the schematic cortical circuit). Projections from sensory receptors under the skin of the forearm converge on the cortical cell by means of intermediate synapses in the brain stem and thalamus. Consequently the neuron responds only to stimulation in that region of the body (shaded area).

**Figure 3.5 (as-is)**

Projections from receptors in area A of the receptive field are excitatory, and projections from receptors in area B provide inhibition, by means of inter-neurons coloured black in the figure. This kind of inhibition is a common feature in sensory pathways. The connections are organized in such a way that stimulation in the center of the receptive field excites the cell, and stimulation in the periphery of the receptive field inhibits the cell. The top recording trace in the figure shows that neural activity increases in response to stimulation at point A in the receptive field. Stimulation in area B, on the other hand causes a decrease in activity (middle trace), due the inhibition transmitted laterally in the neural circuit. Stimulation at points A and B simultaneously leads to no net change in neural response (bottom trace). Receptive fields of this kind are often called antagonistic center-surround receptive fields, for obvious reasons. Why is the receptive field organized in this way? Centre-surround antagonism means that the cell responds best to relatively small stimuli that fill the central excitatory area of its receptive field but do not encroach on the inhibitory surround. This makes the cell’s response very sensitive to very small changes in the position and/or size of the stimulus.
**Cortical organization** Neurons connected to receptors on the left half of the body project to somatosensory cortex on the right-hand hemisphere, and neurons connected to receptors on the right half of the body project to the left-hand hemisphere. Are the properties of neighbouring cells in somatosensory cortex related to each other in any way? Anatomical and electrophysiological studies over the last half-century have revealed that the cortex is highly organized, both vertically and horizontally. Vertically, the mammalian cortex can be split into six distinct layers (see Figure 3.4 bottom left), on the basis of variations in cell number, density, and morphology.

[Incidentally – the division of the whole neocortex into six layers and about 50 different areas, on the basis of histological features, was first described by the neuroanatomist Korbinian Brodmann in the early 1900’s.]

The axons of thalamic neurons terminate in layer 4 of Brodmann’s areas 3a and 3b. Layer 4 cells connect with cells in other layers, which in turn project to cells in areas 1 and 2 (Smith, 2000). Mountcastle (1957) found that all the cells lying within a thin column running down vertically from the surface of the cortex were connected to the same type of sensory receptor. Cells in each neighbouring column were all connected to a different receptor type, as illustrated in Figure 3.4 (bottom-left). In addition, the cells within a group of neighbouring columns have receptive field locations that largely overlap on the body surface. Receptive field size varies between cortical cells, in a way that is related to the part of the body on which the receptive field lies. Receptive fields on the finger tips are very small (3-4 mm in diameter), but those on the trunk are over 100 times larger. As one progresses horizontally (parallel to the surface of the cortex within a particular layer) along the strip of cortex devoted to somatosensation, there is a very orderly progression in the part of the body covered by the receptive fields. This horizontal organization was first described by Penfield, a neurosurgeon who performed brain surgery during the early 1950’s to relieve epilepsy. The patient was anaesthetised but awake during the operation, and Penfield applied small electric currents to the exposed surface of cortex by means of a small electrode. The patient reported any experiences that resulted from the stimulation. The purpose of the procedure was to identify critical areas of cortex to be avoided during surgery, but in the process Penfield made some startling discoveries. When stimulation was applied to the brain area now identified as somatosensory cortex, the patient reported tactile sensations on specific parts of the body. As Penfield systematically moved the electrode across the surface of the cortex, the bodily location of the sensation also moved systematically. Figure 3.4 (right) is re-drawn from Penfield (1953), and represents a cross-sectional view of the cortex along the line B-B’ in the figure. Notice that the body is mapped out across the surface of the cortex. The area of cortical surface devoted to different body parts is not in proportion to their size. For instance, a relatively small area of cortex contains cells with receptive fields on the back, or on the leg, whereas very large areas of cortex are devoted to the hands and to the lips. This effect is known as cortical magnification. Research on other species has discovered very different patterns of cortical magnification. In rodents, for example, the large facial whiskers are disproportionately represented in somatosensory cortex. The large spots or ‘barrels’ apparent in the somatosensory representation of the star-nosed mole (Figure 1.x in chapter 1) each represent an individual whisker. The extent of cortical
representation of a body part seems to reflect the importance of that body part for the survival of the animal.

**Cortical representation of pain** Although thalamic neurons conveying information about pain do project to somatosensory cortex, the cortical representation of pain is not well understood. Removal of the relevant region of cortex to alleviate chronic pain is not usually successful, though tactile sensation is impaired. There is a parallel projection of pain signals from the thalamus to the reticular formation, pons, and midbrain that is probably responsible for the arousing effects of pain. These projections would not be affected by cortical ablation. There are also descending projections from the cortex to the spinal cord, particularly to Rexel’s lamina II. These projections are thought to play a role in the central control of pain, such as the surprisingly low intensities of pain reported by soldiers in battle.

