CHAPTER 7

Orienting to the Environment and Controlling Upright Stance
7.1 Sensorimotor Orientation to the Gravitational Vertical

7.1.1 Introduction

We orient our bodies with respect to our environment in characteristic ways. When we stand, we normally adopt an upright orientation in which our feet are in contact with the ground and our legs, trunk and head are aligned more or less vertically. When we walk around, we hold our heads and trunks in somewhat similar vertically upright orientations. Most other animals also orient themselves in characteristic upright postures. Mammals, birds, lizards and fish all adopt upright body postures for most of their waking hours: Figure 7.1 shows a blue shark and a heron in characteristic upright orientations (the vertical direction is up the page).

Figure 7.1: Blue shark and heron in ‘upright’ orientations (not drawn to scale!).

Note that the shark is darker on its back (dorsal surface) than on its belly. This is called countershading and it is a characteristic that the shark shares with many other animals. It has been suggested that countershading makes animals more difficult to see, increasing the chances that a prey animal will not be seen by a predator or that an approaching predator, such as a shark, will not be seen by the prey – it is a form of camouflage. Figure 7.2 reproduces one of the first photographic illustrations of the effectiveness of the camouflaging effect of countershading: a grouse (a ground-nesting bird related to the chicken) with normal countershaded plumage is located within the scene in panel A, and with its countershading removed by dyeing the ventral plumage in panel B. Countershading will only work as camouflage if the animal orients itself with the dark side facing towards the light source and the pale side facing downwards towards the earth, as in the case of the grouse in panel A of Figure 7.2 and the shark in Figure 7.1.

Figure 7.2: A grouse with countershading (A) and without it (B). From Thayer (1896).
How do people and animals achieve and maintain their characteristic upright postural orientations? To what exactly are they orienting themselves; how do they determine what is upright? In this part of the chapter we will look at the second question. We will look at the first question in subsequent parts of the chapter.

7.1.2 How should ‘upright’ and ‘vertical’ be defined?

We normally use the word upright to mean \textit{vertically oriented} or ‘placed in a vertical position’, which assumes that we already know the meaning of the term \textit{vertical}. However, a clear and unambiguous definition of vertical seems hard to come by. For example, the Oxford English Dictionary defines \textit{vertical} to mean ‘at right angles to a horizontal plane; in a direction, or having an alignment, such that the top is directly above the bottom’\textsuperscript{4}. Yes, certainly, but what does it mean for something to be ‘directly above’ something else, or to be horizontal? In order to provide a complete definition of vertical, we need a frame of reference within which a specific direction is defined to be the vertical direction.

The obvious way to define the vertical direction in natural environments is to identify it with the direction opposite to that of the Earth’s gravitational pull. This is the \textbf{gravitational vertical}, often just referred to as \textit{the vertical} since no other sorts of vertical are usually relevant:

\begin{center}
\textbf{GRAVITATIONAL VERTICAL} (at a particular location): the direction opposite to that of the Earth’s gravitational force.
\end{center}

To say that an object is \textit{upright with respect to the (gravitational) vertical} means that an important axis associated with the object is oriented so that it is parallel to the vertical direction, usually with the additional requirement that some part of the object identified as its ‘top’ be above the part identified as the ‘bottom’. Figure 7.3 shows a bottle in an upright orientation: its longitudinal axis of symmetry is parallel to the vertical direction, and the top is directly above the bottom.

It is not quite so straightforward to define an upright orientation for an animal. The heron in Figure 7.1, for example, possesses no obvious axis that is oriented vertically. One basic feature of the vertically upright postures commonly adopted by both animals and people is that the sagittal plane of the trunk (abdomen and thorax) is vertically oriented. This alone is not sufficient; the animal must also be the right way up – feet at the bottom, head at the top, in the case of the heron or a person; dorsal surface up, ventral surface down, in the case of the shark. Of course, people are able to adopt standing postures in which no single body segment is oriented vertically (like the heron in Figure 7.1). As we will see in section 3 of this chapter, the requirement for a standing posture is that the center of gravity of the body (defined in section 7.3.2) lies vertically above the base of support (defined in section 7.3.6) formed by the feet. Thus, we can say that a standing posture for a person is one in which the feet are on the ground and the body’s center of gravity is vertically above the base of support; an upright standing posture is one in which the sagittal plane of the trunk is vertically oriented.

![Figure 7.3: An upright bottle.](image)
7.1.3 Information about the gravitational vertical can be obtained from the vestibular, somatosensory and visual systems

We naturally adopt upright postures of the body when standing and walking, and we can move a limb segment into a vertical or horizontal orientation. For instance, if you are asked to stretch out your arm horizontally (perpendicular to the gravitational vertical) as shown in Figure 7.4, you can do it quite easily (see section 7.1.4). In order to do these things, we need to obtain information about our orientation with respect to the gravitational vertical. This kind of information must be supplied by our sensory systems. Three sensory systems can provide relevant information: the vestibular system, the somatosensory system and the visual system.

Figure 7.4: Arm held out straight and horizontal.

In Chapter 3, we saw how the otolith organs, particularly the utricles, are able to provide information about the orientation of the head with respect to the gravitational vertical (head tilt). In Chapter 6, we saw how the signals from the utricles can be used to maintain an upright orientation of the head with respect to gravity, via the mechanism of the vestibulocollic reflex. If we can obtain information about how the head is oriented with respect to the vertical, then it is possible to obtain information about the orientation of any body part with respect to the vertical. For example, to determine the orientation of the trunk with respect to the vertical, we need to combine information about the head's orientation with information about the orientation of the head relative to the trunk. Figure 7.5 illustrates the idea: the head is oriented at an angle $\theta$ to gravity and the head is oriented at angle $\beta$ relative to the trunk. Therefore, the trunk is oriented at an angle $\theta + \beta$ to the vertical: sensory information about the angle $\theta$ is obtained from the otoliths, while information about the angle $\beta$ is obtained from proprioceptors in the neck.

