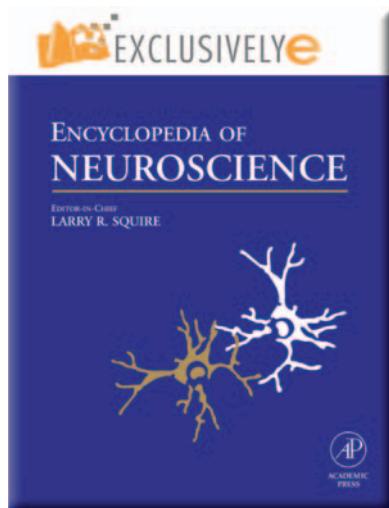


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Visual–Vestibular Interactions

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Introduction

The visual and vestibular systems together form a consortium that informs an organism about its motion and orientation relative to gravity. The visual and vestibular contributions are complementary, with each system tending to make up for inadequacies and ambiguities in the other. Their combined information is used for three main purposes: eye movement control, posture control, and perception. Other systems, such as the somatosensory system indicating the sites of pressure resulting from the weight of the body against a support surface, and the auditory system, can also inform about the relationship of the body to the world. This article concentrates on the use of visual and vestibular information in humans.

Visually Transduced Information Concerning Self-Motion and Orientation

The visual system provides continuous and usually unambiguous information about motion and orientation of the body relative to the world. However, visual information is subject to delays, because of the time needed for retinal processing and for combining signals across time and space to derive motion information. Visual information can also sometimes be irrelevant or misleading for deducing motion and orientation, such as when looking at anything other than features of the environment, for example, when watching films or looking at pictures. It is also subject to interruption in low light, during eye blinks, or when the eyes are closed.

Visual information about the movement of a person comes from the systematic displacement of the visual directions of all visible features as a consequence of movement relative to them. This pattern of motion is called ‘optic flow.’ Optic flow generated by ‘translation’ (movement from one place to another) contains enough information to determine in which direction a person is ‘heading.’ The direction of heading during translation can be determined from the location of the ‘focus of expansion’ of the optic flow, as JJ Gibson told us. When a person moves toward a particular point, the visual direction of that point (and the point in the diametrically opposite direction) does not change relative to the mover. The images of all other points move by an amount that depends on each

point’s angular distance from the heading direction and its distance from the observer. Because of this systematic arrangement, the location of the focus of expansion can be deduced from even a small area of visible optic flow. The relative distance a person has traveled (e.g., movement halfway to some visible object) can be extracted from optic flow. But determining the absolute distance (e.g., movement of 1 m) requires additional information about the distance of visible objects, since the motion of an object’s image on the retina depends not only on the velocity and direction of self-motion but also on these distances. There are therefore high computational demands in reconstructing the self-motion that created a given optic flow pattern. Furthermore, optic flow evokes compensatory movements of the eyes. This complicates the process of determining the underlying optic flow since the retinal motion is affected by both the movement of the eyes in the head and the overall motion of the person. Nonvisual information about compensatory eye movements can often be helpful, and in some cases is indispensable, for distinguishing these components.

Optic flow generated by ‘rotation’ (movement that does not involve an overall change in position) contains information about the axis of rotation and instantaneous rotational velocity. This also has to be interpreted in the context of evoked eye movements which can remove most of the rotational optic flow from the retinal image. Optic flow can be experienced in the absence of physical motion, for example, when a neighboring car or train moves. Such visual movement can generate a compelling sensation of self-motion called ‘vection.’ Vection can have both translational (‘linearvection’) and rotational (‘circularvection’) components and generally takes several seconds to build up. The onset ofvection is speeded by the presence of actual motion even if it is a pulse or a vibration unrelated to the self-motion signaled by the optic flow.

Visual information relevant to orientation of a person relative to gravity includes: (1) the ‘visual frame,’ comprising the ground plane and the view of features known to be approximately vertical or horizontal relative to gravity, such as trees, walls, ceilings, and floors; (2) the orientation of the ‘visual horizon’; (3) the assumption that light generally comes from above; (4) ‘support relationships’ between objects, determined by the laws of physics, such as objects resting on other objects or supported by the ground; and (5) ‘visual polarity’ cues of objects with recognizable tops and bottoms such as faces, lamps, and chairs that have a most-familiar orientation relative to gravity. Some of these properties, such as the direction from