[Incidentally – Neurons in the spinal cord conveying pain signals from the internal organs also convey information about pain near the body surface. As a result, pain from internal organs is often ‘referred’ to a more superficial part of the body sharing the same afferent neurons. Pain in the heart muscle, for instance, is referred to the chest wall and left arm (Purves et al., 2001)]

**Somatosensory Perception**

**Two-point Acuity**

Our ability to discriminate fine differences in touch stimulation can be measured using a pair of calipers, placing one or both points on the skin of the subject (Figure 3.6, top). The subject’s task is to report whether they can feel a single point or a pair of points. As figure 3.6 (bottom) shows, performance varies markedly in different regions of the body. Acuity is highest on the tongue and hands, where points separated by as little as 2 or 3 mm can be discriminated. Performance is worst on the back and legs, where points have to be over 50 mm apart to be discriminated. This pattern of performance closely reflects the variation in receptive field size and cortical representation mentioned earlier in the chapter. The area of cortex devoted to the fingers contains a great many neurons having small receptive fields, typically 1-2mm in diameter. Consequently, if the calipers are placed on the fingers and gradually moved further apart, over a range of 3 or 4 mm, the activity of an individual neuron will change markedly (refer back to figure 3.5). In addition the points of the calipers will very soon stimulation different neurons, since the receptive fields are so small. These changes in cortical activity mediate fine touch discrimination at the fingers. The cortical representation of the back is relatively sparse, and receptive fields are large. Consequently, a change in position of 3 or 4 mm will have very little effect on the activity of individual cells, and therefore on discrimination.

**Object Recognition**

Although humans normally rely on vision for object identification, touch can also be used effectively. The perception of object properties on the basis of touch and kinesthesia is sometimes called haptic perception. When subjects are allowed to touch and manipulate objects without visual information, recognition rates are very high. Klatzky et al. (1985)
investigated the ability of 20 blindfolded students to identify one hundred common objects by touch. Objects included, for example, a ring, a golf ball, a sock, a tea bag, scissors, a fork, a key, and a screwdriver. Identification was 96% accurate, and 68% of responses occurred within three seconds of initial contact with the object. Subjects were clearly able to gather a great deal of useful information regarding object properties from a relatively brief manual inspection. Two objects in particular accounted for a high proportion of the errors, rice and a T-shirt.

**The Vestibular System**

Information about the position and movement of the body with respect to the external environment is vital for normal bodily function. It allows us, for example, to walk and run upright without falling over, and at the same time to maintain steady fixation on an object that may itself be moving. The speed and precision with which the mammalian brain can gather and use this information is evident in the supreme body control displayed by predators such as cats. When a cat falls from a tree or ledge, it can sense the orientation of its body relative to the ground and manoeuvre itself to land feet-first, even when falling from an inverted position. [On the CD – video of a falling cat]

**Physiology of the Vestibular System**

The neural system responsible for such beautifully executed movements, the vestibular system, is a prime example of exquisite biological engineering. It employs receptors that are sensitive to the forces of gravity and acceleration acting on the head. The two organs housing these receptors lie buried in deep openings on either side of the skull known as vestibules. Consequently they are called the ‘vestibular organs’.

**Figure 3.7 (re-draw?)**

Figure 3.7 (top-right) shows the position of the vestibular organs in the head. Each organ consists of a complex set of interconnected canals, known as the vestibular labyrinth. Another organ, the cochlea, is connected to each vestibular organ, and shares its afferent nerve, the eighth cranial nerve (see Figure 3.7, top-left). The cochlea is a complex spiral-shaped canal that mediates hearing (discussed in the next chapter). In both the vestibular organ and the cochlea sensory reception is based on minute displacements of hair cells, caused by the movement of fluid inside the organ. In the case of the vestibular system, fluid movement is caused by accelerations of the head, or by gravity. In the case of the cochlea, fluid movement is caused by air pressure waves transmitted through each ear. [Incidentally – The contiguity of the vestibular organ and the cochlea led to early ideas that both organs were devoted to hearing, with the vestibular organ mediating auditory localization. See Wade (2000)]

**Figure 3.8 (re-draw)**

**Vestibular Receptors**

Figure 3.8 depicts a group of vestibular hair cells on a patch of sensory epithelium. Notice that each hair cell gives rise to a single tall, thick hair known as a kinocilium, and a number of smaller, narrower hairs (stereocilia) grouped together on one side of the
kinocilium. The stereocilia decrease in size with distance away from the kinocilium, and thin filaments connect the tip of each cilium to the side of its taller neighbour. This arrangement is crucial to the sensory properties of hair cells. Unlike mechanoreceptors, hair cells do not have axons, and do not generate action potentials. Instead, pre-synaptic active zones around the base of each hair cell make synaptic connections with afferent nerve cells forming part of the VIIIth cranial nerve. Stimulation of a hair cell increases its receptor potential and causes the release of chemical neurotransmitter from its pre-synaptic zones. This transmitter influences the pattern of action potentials generated by the sensory neuron. Movement of the stereocilia towards the kinocilium depolarizes the hair cell and results in increases in sensory nerve activity. Movement of the stereocilia away from the kinocilium hyperpolarizes the cell, reducing sensory nerve activity. In the patch of sensory epithelium shown in Figure 3.8 all the hair cells are aligned so that deflection to the left causes excitation, and deflection to the right causes inhibition. Resting potentials in hair cells generate a high level of spontaneous neural activity in sensory nerves (about 110 spikes per second), so the firing rate of vestibular nerve fibres can faithfully reflect the change in receptor potential, increasing or decreasing in accordance with the movement of the cilia. The significance of this biphasic response is that it allows nerve fibres to signal the direction of displacement of the hairs, which depends directly on the direction of tilt or acceleration of the head, as we shall see.