Figure 7.5: A person leans so that the head and trunk are at different angles with respect to the gravitational vertical.
Gravity pulls on all the parts of a person’s body, which creates stresses and strains within the tissues that can stimulate somatosensory mechanoreceptors of various sorts. For example, joints between bones that support weight, such as the ankles, knees, hips and the intervertebral joints of the spine, are compressed by the weight they support, which deforms the soft tissues and stimulates joint receptors. Similarly, skin and subcutaneous tissues of the body parts that make contact with the surface of support will be compressed, and cutaneous mechanoreceptors will be stimulated. Finally, gravity will pull on tissues that are suspended from bones and other supporting structures; these tissues will be stretched, and mechanoreceptors embedded within them will be stimulated. Such tissues include muscles and their associated connective tissue, and also various internal organs such as the abdominal viscera, the large blood vessels of the trunk, and associated suspensory connective tissue. There is evidence that people are able to make use of information from all these different somatosensory sources, including information provided by visceral mechanoreceptors.

Finally, the visual system is also able to provide information about the body’s orientation with respect to the gravitational vertical. Of course, gravity does not stimulate the photoreceptors in any way, but it does have an effect on the structure of the visible environment. This structure provides cues to the gravitational vertical. In the urban environment, most walls are vertical and floors horizontal; there are vertical edges to doors and windows, vertical lampposts, and various vertical supporting struts, legs and members. The natural environment also contains cues to the gravitational vertical: tree trunks and the woody stems of various plants are often vertical; the horizon is horizontal, as are the surfaces of standing bodies of water.

7.1.4 Non-visual information contributes to orientation to the gravitational vertical

One way to investigate people’s ability to use vestibular and somatosensory information about the direction of the gravitational vertical is to use kinesthetic or haptic orientation tasks. These tasks involve blindfolding a person and having them try to position something so that it is oriented horizontally or vertically with respect to gravity (or possibly some other specified orientation). In a kinesthetic orientation task, the person attempts to move a body part, such as an arm or hand, so that its orientation matches the required orientation. The haptic orientation task is similar, except that the person attempts to move a hand-held rod into an orientation that matches the required orientation. The rods used in these experiments are normally gravity-neutral, in the sense that their weight does not provide information about their orientation relative to gravity. Figure 7.6 illustrates the two kinds of task for a person in a seated posture. Panel A shows a person engaged in a kinesthetic orientation task: they are attempting to move their arm into a horizontal orientation when seated upright (top) and when they are tilted backwards (bottom). This kind of tilt is called pitch tilt. Panel B shows a person engaged in a haptic orientation task: they are attempting to move a hand-held rod into a vertical orientation when seated upright (top) or tilted to their left (bottom). This kind of tilt is called roll tilt. People’s ability to orient a limb segment or a rod to the vertical can be interpreted as a measure of their perception of the vertical. Thus, these tasks are frequently used to assess people’s perception of the vertical direction.

Experiments have shown that people’s performance in both kinesthetic and haptic orientation tasks is reasonably accurate over a wide range of both pitch and roll tilts. Example results from a haptic orientation task are shown in Figure 7.7. Participants in the experiment were strapped to a bed that could be pitched forwards and backwards or rolled side to side. They were held at different angles of pitch or roll, and their task was to indicate the perceived vertical using a gravity-neutral, hand-held rod. Panel A of Figure 7.7 shows the angle at which participants oriented the rod relative to their midlines (medians for the group) for different angles of pitch tilt (from 100° backwards to 80° forwards). The insert shows how the angles of tilt and rod orientation are defined. The angle of tilt is the angle between the gravitational vertical (blue line) and the midline of the person’s head and trunk (dotted line); the rod angle is the angle between the midline and the rod’s long axis (dashed line). Perfectly accurate
(A) Kinesthetic orientation task

seated upright with respect to gravity

pitched backwards by about 45°

(B) Haptic orientation task

roll tilted to the left by about 45°

**Figure 7.6:** Orientation tasks that involve orienting a body part (A) or an object (B) with respect to the vertical (based on Figure 3 of Carriot, DiZio, Nougier, 2008).

Performance is represented by the straight diagonal line in the graph (rod orientation angle equal to the angle of tilt). Panel A shows that participants were able to orient the rod to the vertical quite accurately. Panel B plots the data for variations in roll tilt (from 90° left to 90° right) and shows that performance is again quite accurate.

The data shown in the graphs in Figure 7.7 demonstrate that people are able to accurately perceive the vertical using information gained from the vestibular and somatosensory systems.

**Figure 7.7:** Results from haptic orientation experiments in which pitch (A) and roll tilt (B) were varied. The rod angle (β) provides a measure of the perceived direction of the vertical. (Data from Bartolami et al., 2006a.)
Detailed experimental studies have shown that people are able to make use of all the different sources of information available, including information from the viscera, though it seems that the otoliths are a particularly important source of information. Many of these studies have manipulated ‘gravity’ using centrifugation: we will discuss how this works later in the chapter.

Although performance in the kinds of tasks described here is often quite accurate, people have been found to show systematic biases in their perceptions of the vertical when their heads or bodies are tilted. There are two types of bias that are commonly observed; these are called A-effects and E-effects, which may be defined as follows:

1. **A-effect**: a bias to indicate that the vertical direction is tilted towards the midline of the body in the plane of the body’s tilt (i.e., in the same direction as the body tilt). The stick figure insert at the top of panel A in Figure 7.7 is exhibiting an A-effect: the rod angle (β) is less than the angle of body tilt (α).

2. **E-effect**: a bias to indicate that the vertical is tilted away from the midline of the body in the plane of the body’s tilt (i.e., in the direction opposite to the body’s tilt). The stick figure insert at the top of panel B in Figure 7.7 is exhibiting an E-effect: the rod angle (β) is greater than the angle of body tilt (α).

The data shown in Figure 7.7 show evidence of both types of bias. In panel A there is evidence for a small A-effect (<5°) for large backward tilts (>50°); in panel B there is evidence of an E-effect (between 10° and 15°) for tilts to the left, and a smaller E-effect (<5°) for tilts to the right greater than 50°.

![Figure 7.8: A- and E-effects in a visual orientation task.](image)

Both these biases were originally discovered in tasks where people were tilted (either whole body tilts or head only) in complete darkness and asked to judge the orientation of a self-
luminous line\(^1\) (visual orientation task). If a line that is aligned with the gravitational vertical — a truly vertical line — appears to be tilted in the opposite direction to the tilt of the body, then there is an A-effect. This means that if a person adjusts the orientation of the line until it appears to be vertical, then it will be tilted in the same direction as the head or body, which corresponds to the definition of the A-effect given above. A pictorial illustration of both the A- and E-effects in a visual orientation task is presented in Figure 7.8.