The Vestibular Labyrinth

The labyrinth consists of two chambers (otolith organs), the utricle and the saccule, and three semicircular canals (see figure 3.7). All of these membranous structures are interconnected and filled with fluid (endolymph). In each structure there is a small area of sensory epithelium containing hair cells. Displacement of these hair cells provides the stimulus for vestibular responses. The precise arrangement of the otolith organs and canals in the head is shown in the lower part of figure 3.7. In the saccule, the sensory epithelium is oriented vertically, and in the utricle it is oriented horizontally. The three semicircular canals are oriented at right-angles to each other, as shown in the figure. The two vestibular organs on either side of the body are mirror images of each other. The significance of this arrangement becomes apparent when one considers the physics of head movement and the vertical direction of gravitational force. Head movements can be defined in terms of three principle planes and three axes passing through the head, as illustrated in Figure 3.9.

Figure 3.9 (re-draw?)
The median plane passes vertically through the head from front to back. The frontal plane passes vertically through the head from side to side. Finally, the transverse plane passes through the head horizontally. The x-axis runs from front to back, the y-axis runs from side to side, and the z-axis runs vertically (see Howard, 1982). Within this framework, there are six possible ways that the head can move, usually called six degrees of freedom, also shown in figure 3.9. There are three possible linear (translatory) movements, corresponding to translation along one of the three axes (backward and forward along the x-axis; sideways along the y-axis; up and down along the z-axis). There are also three possible rotational movements corresponding to rotation in one of the three planes.
Rotation in the median plane, as in a ‘yes’ nod, is called ‘pitch’. Rotation in the transverse plane, as in a ‘no’ shake, is known as ‘yaw’. Rotation in the frontal plane, as in a side-ways tilt of the head, is known as ‘roll’. Each of these six different possible movements can occur independently of the others. Complex natural movements of the head can be considered to contain a combination of two or more of these movement components. For example, as you bend down to tie a shoe lace, your head might move in a way that combines linear downward motion in the median plane and rotational movement about the y-axis as the head tilts forward. A turn of the head to one side during this movement would add a second rotational component about the z-axis. The otolith organs and semicircular canals are shaped and positioned very precisely so that their responses during natural three-dimensional head and body movements effectively decompose complex movements into their translatory and rotational components. This decomposition is crucially important for proper control of body and eye position. For example the presence of a translatory component of body movement may indicate a need to adjust one’s balance, while the presence of rotational component may require compensating eye movement to maintain steady fixation on an object. The vestibular labyrinth is beautifully designed to achieve this decomposition. The otolith organs provide information about linear movement components, and the semicircular canals provide information about rotational components. Precisely how they achieve this decomposition is explained in the following paragraphs.

**Figure 3.10 (re-draw)**

**Otolith Organs** The patch of hair cells in each otolith organ is called the macula. It is covered in a gelatinous layer, which in turn is covered by a heavy fibrous carpet (otolithic membrane) containing calcium carbonate crystals (otoconia; see figure 3.10). Linear acceleration of the head causes a shifting or shearing motion between the layer of hair cells and the otolithic membrane above them (similar to the movement of a loosely-fitting hat placed on the head when the head is moved or tilted). The shearing motion displaces the hair cells and results in a sensory response, as shown in Figure 3.10 (right). Recall from the previous section that individual hair cells are directional in the sense that deflections toward the kinocilium are excitatory and deflections away from the kinocilium are inhibitory. Close examination of the arrangement of hair cells in the saccule and utricle reveals that the macula in each is split down the middle. All hair cells on one side of the division are excited by deflection in one direction but inhibited by deflection in the opposite direction, whereas hair cells on the other side of the division show the opposite pattern of response. This arrangement allows the organs to distinguish between opposite directions of shear on the basis of the pattern of excitation. Since the macula of the utricle is approximately horizontal, and the macula of the saccule is roughly vertical, the two organs together can signal linear acceleration along any axis, since one or the other or both will always be activated. The otolith organs respond to acceleration rather than to movement at a constant velocity, because displacement of their hair cells is due to the initial inertia of the otolithic membrane. Once a steady speed of bodily motion is reached, the otolithic membrane catches up with the macula, so the hair cells return to their resting position.

It is important to note that the otolith organs provide static information about gravitational vertical as well as dynamic information about linear acceleration. This
property arises from Einstein’s equivalence principle, according to which a gravitational force field is equivalent to an artificial force field resulting from linear acceleration (the effect of gravity can, of course, be described in terms of acceleration toward the ground at a specific rate). Consequently, as illustrated in Figure 3.10, the shearing motion of the otolithic membrane produced by horizontal acceleration is identical to that produced by a static tilt of the head at an angle of 15 deg. This equivalence has important consequences for perception, described later in the chapter.

[Incidentally – Invertebrates possess a structure called the statocyst, which performs the same function as the vertebrate otolith organ. In shrimps, the statocyst has an opening through which the creature takes in grains of sand that perform the same function as otoconia. In a classic study in 1893, the sand in the creature’s aquarium was replaced with iron filings. The shrimp’s bodily orientation could then be influenced by the presence of a strong magnet placed outside the tank (Shepherd, 1988)]

**Semicircular Canals** In each semicircular canal the bundle of hairs cells (known as the crista) stretches across the canal inside a gelatious mass (the cupula) that blocks the flow of fluid around the canal. Rotational acceleration of the head causes a flow of fluid around the canal, due to the inertia of the fluid. The cupula is distorted by the force of these currents, displacing the hair cells by a very small amount (about 10 millimicrons for a relatively slow head movement), as shown in Figure 3.10 (bottom). The curved shape of the semicircular canals allows them to signal rotational acceleration of the head, because this movement will set up strong current flows around the canals. Since there are three degrees of rotational movement, three canals in each labyrinth are sufficient to detect any combination of the components. The canals are roughly at right-angles because this is the optimal arrangement to signal movement about the three possible axes, which are also at right-angles. Unlike hair cells in the utricle and saccule, hair cells in each canal are arranged with their kinocilium pointing in the same direction, so all cells within a particular canal will be excited or inhibited together by movement of fluid in a particular direction through the canal. It is important to note that each canal works in partnership with its mirror-image canal on the other side of the head, whose hair cells point in the opposite direction. Rotation of the head about any axis will set up strong current flows in the canals on each side of the head, but the resulting responses from canals on opposite sides will be in opposition. For example, a leftward head turn will cause an increase in firing rate in the left vestibular nerve, connected to the left horizontal canal, but a decrease in firing rate in the right vestibular nerve. Rightward rotation reverses the pattern of firing. This arrangement also applies to the other two pairs of canals (left anterior and right posterior, left posterior and right anterior), which respond well to rotation in the x- and z- axes.

The semicircular canals respond only to angular acceleration, not to a constant angular velocity of rotation. As in the case of the otolith organs, this property arises because of the initial inertia of the endolymph fluid at the start of the rotation. Once a steady rotational velocity has been reached, the fluid catches up with the canal movement, and the cupula returns to its rest position.

10
Central Vestibular Pathways

Hair cell responses are transmitted along the vestibular branch of the VIIIth cranial nerve. There are about 20,000 fibres on each side of the head (Shepherd, 1988), most of which terminate in several large groups of neurons in the brainstem called the vestibular nuclei. The remainder project directly to the cerebellum (see below). Projections from the vestibular nuclei can be grouped into four systems (see Figure 3.11), two ascending (thalamic and cerebellar), and two descending (spinal and ocular).

**Figure 3.11 (as-is)**

**The vestibulo-cerebellar system** Cells in the vestibular nuclei project to, and receive projections from the flocculonodular lobe of the cerebellum (see Carlson, 1998). The cerebellum is a large, complex neural structure that receives projections from and projects to many neurons in the cortex, brainstem, and spinal cord. Its main function is to control movement by detecting and reducing differences between intended and actual movements. The vestibulo-cerebellar system regulates the movements that control posture and bodily equilibrium.

**The vestibulo-thalamic system** Thalamic cells receiving inputs from the vestibular nuclei project to two areas of cerebral cortex (Purves et al., 2001). One area is just posterior to the primary somatosensory cortex near the representation of the face, and the other area is on the border between the somatosensory cortex and the motor cortex. These cortical projections may mediate perception of balance.

**The vestibulo-spinal system** carries projections to motoneurons in the spinal cord along two tracts, medial and lateral. The medial tract carries projections mainly from the semicircular canals to motoneurons controlling muscles in the neck and trunk. These projections are thought to be involved in reflexive control of body posture and head position in space. The lateral tract carries projections mainly from the otolith organs to motoneurons controlling limb muscles. These projections are thought to be important for the limb movements necessary to maintain balance. The small number of synapses between the vestibular organs and the motoneurons allows these reflexive movements to occur very rapidly. The high rate of resting discharge in vestibular afferent fibres supplies a continuous flow of excitation to the motor centers that control posture, helping to maintain the muscles in a steady state of contraction.

**The vestibulo-ocular system** carries projections to other nuclei in the brain stem, containing motoneurons that control eye movements. This neural circuit mediates reflexive eye movements (vestibulo-ocular reflex) that compensate for head movement and stabilize the visual image. The importance of the vestibulo-ocular reflex can be demonstrated easily. Hold your head stationary, and oscillate this book rapidly from side to side. Notice that the print becomes an unreadable blur. Now keep the book stationary but oscillate your head from side to side at the same rate, while fixing the page. The print should remain perfectly stable and readable, because your eyes move to stabilise the image. Signals from the vestibular organs are used to drive eye movements that compensate perfectly for the head movement. The eye movements are actually driven directly by differences in firing rate between the left and right vestibular organs, without the involvement of higher brain areas.

**Figure 3.12 (re-draw)**
Figure 3.12 illustrate what happens when the head is rotated about the z-axis, as in turning your head to the left. The leftward rotary acceleration displaces fluid in the left and right horizontal canals. The direction of fluid motion in the left horizontal canal causes an increase in firing rate in its afferent fibres. Fluid motion in the right horizontal canal has the opposite effect, decreasing firing rate. Note the direction of fluid motion in each canal in relation to the kinocilia. These responses are collected by the lefthand and righthand vestibular nuclei in the brainstem. Projections from the vestibular nuclei innervate the muscles surrounding each eye. There are both excitatory (+) projections and inhibitory (-) projections from each nucleus. Consequently, when the activity level in the two nuclei is equal, the eyes remain stationary. However, an imbalance between the nuclei leads to a bias in favour of signals to the muscle on one side of each eye, and a resulting eye movement. The greater level of activity in the lefthand vestibular nucleus during a leftward head turn, shown in figure 3.12, results in compensatory eye movement to the right. Damage to the vestibulo-ocular system can result in unwanted jittering eye movements, even when the head is stationary, due to pathological differences in firing rates between the vestibular nuclei. Damage can also result in visual disturbances such as blurred vision during head movements, due to loss of image stabilization.