A- and E-effects are typically larger and more consistent in visual orientation tasks than they are in haptic or kinesthetic orientation tasks\(^2\). In roll tilt, the effects in haptic and visual tasks are opposite: E-effects are observed in haptic tasks (Figure 7.7B), A-effects in visual tasks\(^3\). The reasons for these effects are not fully understood. One early suggestion was that they could be explained in terms of the variation in the responses of the utricules to different angles of body tilt\(^4\). The typical patterns of data were subsequently found to be inconsistent with this explanation\(^5\), but consistent with the idea that the ratio of utricular and saccular responses contributes to the perception of the vertical\(^6\). However, this cannot be the complete explanation, since both E-effects and A-effects have been found to be present in people who have lost vestibular function\(^7\), indicating a role for other sources of information. It is clear that the two effects could be interpreted as the results of a misperception of the tilt of the head and/or body. If a person underestimates their head/body tilt, they should experience an A-effect; if they overestimate their tilt, they should experience an E-effect. However, there is little evidence that people do systematically misperceive the orientation of their heads or bodies\(^8\). It has also been reported that an A-effect present in judgments of the vertical was accompanied not by an underestimation of body tilt, but by an overestimation\(^9\), indicating that the effect is not due to a misperception of body position.

7.1.5 Visual information contributes to perception of and orientation to the vertical

As described in section 7.1.3, terrestrial environments typically contain numerous vertically and horizontally oriented contours that provide visually available information about the direction of gravity, and features such as the sky and the ground that establish what is up and what is down. These visible contours and features define a spatial frame of reference called the visual frame of reference. What does the visual frame of reference contribute to our ability to orient to the vertical?

We can easily stand upright without vision, and as described in the previous section, we are quite accurate at orienting body parts or hand-held objects in vertical or horizontal directions without vision. Thus, visual information is not necessary for successful performance of these tasks. However, there is no doubt that when visual information is available, it contributes to our perception of the vertical and to the performance of orientation tasks. One demonstration of this is provided by the tilted rooms sometimes found in amusement parks, science museums\(^10\) and ‘Mystery Spot’ attractions\(^11\). The walls and furnishings of these rooms are all tilted by the same amount in the same direction; the ceilings and usually the floors are perpendicular to the tilted walls (Figure 7.9). The visible contours of the room establish a visual frame of reference in which the vertical direction (room vertical) is the direction from floor to ceiling parallel to the walls. In a tilted room, the visual frame of reference is not aligned with gravity, so the ‘room vertical’ differs from the gravitational vertical, as indicated in Figure 7.9.

If people use visual contours as information about the vertical direction, then they should show a tendency to orient themselves so that they are upright with respect to the room vertical, and they should perceive the vertical to be displaced from the gravitational vertical towards the room vertical. This is exactly what happens for modest angles of tilt (less than about 30°); upon entering such a room for the first time, people perceive themselves to be tilted and the room to be oriented in the normal way (i.e., vertically). They typically make adjustments to their postural orientation to compensate, leading to stumbling or falling over\(^12\). People can quickly learn to adapt their postural orientation so that their bodies are close enough to upright to prevent the loss of balance. However, the impression that they are
in a room that is vertically oriented or close to vertical persists. This leads to some curious visual perceptions that appear to defy the law of gravity: objects and people appear to lean at impossible angles, water can appear to flow uphill, and balls to roll uphill. The reasons for these effects are explained in Figure 7.10. In each case, the perception of a person within the tilted room is shown on the left: the room is perceived to be vertical, or very nearly vertical. In panel A, another person standing on the table appears to lean over in a physically impossible fashion, in panel B, a ball appears to roll up an incline. The true situation is shown on the right: the person is actually standing upright with respect to the gravitational vertical, and the incline is actually a slight decline, so the ball is really rolling downhill.

Laboratory studies of the effects of the visual frame of reference on people’s perception of the vertical have typically used either a tilted room, or an apparatus that resembles a tilted room to some degree. The simplest such apparatus consists only of a self-luminous rectangular or square frame viewed in complete darkness. The general finding in these experiments is that the perceived vertical is affected by the extent of the visual field and the number of contours within it: the smaller the field of view and/or the fewer contours it contains, the less the perceived vertical deviates from the gravitational vertical. For example, in one study participants looked into a small room (1.22 meters square) containing a table, a chair and a shelf with a book on it. With the room tilted 22° to the left or right, participants perceived a visible test rod to be vertical when it was tilted 15° in the same direction as the room. In a second part of the study, participants saw only a self-luminous square frame. With the frame tilted 28° left or right, participants perceived a visible test rod to be vertical when tilted only 6° in the direction of room tilt, with some participants showing no effect of the frame. Results of this kind suggest that a larger number of contours distributed over a larger region of the visual field provide a more powerful cue to the vertical than a smaller number of contours within a smaller region of the visual field. This is what might be expected: reliable visual information about the vertical is not provided by just one or two contours or from within small regions of the visual field, because individual objects and surfaces are often tilted. For example, tree branches normally grow at an angle to the vertical; the trunks of some trees are not vertical; small regions of the ground surface are seldom horizontal; and the contours of many objects are neither vertical nor horizontal. Reliable visual information about the vertical can only be obtained as a kind of average over a number of different contours distributed over the whole visual field.

The effects and results described in this section imply that visual information is used in combination with other sources of information to determine people’s perception of the vertical and their orientation to it. This combination is discussed next.
7.1.6 Various sources of information are combined to determine the perceived vertical

Imagine the visual orientation task described at the end of section 7.1.4 (Figure 7.8). You can see nothing except a luminous line, and you have a clear, unambiguous perception of the line being in a particular location in space and having a particular orientation with respect to the vertical. You experience the line within a visual space with definite vertical and horizontal directions – a frame of reference with respect to which the orientation of the line is perceived. There is nothing visible to inform you about these directions, which means that they must be determined by other, non-visual sources of information about the vertical. As we have seen, such information is provided by the vestibular and somatosensory systems. Thus, we can conclude that the spatial frame of reference for visual perception of a self-luminous line is established by information provided by these other sensory systems\(^2\). In other words, what is described as a visual percept – the percept of the luminous line’s orientation – is, in fact, a percept to which at least two different sensory systems are contributing.