**Vestibular Perception**

As we have seen above, the sensory information supplied by the vestibular system is used largely to control reflexive movements of the eyes and limbs. Its cortical representation is small relative to the representation of the other senses. In addition, information about the body’s position and movement in the environment is available from vision as well as from the vestibular system. For example, contour orientation and texture gradients offer cues about the orientation of the ground plane relative to the body, and large-scale patterns of movement in the image (‘optic flow’, see Chapter x) offer reliable information on bodily movement. Vestibular responses tend to intrude on conscious experience only when there is a discrepancy between visual information and vestibular information. The resulting sensations of ‘motion sickness’ can, however, be very powerful, often inducing confusion, disorientation and nausea. The situations giving rise to such discrepancies typically involve subjecting the body to movements outside the range normally experienced.

**Perceptual effects attributable to vestibular responses**

**The oculogyral illusion and Coriolis effects** Everyone has experienced the dizziness that results from rotating the body about the z (vertical) axis very rapidly. Just as the spin stops there is a strong illusory sense of bodily movement, and loss of body equilibrium, accompanied by apparent visual movement in stationary objects and reflexive movements of the eyes. Graybiel and Hupp (1946) called the illusory visual movement the ‘oculogyral illusion’. These effects can be attributed to responses in the semicircular canals. During initial acceleration into the spin, ‘backward’ deflection of the cupula due to its inertia leads to appropriate vestibular signals concerning angular acceleration. During sustained rotation the cupula returns to its resting position. During and after deceleration as the spin stops, momentum in the fluid deflects the cupula ‘forwards’ in
the direction normally associated with a spin in the opposite direction. The resulting erroneous signals lead to disorientation and dizziness. The illusory impression of turning can persist for up to 30 or 40 seconds after stopping, during which time the vestibular system recovers to its resting state (Parsons, 1970).

Coriolis effects are experienced when the head is moved during a spin. Head movements modify the effect that the spin has on the semicircular canals. If the head rotates about the same axis as the spin, there is a momentary increase or decrease in the total angular acceleration of the head. If the head rotates about a different axis, then the angular accelerations produced by the spin and by the head rotation interact in a complex way, under forces known as Coriolis forces (similar to the forces that act on a spinning wheel if you try to turn its axis at right angles to itself). For example, if you are spinning in a leftward direction, and incline your head forward during the spin, the resultant stimulation of the canals produces a sensation that the head is being tilted sideways toward the left shoulder (see Howard, 1982, for more details). The mismatch with information supplied by the otolith organs and by vision induces dizziness and nausea.

**The oculogravic illusion** Illusory tilt that is perceived during linear acceleration is known as the oculogravic illusion. For example, a seated individual undergoing horizontal linear acceleration will experience a strong sensation of backwards tilt, and a corresponding apparent elevation of visible points positioned at eye level (eg. Cohen, 1973). The illusion can be attributed to responses in the otolith organs. As discussed earlier, and illustrated in Figure 3.10, the macula cannot distinguish between displacements due to horizontal acceleration and displacements due to static head tilt. As a result, a displacement of the macula during acceleration may be attributed, at least partially, to head tilt. This illusion can have potentially disastrous consequences in modern transportation, as discussed in the tutorial section.

**Vection** Wood (1895) described a visit to a fairground attraction called the ‘Haunted Swing’ at the San Francisco Midwinter Fair. Visitors entered a large cubical room containing various items of furniture, and sat on a large swing that hung in the centre of the room. The swing was set in motion, eventually turning a complete revolution. Participants experienced a compelling sensation of bodily movement, but in reality the swing was stationary, and the room moved (the furniture was fastened to the floor). Wood reports that “many persons were actually made sick by the illusion...[and could]...scarcely walk out of the building from dizziness and nausea”. This kind of illusory motion is sometimes known as vection (Howard, 1982). Lishman and Lee (1973) constructed a moveable room similar to that used in the Haunted Swing to study one form of vection, apparent translation or ‘linearvection’. The subject stood on a stationary platform inside the room, the walls and ceiling of which swung back and forth slowly. Adults experienced a sensation of body sway, and tended to sway in synchrony with the room to compensate for the apparent movement of the body. Infants who had recently learned to walk fell over as soon as the room began to move. Illusions of rotary movement of the body (‘circularvection’) can be induced by placing the subject inside a large textured cylinder, and setting the cylinder to rotate around the subject very slowly. One could argue that vection is not truly a consequence of vestibular responses, because the subject is stationary, and the illusion is induced by movement of the scene surrounding her. However, visually induced sensations of body motion (involving no
direct stimulation of the vestibular organs) are indistinguishable from sensations induced by actual body motion. For example, if a person tilts his head while experiencing visually induced rotation of the body, he experiences the same Coriolis effect that would be induced by real rotation (Dichgans and Brandt, 1973). The equivalence of visual and vestibular stimulation probably arises because neurons in the vestibular nuclei respond both to vestibular stimulation and to visual stimulation, perhaps via signals from the cerebellum (Henn et al., 1974).

Chapter Summary
The body senses provide information about surfaces in direct contact with the skin, about the position and movement of body parts, and about the position and movement of the body relative to the outside world.

The somatosensory system
The somatosensory system contains eight different types of receptor distributed throughout the body, whose responses are conveyed to the brain along two parallel neural pathways. Each cortical neuron receives signals from just one of the eight receptor types, in a confined area of the body surface which defines the neuron’s receptive field. Receptive fields on the hands and face are much smaller than those on the trunk and limbs. Cells with receptive fields at nearby body locations are themselves located near to each other in the cortex. Receptive field location changes systematically from cell to cell, so that the body is mapped out in an orderly manner across the cortex. The map is distorted so that a much larger area of cortex is devoted to some parts of the body than to others. Human ability to discriminate small differences in tactile stimulation varies in different regions of the body in a way that closely reflects the distortion of the cortical map.

The vestibular system
The sense of balance is mediated by sensory responses from hair cells in the vestibular organs. Separate neural structures within each organ signal angular acceleration and linear acceleration of the head through space. Signals from the vestibular organs are used largely to control reflexive movements of the muscles. The vestibular nuclei in the brainstem are major distribution centers for vestibular signals. Descending projections to the spinal cord control reflexive movements of the head, neck and limbs. Projections to the extra-ocular muscles control eye movements that compensate for head movement. The vestibular nuclei also project to the cerebellum and to the cortex (via the thalamus). Mismatches between vestibular information and visual information often induce ‘motion sickness’ - feelings of disorientation, dizziness, and nausea.
Tutorials

Phantom Limbs

A physician treating wounded soldiers during the American Civil War noticed that his patients reported the illusion that their amputated limb was still present. He used the term ‘phantom limb’ to describe the effect (Ramachandran and Blakesee, 1998). Nine out of ten amputees have such experiences. The phantom limb feels much the same as a real limb in terms of its size, movement and tactile sensations such as itching, sweating, and pain. Indeed pain is felt in about 70% of cases over the first few weeks following amputation, and persists for years in 50% of cases (Melzack, 1990). Over time, sensations from the phantom limb may change. It may, for example, appear to telescope into the stump so that the foot is perceptually located on the thigh, or the extremity may appear to be present in the absence of an intervening limb. Prostheses such as an artificial arm or leg may appear to be real, or filled with the phantom limb. Sensations from phantom body parts are not restricted to limbs, but can include many other innervated regions of the body such as the penis, breast and bladder.

The traditional explanation for phantom limbs is based on neural responses arising in the stump of the amputated limb. Nerve endings that once innervated the missing limb may become irritated, and generate signals that duplicate those normally arising from the limb. Once these signals arrive in somatosensory cortex, they are perceptually localized on the missing limb. We know from the work of Penfield described earlier that direct stimulation of somatosensory cortex does evoke sensations of tactile stimulation that are localized on body parts, so this explanation seems plausible. However, phantom sensations occur even in patients whose spinal cord has been cut, so that there is no route for peripheral signals to reach the brain (Melzack, 1990). We must turn to signals within the brain, rather than signals arriving from the region of the stump, for an explanation of phantom limbs.

Figure 3.13 (as-is?)

Merzenich et al. (1984) studied somatosensory cortical maps in adult monkeys before and after surgical amputation of one or two fingers. Before amputation, each finger was represented individually in the cortex (see figure 3.13, top). Two months following amputation of digit three, its cortical representation had disappeared entirely. The areas devoted to the adjacent fingers had expanded to occupy the area previously devoted to the amputated finger (see figure 3.13, bottom). Pons et al. (1991) reported more radical re-organisation in the somatosensory cortex of monkeys whose sensory nerves from one arm had been severed eleven years previously. Stimulation of a monkey’s deafferented hand did not excite the hand area of cortex. However, stimulation of the monkey’s face did evoke a response from the ‘hand’ area. Recall from Penfield’s map (figure 3.4) and from figure 3.13 that the face area of cortex is adjacent to the hand area. The ‘face’ area of cortex had expanded to incorporate an area previously devoted to the hand. These remarkable results demonstrate that even during adulthood the cortex is able to re-organise itself in response to altered sensory input. Recall that human tactile acuity in a particular body region is closely related to the area of cortex devoted to that region (see figures 3.4 and 3.6). If cortical re-organisation also occurs in humans following
amputation, one might expect improved acuity in the region surrounding the amputated limb. Haber (1955) reported just such an improvement in acuity. It is tempting to relate the experimental findings of Merzenich et al. (184) and Pons et al. (1991) to the phantom limb syndrome. On the basis of these studies we can assume that following amputation of a hand, for example, cortical cells formerly responsive to hand stimulation become responsive to stimulation in another part of the body (eg. the face). We must also assume that, despite this re-wiring, activity in these ‘hand’ cells can still evoke a sensation that is localized in the missing hand. As a result, the amputee may experience sensations from a phantom hand when the face is stimulated. Ramachandran and Blakeslee (1998) report observations that are consistent with this explanation. However, cortical re-mapping is unlikely to be a full explanation of the phantom limb syndrome. Haber (1958) did not find perceptual localization errors with stimulation of the area surrounding an amputation. In addition, pain is a prominent feature of the syndrome and, as we saw earlier in the chapter, the central representation of pain is complex.