In the previous section we saw that vision can contribute information about the vertical, and that the stronger the visual cues, the closer the perceived vertical will be to that specified by those cues. This means that the frame of reference with respect to which vertical
judgments are made must be derived from two or more different sources of information about the vertical direction; the relative contributions of those sources depends on their availability and reliability. In the absence of visual information, information provided by the vestibular and somatosensory systems establishes the vertical direction for the frame of reference. It is generally agreed that the otoliths are the most important source of non-visual information about the gravitational vertical, but other information sources can make a contribution. As discussed earlier (section 7.1.3), somatosensory information is provided by muscle and joint proprioceptors, cutaneous mechanoreceptors and visceral mechanoreceptors, and there is empirical evidence that all these sources can make a contribution to the perceived orientation of a luminous line viewed in darkness and to the perceived orientation of the body in space.

### 7.1.7 Postural orientation and perception of the vertical can involve different information

From the description of people’s experiences in tilted rooms given in section 7.1.5, it is apparent that after an initial period of disruption, people adjust their postural orientation so that they stand upright with respect to the gravitational vertical (if they did not do this, they would fall over). However, their visual perception of the room as vertical persists, and so their visually perceived vertical does not correspond to the postural upright. This suggests that postural control in a tilted room comes to be somewhat independent of static visual cues to the vertical. When a person initially enters the room and experiences postural disturbances (stumbling or falling), visual cues are presumably influencing postural orientation. When the person has been in the room long enough to be able to stand upright with respect to gravity without experiencing any disturbances, their postural orientation must be based on vestibular and somatosensory information about the vertical, which is unaffected by the room tilt.

Several empirical studies have found that when people are required to orient their bodies either vertically or horizontally, their orientations are very close to the veridical (gravitational) vertical or horizontal, whereas their perceptions may not be veridical. For example, in one study, participants lay on their sides on a flat board and could adjust the orientation of the board by remote control. In complete darkness (no vision) and starting from either a head-higher-than-the-feet position or head-lower-than-the-feet-position, participants were required to adjust the board so that they felt that they were lying in a horizontal position. They were found to be able to do this very accurately (to within a degree or two on average) and precisely (standard deviation of about 1.5° on average), but when asked to adjust a luminous line so that it appeared to be vertical, they showed a pronounced A-effect: their settings were biased towards their body orientation by about 10°. Results of this kind suggest that the information used for perception of the vertical can differ from that used for control of body orientation.

An obvious question to ask is why the visually perceived vertical does not always correspond to the true gravitational vertical, whereas postural orientation to the vertical or horizontal is close to veridical. The reason probably has to do with the different requirements of postural and perceptual tasks. The postural control system needs to have access to veridical information about the body’s orientation to gravity in order to maintain balance: if the body is not properly oriented to the gravitational vertical when a person stands up, then they will fall over. Perceptual tasks appear to have different requirements. For example, if a picture on the wall is tilted to one side, then in order to look at it, we either turn it so that it is vertical or we tilt our heads into the same orientation as the picture. Tilting of the head is also commonly observed in tilted rooms: the body is oriented to the gravitational vertical, and the head is tilted so as to be more closely oriented to the room vertical. This indicates that we prefer to perceptually orient ourselves to the visual frame of reference when we visually inspect our surroundings. We perceptually orient to the visual frame of reference and posturally orient to the gravitational frame of reference. Of course, the two frames are normally congruent – the vertical specified by visual cues is the same as the gravitational vertical – but in very unusual
situations like tilted rooms, the two frames are different, and then a dissociation between visual and postural orientation can occur.

An interesting example of the power of the visual frame of reference to determine a person's perception of the vertical has been reported in the situation shown in Figure 7.11. Experimental participants lay horizontal on a padded bed with their arms unsupported inside a room rotated through 90°. The room contained a variety of everyday objects fixed into their normal positions with respect to the room. In short, the room contained numerous visual cues to the vertical and horizontal directions. In these conditions people's perception of the vertical was largely determined by the visual information: they typically perceived themselves to be upright within a vertically oriented room, despite the fact that vestibular and somatosensory cues were in conflict with this interpretation. Thus, vision dominates the vestibular and somatosensory system. When participants held out their arms to their sides in an extended position and oriented horizontally with respect to gravity, they experienced what the authors of the study called a levitation illusion: they felt their arms to be weightless and floating in space. The reason for this experience was presumably due to the absence of gravity in the direction consistent with their perceived vertical orientation: gravity was not pulling the arms towards the floor of the room.

Figure 7.11: Person in a room rotated through 90°.

In the zero-gravity environments encountered in space, we would expect people's perception of the vertical to be determined by the visual frame of reference (if such a frame is present), given that no other sensory cues are present. Inside the cabin, visual cues to the vertical are provided by the horizontals and verticals of the walls and floor and by the orientations of instrument panels and furniture (if present). In cabins that lack a significant number of objects or features with obvious tops and bottoms, astronauts’ perception of the vertical is strongly determined by the body's orientation within the cabin: they tend to perceive the side of the cabin beneath their feet as the floor and the side above their head as the ceiling. Thus, if the astronaut turns through 180°, the vertical direction flips 180° as well – the floor becomes the ceiling and the ceiling becomes the floor. Such flips in the orientation of the vertical can also be induced if another astronaut enters the cabin upside down with respect to the first: the second crew member provides a strong visual cue to which direction is 'up', and the first astronaut's perception flips accordingly.

An astronaut is weightless within a spacecraft provided that the spacecraft is not accelerating. Once the craft accelerates, a kind of artificial gravity is produced. We consider the way in which accelerations can alter the force environment experienced by a person in the next part of the chapter.
7.2 Orientation to the Gravitoinertial Vertical

7.2.1 ‘Upright’ can be defined with respect to the direction of an inertial force vector

If a spacecraft accelerates at a constant rate, then the direction of the acceleration vector can be used to define what is up and what is down. Inside the cabin, the acceleration produces what is called pseudo-gravity, which defines a ‘pseudo’ vertical – the direction parallel to the acceleration vector. Figure 7.12 helps to illustrate the idea. Panel A shows a spacecraft that is not accelerating; the side has been cut away so that we can see an astronaut inside. There is zero gravity, and the astronaut is shown floating freely in a position that is upright with respect to the cabin walls. If the drive rocket fires, the spacecraft will accelerate as indicated by the double-headed arrow in panel B. The spacecraft accelerates, but an astronaut who is not in contact with the cabin but floating within it does not accelerate. As a result, the shaded wall of the cabin accelerates towards the astronaut, who collides with it. From the astronaut’s point of view, the floor accelerating towards him is indistinguishable from him accelerating towards the floor, as if he were being pulled by a gravitational force.

![Figure 7.12: A rocket capsule in space. (A) The astronaut floats freely in the cabin. (B) The capsule accelerates in the direction of the arrow.](image)

If a spacecraft accelerates at 9.81 m/s² (the normal gravitational acceleration at the Earth’s surface), then the astronaut is unable to tell whether the craft is accelerating through space or sitting on the surface of the Earth unless s/he looks out of the cabin window. As first recognized by Albert Einstein⁶, someone inside a windowless cabin has no way to distinguish between the situations shown in panels A and B of Figure 7.13: everything inside the cabin behaves in exactly the same way in the situation shown in panel A as it does in panel B. For example, if the astronaut in the accelerating cabin in Figure 7.13B holds an object in one hand and releases it, he will see it fall to the floor in exactly the same way as an object falls to the floor when it is dropped on Earth. The difference is that on Earth the object falls because it is attracted to the Earth by the force of gravity, whereas in the spacecraft it is the floor of the cabin that is accelerating up towards the object. Without looking outside, the astronaut cannot know for sure which situation he is actually in.
From the foregoing discussion, we can see that an astronaut in a cabin accelerating through empty space at 9.81 m/s² experiences the situation exactly as does a person standing inside a stationary cabin sitting on the Earth. Consequently, from the astronaut’s point of view, there is a gravitational force; because it is not a real gravitational force it is called pseudo-gravity. The astronaut in panel B of Figure 7.13 is in an upright position with respect to the direction of pseudo gravity.

Pseudo gravity is an example of what is called a pseudo force or an inertial force in physics, a concept that many people find difficult to understand. In the study of human and animal movement, the latter term is more generally used. Inertial forces are not ‘real’ forces (like gravity) but arise because the frame of reference is accelerating. Within this frame of reference, a pseudo force behaves exactly like a real force and cannot be distinguished from a real force. Thus, gravity can be created artificially in a spacecraft simply by accelerating it. Accelerating in a straight line is not a very good way to create artificial gravity for a space station, because you have to keep accelerating, and so you move away from where you want to be at an ever increasing rate. Another way to produce artificial gravity is to make the spacecraft in the shape of a wheel, and spin it at a constant angular velocity.

An astronaut on the inside surface of the rim in a spinning space station is subjected to a real force applied to them by the rim itself. This force pushes the astronaut around in a circle (if the force were not there, the astronaut would move in a straight line; see Chapter 2, section 2.4.15). A force that acts to move something around in a circle is called a centripetal force, and it points towards the center of the circle. Although the centripetal force does not change the speed at which the astronaut is moving, it continuously changes his direction of motion, which is a kind of acceleration (a change in velocity) called the centripetal acceleration. This acceleration is also directed towards the center of the circle. Figure 7.14 shows an astronaut standing on the inner surface of the rim of a space station, with a double arrow representing the centripetal acceleration. From the astronaut’s perspective, there seems to be a force pulling him directly towards the rim; its direction is opposite that of the centripetal acceleration – away from the center of the circle. This is an inertial force called the centrifugal force. To the astronaut on the rim, the centrifugal force provides artificial gravity; the astronaut in Figure 7.14 is upright with respect to it.

The centrifugal force is not a real force; it arises due to the fact that the astronaut is in an accelerating frame of reference. It can also be experienced in more familiar terrestrial circumstances. When traveling in a car that turns a sharp left corner, you feel as if there is a force pushing you towards the door of the car. This is a centrifugal force. It arises because you are continuing to travel in the direction the car was going before it started to turn. As the car turns, you continue onward, and so find yourself heading towards the door or pressed up against it. In reality, there is no force pressing you against the door; it is simply that the door is preventing you from continuing to move in your original direction.
Figure 7.14: Artificial gravity in a spinning space station is provided by the centrifugal force ($a_c$ is the centripetal acceleration).

To summarize, we have seen that an upright orientation can be defined not only with respect to gravity (the vertical) but also with respect to the direction of inertial forces (pseudo gravity) that exist within an accelerating frame of reference. You may be asking what this has to do with adopting an upright orientation in a terrestrial environment. We address this question next.

7.2.2 The gravitoinertial force is the sum of gravitational and inertial forces

Whenever you accelerate, you are subject to inertial forces. Whenever you drive a vehicle and push on the accelerator to speed up, you will experience an inertial force – a force that seems to be pushing you back into your seat. When you push the brake to slow down, you experience an inertial force – a force that seems to be throwing you forwards out of your seat. In both cases, the inertial forces are not real forces but are consequences of your being in an accelerating frame of reference (the vehicle), and your tendency to keep moving in the way you were before the accelerator or brakes were applied. These two examples of inertial forces are encountered when your speed changes but not your direction of motion, and so they are similar to the inertial force experienced by the astronaut in panel B of Figure 7.12.

Figure 7.15: The gravitoinertial force acting on a person’s head is the vector sum of the gravitational and inertial forces.
Centrifugal forces are experienced whenever you change direction, whether driving a car or motorcycle, or riding in a bus, a boat or an airplane. In each case, the vehicle is accelerating because its direction of motion is changing. Unlike the astronaut, a person in an accelerating vehicle is subject not only to the inertial forces due to the acceleration, but to gravity as well. The inertial force adds to the gravitational force in the normal way to produce a combined force called the gravitoinertial force (usually abbreviated GIF). Figure 7.15 illustrates the idea for the case of a person’s head that is being accelerated forwards (to the left across the page) – the person might be a passenger in an aircraft that is accelerating along the runway prior to taking off. The vector sum of the gravitational and inertial forces yields the gravitoinertial force vector.