**Modern Transportation and the Vestibular System**

The vestibular system evolved to deal with the restricted range of conditions that apply to natural bodily movements. The fastest human being can run no faster than about 50 km/h (31 mph), and gravitational acceleration is 9.8 m/sec\(^2\) (32.2 ft/sec\(^2\), or 1G). Modern transportation can subject the body to velocities and accelerations far beyond these values. Surface transportation can reach speeds in excess of 500 km/h (310 mph), whereas the escape velocity for spacecraft is 40,000 km/h (25,000 mph). To reach this speed during take-off, spacecraft accelerate with a force of up to about 9 G. This means that the astronaut is pressed back into his seat by a force equal to nine times his body weight. Modern fairground attractions generate accelerations of several G. Velocities and accelerations outside the natural range can create abnormal vestibular responses that result in dizziness, disorientation, nausea, unstable vision, and disturbed motor control. These disturbances can obviously have disastrous consequences when experienced by a person in control of a vehicle.

[Incidentally - Sustained acceleration in excess of about 5 G actually causes loss of vision and consciousness, if applied in a standing position; astronauts lie in a reclined position during take-off, to avoid black-out]

**Effects of constant velocity** As we saw earlier in the chapter, movement at a fixed velocity does not generate a vestibular response. Consequently humans can subject themselves to extreme velocities with no perceptual disturbances. Passengers in cars, airliners, and spacecraft feel no vestibular sensation of speed even at extreme velocities, provided that the velocity is constant. One can argue that it would make no sense to possess a vestibular system that was sensitive to constant velocity. As Einstein’s theory of relativity made clear, in an abstract sense any measure of movement at a constant velocity is arbitrary since it depends on the frame of reference. If humans possessed a vestibular system that did signal constant velocity, would it report our speed relative to the surface of the earth, or the speed of the earth traveling in space? Humans can, of course, gain some sense of movement at constant velocity from the visual system. However, this information specifies *relative* velocity; speed in relation to the visible surroundings. Our
perception of constant velocity movement is therefore vulnerable to variation in visual input. Under-estimation of road vehicle speed in foggy conditions is due to the lack of both visual and vestibular information regarding velocity. A heightened sense of road speed is experienced in open or low-slung vehicles such as motorcycles and racing cars, where visual movement cues are particularly powerful.

**Effects of variation in velocity** Perceptual disturbances due to abnormal vestibular responses all arise from *changes* in vehicle velocity. Aircraft pilots are at particular risk of perceptual disorientation, leading to inaccurate perception of the attitude or motion of the aircraft relative to the earth’s surface. According to one estimate (Benson, 1974) disorientation accounted for nearly 40% of fatal accidents in civil aviation in the period 1964-1972. The oculogyral and oculogravic illusions described earlier in the chapter are common experiences for aircraft pilots.

The oculogyral illusion can occur following aircraft manoeuvres that involve complete revolutions in any of the three principle axes (turns, rolls, and spins). The pilot may experience an illusion of turning in the opposite direction just after the turn is completed. During and after such manoeuvres, the vestibulo-ocular reflex is likely to trigger eye movements, in an attempt to stabilize vision during the spin. Since the aircraft’s cockpit instrumentation obviously remains in a fixed position relative to the pilot’s head, such eye movements succeed only in producing visual instability that obscures the instruments. Any head rotations executed during the spin heighten disorientation, due to Coriolis effects discussed earlier.

The oculogravic illusion can lead to the pilot mistakenly perceiving the aircraft to be level when it is in fact banking, or tilted when it is actually level. In the situation illustrated in Figure 3.14a, the aircraft is executing a bank and turn. The pilot is subject to both gravitational and centrifugal forces which combine to create a resultant force that is slightly tilted from gravitational vertical. The pilot may interpret this resultant force as gravitational vertical, and therefore perceive the plane to be flying straight and level. A second example is illustrated in Figure 3.14b. During a catapult launch from an aircraft carrier, the aircraft is subjected to a peak forward linear acceleration that presses the pilot back in his seat with a force equal to 4.5 G. When combined with the downward gravitational force of 1 G, the resultant force acting on the otolith organs indicates a backwards tilt of the aircraft (though perceived tilt is much less than would be predicted by the direction of the resultant force). Inexperienced pilots may attempt to compensate for this apparent tilt by pitching the plane down towards the sea. The extreme disorientation experienced by pilots can impair and confuse their motor control to such an extent that they report an invisible ‘giant hand’ interfering with their command of the control column.

**Figure 3.14 (re-draw?)**

Flying instruction draws attention to the dangers of misinterpreting vestibular signals. Pilots are taught to avoid flying ‘by the seat of the pants’, but to rely on instrumentation for information about the attitude and motion of the aircraft.
Figure Captions

Figure 3.1
Direct physical contact mediates some of our most powerful sensory experiences.

Figure 3.2
Cross-section through a region of hairless skin revealing five different types of touch receptor.

Figure 3.3
Sensory pathways in the somatosensory system. Responses from free-nerve endings, mediating pain and temperature sensations, travel along the spinothalamic tract. Responses from mechanoreceptors mediating touch and proprioception travel along the lemniscal tract. Branching connections in Rexed’s laminae of the spinal cord mediate reflexes withdrawal responses to harmful stimuli.

Figure 3.4
Cortical representation of somatosensation. Thalamic neurons project to cells in a long thin strip extending across the cortex from ear to ear (top-left; a view of the cortex from the left side). Cross-sections along the line A-A’ are shown in the lower left of the figure. In common with other areas of cortex, somatosensory cortex can be sub-divided into six different layers, labeled 1-6 moving down from the surface. Thalamic axons terminate in layer 4 of area 3. Within a thin column of cortex, cells in all layers receive inputs from just one receptor type. A larger scale cross-section along line B-B’ is shown at the right of the figure. Each cell is selectively responsive to stimulation in a particular region of the body. Moving across the cortex from B to B’, there is an orderly progression in the body part covered by the cells. Re-draw from Smith (2000) and Penfield (1953).