7.2.3 People should orient themselves so that they are upright with respect to the gravitoinertial force vector

In the normal standing posture, the body is oriented upright with respect to the gravitational force vector. When an astronaut stands up in an accelerating space vehicle or satellite when there is no true gravity, they adopt the normal standing posture, but are upright with respect to the inertial force vector (pseudo gravity).

![Diagram of forces acting on a person's center of mass in an accelerating train car.](image)

Figure 7.16: Forces acting on a person's center of mass in an accelerating train car.

In both true and pseudo gravity, if the standing posture were not upright with respect to the vector, the person would topple over. When both gravity and inertial forces are present, a person must stand upright with respect to the gravitoinertial force vector to avoid toppling over. For example, if a person stands in a train carriage as the train accelerates forwards, then they need to lean forwards so as to be upright with respect to the gravitoinertial force (GIF) vector, as shown in Figure 7.16 (the GIF vector is represented by the white arrow). If they did not lean forwards, they would fall over backwards. Similarly, when standing on a train as it goes around a bend in the track, a person needs to adopt an upright orientation with respect to the GIF, which is the sum of gravity and the centrifugal force. This is easier to do in a tilt-train, because as the train negotiates a bend, the train cars tilt so that the floor is perpendicular to the GIF. Figure 7.17 shows a cross-sectional cutaway of a tilt-train carriage as it negotiates a curve: a person is shown standing upright with respect to the GIF. If the person tried to stand upright with respect to the gravitational vertical when the train was going around a curve, they would risk falling over – in Figure 7.17 they would fall towards the higher side of the carriage.

A particularly clear illustration of people orienting themselves to the gravitoinertial force vector and not to gravity can be observed in a velodrome. The velodrome arena contains a steeply banked circular or oval cycling track. A cyclist traveling around the track at high
speed has a significant centripetal acceleration towards the center of the track and perpendicular to the direction of gravity. The cyclist is subject to gravity and a centrifugal force that sum to give the GIF shown in Figure 7.18. As the cyclists travel around the track, they orient themselves in the direction of the gravitoinertial force vector and may be quite tilted relative to gravity, as shown in the figure.

Figure 7.17: Cross-section through the car of a tilt-train as it travels around a curved section of track.

When traveling as a passenger in a tilt-train or in an aircraft you can usually tell when the train or plane starts to turn: your vestibular and somatosensory stimulation changes as the plane banks or the train tilts. Once the vehicle is traveling in a wide turn, however, you no longer have any vestibular or somatosensory information to tell you that you are going along a curved path. The cabin will be oriented to the gravitoinertial force vector, as in Figure 7.17 for the tilt-train: from the point of view of a person within the train car or airplane cabin, they are upright in an upright vehicle. If you looked out of the window of the train or plane, you might be able to see that the vehicle was actually tilted and traversing a curved path, but not necessarily: the plane might be in dense cloud, or it might be a pitch-black night outside. In such circumstances, it is impossible for a passenger to know whether they are traversing a curve or traveling in a straight line. The responses of the sensory systems in such conditions are the same as they would be if the person were traveling in a straight line, which is what they perceive to be the case.

Figure 7.18: A cyclist traveling around a curve on a banked track.
PART II  SENSORIMOTOR CONTROL

It does not really matter whether a passenger in an aircraft can tell whether they are traversing an extended turn or traveling in a straight line, but it does matter for the pilot. If the pilot were to act on the perception of traveling in a straight line when the plane was actually traversing a turn, then the plane could end up seriously off course. To avoid problems of this kind, aircraft are equipped with various devices that inform the pilot about the vehicle’s motion and orientation with respect to the Earth. Nevertheless, unless a pilot is properly trained and experienced, their perceptions may be so compelling that they act on them rather than on information from the instruments. In such situations, the pilot is said to be spatially disoriented. There are several situations in which spatial disorientation can have catastrophic consequences; one example will be described later (section 7.2.7), but first we will describe some relevant results from studies of human centrifugation.

7.2.4 The effects of changing the gravitoinertial force vector can be studied using the human centrifuge

People’s sensorimotor orientation to changes in the gravitoinertial force is often studied using a human centrifuge apparatus. This consists of a cabin mounted at the end of a beam that is spun around a central bearing by means of a large torque motor, as shown in Figure 7.19. The cabin moves around in a circle, and a person sitting in the cabin is subjected to gravity and to the centrifugal force produced by the spin. The person might sit facing the axis of rotation, as shown in panel A of Figure 7.19, or they might sit facing the instantaneous direction of travel, as shown in panel B. The centrifuge cabin in the figure has no windows, so the person cannot see out; in each panel of the figure, the side of the cabin has been cut away to reveal the person inside.

(A) Person in a ‘human centrifuge’ facing the axis of rotation.

(B) Person in a ‘human centrifuge’ facing the instantaneous direction of travel (perpendicular to the axis of rotation).

Figure 7.19: The human centrifuge apparatus.
Once the centrifuge is spinning at constant angular speed, the person in the cabin will be subjected to a gravitoinertial force vector that is not in line with gravity (as indicated in Figure 7.19). The angle between the GIF vector and gravity ($\theta$ in the figure) depends on the speed with which the centrifuge spins: the greater the speed, the larger the angle. Inside the frame of reference of the centrifuge cabin, the GIF vector is an artificial gravity (cabin gravity). In Figure 7.19 the person is not upright with respect to cabin gravity, but tilted through an angle $\theta$: in panel A he is pitched backwards with respect to cabin gravity, whereas in panel B he is roll-tilted to his left. His vestibular and somatosensory systems will be signaling that he is tilted with respect to cabin gravity. Given that the cabin has no windows so the person cannot see outside, they should feel that they are tilted, particularly if the cabin is dark inside. This is exactly what has been reported in experimental studies of the effects of centrifugation: people facing the axis of rotation feel pitched backwards; people facing the opposite direction feel pitched forwards. People facing the instantaneous direction of travel feel roll-tilted to their left; people facing the opposite direction feel tilted to the right. Panel A of Figure 7.20 shows the effect in cartoon form for a person facing the axis of rotation: the contents of the 'think bubble' indicate the person's perception of being tilted backwards. If the cabin is in darkness and the person's perception of the vertical (or horizontal) is assessed using a haptic, kinesthetic or visual orientation task (see section 7.1.4), then they indicate that the vertical is close to the direction of the GIF (horizontal perpendicular to it), and they typically show the same kind of A- and E-effects as they do when tilted in normal gravity. Panel B shows the visual effect in cartoon form for a person being centrifuged in darkness and facing the instantaneous direction of motion: the person feels tilted to the left, and a luminous line that is vertical with respect to gravity is seen to be tilted in the opposite direction (to the right).