Figure 3.5
Cortical receptive fields. Stimulation of a small region on the forearm (left) generates a response that is recorded from the middle cortical cell on the right. This region of body surface represents the cell’s receptive field. Excitation from receptors in region A of the receptive field is relayed via ascending projections in the spinal cord, brainstem, and thalamus. Inhibition from receptors in region B of the receptive field is generated by lateral connections (black in the figure). Stimulation in the central region (A) generates an increase in firing rate (top trace in the box). Stimulation in the outer region of the receptive field (B) causes a decrease in activity (middle trace). Stimulation in both A and B simultaneously does not change the activity level of the cell (bottom trace).

Figure 3.6
Two-point acuity for touch. A pair of calipers is placed on the skin surface, and the subject is required to report whether they feel a single point or a pair of points (top). The calipers are adjusted until the subject can just report the presence of a pair of points reliably (discrimination threshold). The bar graph shows the discrimination threshold on
various parts of the body. Thresholds are smallest, in the region of 1-5 mm, on the mouth and fingers, and largest on the neck and back (50-70 mm). Data re-plotted from XX.

Figure 3.7
The vestibular organs. The two organs lie in deep openings on either side of the skull. Each organ consists of three canals (posterior, anterior, lateral or horizontal) and two sacs (saccule and utricle), all of which are filled with fluid. Each structure also contains a small patch of sensory hair cells. Head movements result in fluid flow around the five structures, which displaces the hair cells and leads to sensory responses. The lower part of the figure shows the plane within which the head must move in order to excite each structure. P – posterior canal; A – anterior canal; H – horizontal or lateral canal; U-utricle; S – saccule.

Figure 3.8
Vestibular hair cells on a patch of sensory epithelium. Each cell consists of a single tall hair (kinocilium), and a number of smaller hairs (stereocilia) grouped on one side. Displacement of the hairs in the direction of the kinocilium, as shown, increases activity in the sensory nerve fibre. Displacement in the opposite direction decreases activity in the sensory nerve.

Figure 3.9
Principle planes and axes of the human body. The body can move linearly along three possible axes; x, y, and z. The body can rotate within three possible planes; frontal, medial, and transverse. These movements define six degrees of freedom – the body can move in six possible ways, each independent of the others. Natural movements usually a combination of two or more of these movement components.

Figure 3.10
Sensory epithelia in the otolith organs semicircular canals. In the utricle (top row) the hair cells are covered by a gelatinous carpet (otolithic membrane), itself covered with heavy calcium carbonate crystals (otocnia). Head tilts or accelerations lead to shearing motion between the otoconia and the hair cells, due to the inertia of the otoconia. The resulting displacement of hair cells leads to sensory responses. In the semicircular canals (bottom row), the hair cells form a bundle (crista) projecting across the canal inside a gelatinous mass (cupula). Head rotation causes a flow of fluid around the canal in the opposite direction, due to the inertia of the fluid. This current flow displaces the cupula and results in a sensory response. Redrawn from Purves et al. (2001).

Figure 3.11
Sensory pathways in the vestibular system. Sensory nerve fibres from the hair cells project centrally along the vestibular portion of the VIIIth cranial nerve. Most of the fibres terminate in the vestibular nuclei of the brainstem. The vestibular nuclei act as major distribution centers, dividing responses among four major systems; vestibulo-cerebellar, vestibulo-thalamic, vestibulo-spinal, and vestibulo-ocular. These systems
control reflex movements of the eyes and body, and provide a small cortical representation for vestibular signals.

Figure 3.12
Schematic representation of neural circuits in the vestibulo-ocular system. During head rotation to the left, fluid movement increases activity in afferent fibres of the left horizontal canal, and decreases activity in fibres of the right horizontal canal. These responses arrive in separate groups of neurons in the vestibular nuclei of the brainstem. There are both excitatory (+) and inhibitory (-) projections from the brainstem to the external muscles of the eyes. These connections are arranged in such a way that the imbalance in activity between left and right canals is translated into an imbalance in signals arriving at lateral and medial eye muscles. This imbalance produces a rightward rotation of each eye that is sufficient to compensate for the leftward head rotation.

Figure 3.13
Maps of the somatosensory area of monkey cortex, showing the region devoted to the fingers of one hand before (top) and after (bottom) amputation of finger 3. Before amputation, each finger was represented individually in the cortex. After amputation, the representation of finger 3 disappeared, and the region devoted to adjacent fingers expanded to occupy its space. Re-drawn from Merzenich et al. (1984).

Figure 3.14
The oculogyral illusion in aviation. A: During a bank and turn, the vestibular apparatus is subjected to both vertical gravitational force and horizontal centrifugal force. These forces combine to produce a resultant force that is slightly titled from vertical. The pilot may interpret this resultant force as corresponding to gravitational vertical, and consequently perceive the plane to be flying straight and level. B: During a catapult launch from an aircraft carrier, the vestibular apparatus is subjected to vertical gravitational force and to horizontal linear acceleration. The direction of the resultant force is tilted, and can lead the pilot to perceive the aircraft to be tilted backwards.