Figure 7.20: Actual situation and the person's perception (in think bubble) during centrifugation.

The perceptions of body tilt in accelerating frames of reference are usually referred to as somatogravic illusions. The perception that the visual vertical is close to being in line with the GIF vector is usually referred to as an oculogravic illusion. The reasons for calling these perceptions 'illusions' is that the perceived orientation does not correspond to the orientation with respect to 'true' gravity. Figure 7.20 makes this clear: what the person perceives does not correspond to their orientation with respect to gravity (panel A) or the line's orientation with respect to gravity (panel B). However, from the point of view of the person in the accelerating frame of reference, these perceptions are not illusions at all: the person is tilted with respect to the GIF (which for them is gravity), and the line is tilted with respect to the GIF. The person's perceptions are in a frame of reference in which the GIF defines the vertical: in this frame, their perceptions are close to veridical. Thus, to call these perceptions 'illusions' is 'misleading, since no sensory deception is involved. There can be illusory perceptions of tilt as we will see in the next section, but those described above are not illusory. Non-illusory perception of body tilt in an accelerating frame of reference is better described as a somatogravic effect, and the non-illusory perception of the visual vertical being in line with the GIF as an oculogravic effect.
7.2.5 When the magnitude of the gravitoinertial force exceeds gravity, people perceive themselves to be tilted backwards

In the centrifuge cabin, the effective gravity (cabin gravity) is provided by the gravitoinertial force. As we saw in the last section, a person upright with respect to Earth's gravity is tilted with respect to the GIF vector, and they perceive themselves to be tilted accordingly. If this were the only effect of centrifugation, then the human centrifuge would simply be a very expensive and elaborate apparatus for tilting people with respect to 'gravity'. However, centrifugation does have other effects\(^{47}\), one of which is obvious from the force vector diagrams in Figures 7.15 to 7.20: the GIF vector is not only oriented in a different direction to the gravity vector, it is also longer. This means that the GIF is greater than the force of gravity: the human centrifuges used in the training of fighter pilots and astronauts are capable of subjecting a person to forces up to nine times the force of gravity. Thus, the centrifuge can be used to study the effects of increased gravity on a person.

![Diagram of centrifuge cabin and person](image)

Figure 7.21: A human centrifuge that is free to tilt aligns itself with the GIF vector.

The effects of increased 'gravity' can be studied independently of the effects of tilt with respect to the GIF, by using a centrifuge with a cabin that is free to rotate about a horizontal axis perpendicular to the radius of its circular path. A centrifuge of this sort is shown in panel A of Figure 7.21: as the cabin is spun around, it orients itself to the GIF, so the person seated inside is upright with respect to cabin gravity. Once the centrifuge is spinning at constant angular speed, a person in the cabin feels that they are tilted, and makes corresponding responses in orientation tasks even though they are upright with respect to cabin gravity. These perceptions of tilt are different from those experienced by a person spinning in a fixed-cabin centrifuge (Figures 7.19, 7.20). For example, a person facing the instantaneous direction of travel does not feel tilted to the left as they would in a fixed cabin centrifuge, but feels tilted backwards from an upright position, as indicated in panel B of Figure 7.21. If the person is
free to move, they lean forwards with the head and trunk by between about 25° and 30° to compensate for the perceived tilt. Once they have leant forwards by this amount, they no longer perceive themselves to be tilted. If they lean forwards further, they feel that they are tilted forwards and lean backwards to compensate. These perceptions can reasonably be called somatogravic illusions because when the person is actually sitting upright with respect to cabin gravity, they erroneously feel that they are tilted. When they are actually tilted forwards 25° to 30°, they erroneously perceive that they are upright. These illusory effects can all be accounted for in terms of the responses of the utricles to the increased cabin gravity, as described next.

7.2.6 The effects of centrifugation are largely due to altered vestibular stimulation

As described in Chapter 3, when a person’s head is upright, gravity displaces the otoconia of the utricles, which deflects the hair cells and so determines the afferent signals that reach the brain. In the cabin of a centrifuge, it is the gravitoinertial force (cabin gravity) that displaces the otoconia. Since cabin gravity is greater than normal gravity, the otoconia are displaced more by cabin gravity, which deflects the hairs further. The greater displacement of the otoconia would be produced in normal gravity if the head were tilted backwards. This corresponds to the person’s perception in a tilting centrifuge: a person seated with their head upright with respect to cabin gravity feels tilted backwards. Figure 7.22 presents a pictorial account. Panel A shows a person with head upright in normal gravity; their utricular maculae are tilted back by about 30° to the horizontal, and a component of the gravitational force (dotted blue arrow)

(A) Head upright in normal gravity.
(B) Head tilted backwards in normal gravity.
(C) Head upright in cabin gravity.
(D) Head tipped forwards in cabin gravity.

Figure 7.22: Actual situations and perceptions in normal gravity (left, panels A and B) and increased gravity (right, panels C and D).
acts on the otococia parallel to the macular surface, displacing them and deflecting the cilia of the hair cells. The afferent signal from the utricles specifies that the head is upright, which is what the person perceives. Panel B shows the person with their head tilted slightly backwards in normal gravity. The component of gravity acting on the otococia (dotted arrow) is larger and they are displaced further. The afferent signal specifies that the head is tilted backwards, which is what the person perceives. The panels on the right of the figure show two situations in the centrifuge cabin. In panel C, the person’s head is upright with respect to cabin gravity, and a component of the force acts on the otococia (dotted arrow). This component has the same magnitude as the component of normal gravity that acts on the otococia when the head is tilted backwards (the lengths of the dotted arrows are equal in panels B and C). Thus, the afferent signal from the utricles is the same in panels B and C, and the perception of head tilt is the same. This explains why a person feels tilted backwards in the centrifuge cabin of Figure 7.21.

Panel D of Figure 7.22 explains why a person feels upright in cabin gravity when they are actually leaning forwards. Leaning forwards reduces the magnitude of the component of cabin gravity acting on the otococia parallel to the macular surface. This component has the same magnitude as the component of normal gravity that acts on the otococia when the head is upright (the lengths of the dotted arrows are equal in panels A and D). Thus, the afferent signal from the utricles is the same in panels A and D, and the perception of head and body position is the same (upright). This assumes, of course, that the neural mechanisms that process utricular afference to generate estimates of head tilt are calibrated to normal gravity. In other words, these mechanisms associate a particular afferent signal with a particular head tilt that is appropriate provided gravity has the normal terrestrial value. If gravity is different, then the calibration is incorrect, and erroneous perceptions of tilt (somatogravic illusions) will result.

The effects described in this section can only be explained in terms of utricular stimulation; stimulation of other receptors that can contribute to perception of body orientation cannot explain them. The explanation in terms of utricular responses also predicts that the direction the person faces when sitting in the cabin of a centrifuge like that in Figure 7.21 should make no difference to their perceived body orientation: if the person sits upright, they should always feel tilted backwards, regardless of the direction they are facing. This is what is observed50.

7.2.7 Inertial forces can disorient pilots: the case of illusory ‘pitch-up’ during low-visibility takeoffs

People living untechnological lives will seldom be exposed to inertial forces that are more than a few percent of the gravitational force, and will probably never be exposed to sustained inertial forces that persist for longer than a few seconds. For this reason, people in the past would never have experienced somatogravic and oculogravic effects and illusions51. This is no longer true: in our modern era of motorized travel, people can be subjected to large, sustained inertial forces. This is most extreme for astronauts and fighter pilots, who may be exposed to inertial forces many times the force of gravity. Much smaller but still significant inertial forces are routinely experienced by the occupants of commercial aircraft during takeoff and landing and while turning. These forces can lead to spatial disorientation, with potentially catastrophic consequences. Here we will consider one example: a somatogravic effect produced during takeoff and its influence on pilot behavior52.

Figure 7.23 shows a plane traveling along a runway close to the point of taking off: the plane’s engines are running at close to full power, so as to accelerate the plane to takeoff speed. The fact that the plane is accelerating means that the pilot is subjected to a sustained inertial force acting in the direction opposite to the acceleration, as shown in the inset. The pilot is tilted backwards with respect to the gravitoinertial force vector, and so is the cockpit, as shown in panel B. Under these conditions, there is the possibility that a pilot will feel that he or she is tilted backwards (a somatogravic effect), and consequently that the plane is tilted
in a nose-high attitude. However, the pilot will be looking out of the cockpit windows and can see that the plane is traveling along the runway and is not tilted; the visual information dominates any somatogravic effects, and the pilot veridically perceives the plane’s orientation with respect to the Earth.

When the plane leaves the ground the situation is slightly different, because the plane will be starting to climb, so it will have a small vertical component of acceleration\(^\text{35}\). However, the plane will still be accelerating forwards, and the pilot will still be tilted backwards with respect to the gravitoinertial force vector. As before, this does not result in the pilot perceiving the plane to be tilted more than is actually the case, because he or she can still see the horizon and other visible features such as trees and buildings, which permits a veridical perception of the plane’s attitude. What we have described so far is the normal situation during a daytime takeoff, when the pilot can see how the plane is oriented with respect to the environment outside. Dark-night takeoffs or takeoffs into fog are a different matter, because the pilot may be unable to see anything outside. In this situation, the pilot has no sensory information about how the plane is oriented with respect to the outside environment.

Figure 7.23: When accelerating along the runway, the pilot is vertically oriented with respect to gravity, but tilted backwards with respect to the GIF.

Consider the dark-night takeoff situation in more detail. While the plane is traveling along the runway, the pilot will be able to see the runway lights, and so has visual information about the orientation of the plane relative to the ground. When the plane takes off, the runway lights quickly disappear from view: at this point the pilot may be unable to see anything outside the cockpit. If this happens, there is no longer any visual information to override the somatogravic effect: the pilot is tilted backwards with respect to the gravitoinertial force vector, and as a result feels tilted backwards more than is actually the case. Since the pilot is seated upright with respect to the cockpit, the pilot misperceives the plane to be tilted in a nose-high attitude. This can be classed as an illusion, because the plane is perceived to be more tilted than it really is; it is sometimes called the pitch-up illusion.

Figure 7.24 presents a pictorial illustration of the situation. The plane has just taken off, and the pilot cannot see anything outside the cockpit. He is tilted backwards with respect to the gravitoinertial force vector and so perceives himself to be tilted backwards (somatogravic effect), which leads him to perceive that the plane is tilted backwards more than is actually the case (pitch-up illusion). This perception can be very strong. The pilot’s natural tendency is to correct for the perceived excessive pitch-up of the plane by maneuvering the controls to bring the nose down. This is analogous to the leaning-forward response of people in the tilting centrifuge described in section 7.2.5. Bringing the nose down takes the
plane out of the climb, and the engine power goes into accelerating the plane forwards. The increase in forwards acceleration results in a greater inertial force, which increases the pitch-up illusion: so correcting for the perceived excessive tilt does not have the effect of eliminating it. If the pilot does not recognize that the perceived nose-up attitude of the aircraft is illusory, then further corrections will be made. These will quickly result in the plane plunging towards the ground. A cartoon representation of this sequence of events is shown in Figure 7.25.

The pitch-up illusion is clearly very dangerous, and a number of serious aircraft crashes are thought to have been a consequence of the pilot correcting for the illusory nose-up attitude during takeoffs when visibility was very poor. The pilot can avoid such accidents by relying on the flight instruments rather than the `seat of the pants' feel.

Figure 7.24: The pitch-up illusion arises in dark-night takeoffs as a consequence of a somatogravic effect (pilot feels tilted backwards).

Figure 7.25: Consequence of correcting for the pitch-up illusion.