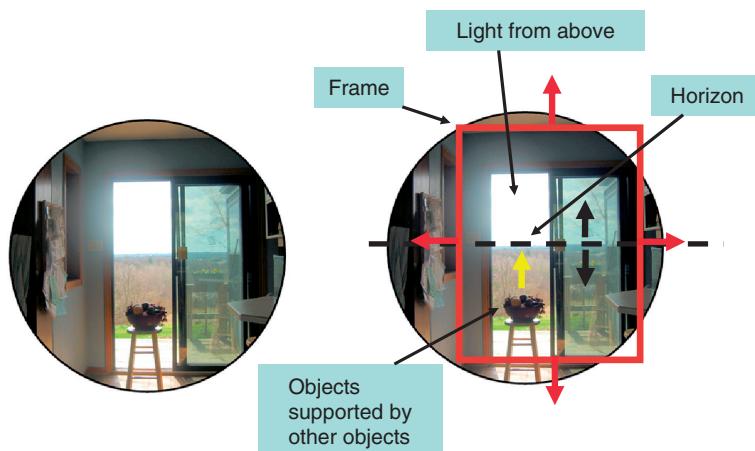


Figure 1 A photograph of a typical scene showing examples of the various visual cues to the direction of gravity. On the right, the possible directions reported by the cues in the photograph are detailed. The four possible directions of gravity signaled by the frame, defined by the orientation of the walls, floor, ceiling, and window stripped of their other cues, are indicated by red arrows. The two indicated by the horizon are shown in black, and the unique direction signaled by the relationships of objects in the world (e.g., the fruit bowl on the stool), the expected orientation of objects (fruit bowl curved side down), and light coming from above is indicated by the yellow arrow.

which light comes or the orientation of the horizon, could have a recognition mechanism with an innate component; others must be learned by association, such as the orientation of writing on advertising signs. **Figure 1** illustrates some of the visual cues that are available to specify orientation in a typical scene.

Figure 1 also illustrates that the various visual cues to orientation have greater or lesser degrees of ambiguity. The frame structure of a room, stripped of visual polarity and support relationship cues, indicates four possible directions of gravity; the horizon indicates two possible directions; whereas the direction of illumination, support relationships, and visual polarity cues signal only one unique possibility.

Vestibularly Transduced Information Concerning Self-Motion and Orientation

The ‘vestibular system’ comprises two sets of mechanical sensors, both of which are activated by physical force. Force, as Isaac Newton told us, is the product of mass and acceleration. Thus, the vestibular system can only detect motion that involves acceleration: movement at a constant speed cannot stimulate the vestibular system. The ‘semicircular canals’ detect angular acceleration of the head, and the ‘otoliths’ detect linear acceleration. Gravity, as Albert Einstein told us, is equivalent to an upward linear acceleration of 9.8 m s^{-2} , and so the vestibular signal also contains information about the orientation of the head relative to gravity.

Since the vestibular system is sensitive only to acceleration, position and velocity information need to be derived from the acceleration. However, such a derivation can only provide relative values of position

and velocity for both rotation and translation. For example, the changes in linear velocity (i.e., acceleration) from 10 to 20 m s^{-1} ; 0 to 10 m s^{-1} ; -10 to 0 m s^{-1} ; and -20 to -10 m s^{-1} are all the same although the final velocities are very different. Before the invention of modern modes of transport, the assumption that the starting velocity was close to 0 was more or less valid, but even so, the need to add assumed starting values makes the vestibular system fundamentally unsuited for tasks such as keeping track of position and orientation during translation and rotations in space. Many disorientation illusions related to aviation can be traced to this limitation.

It might be thought that the constant pull of gravity would provide a reference direction to which the perception of self-motion and orientation could be anchored. However, since gravity cannot be distinguished from linear acceleration, a given signal from the otoliths organs is ambiguous. This signal could be produced by any one of an infinite number of combinations of linear accelerations and tilts of the head as shown in **Figure 2**. Since the accelerations of everyday life are not generally confused with tilt, the gravity vector must somehow be subtracted from the signal. The direction of the gravity vector can be obtained from the visual cues described above.

However, solving the geometrical problem of the double vector requires knowledge not only of the direction of gravity, but also of its magnitude. If its magnitude is not available, then, when acceleration with a component orthogonal to gravity is experienced, it is hard to distinguish the resultant vector from gravity alone after an appropriate tilt of the head. This is the ‘tilt-translation’ ambiguity. The two eventualities

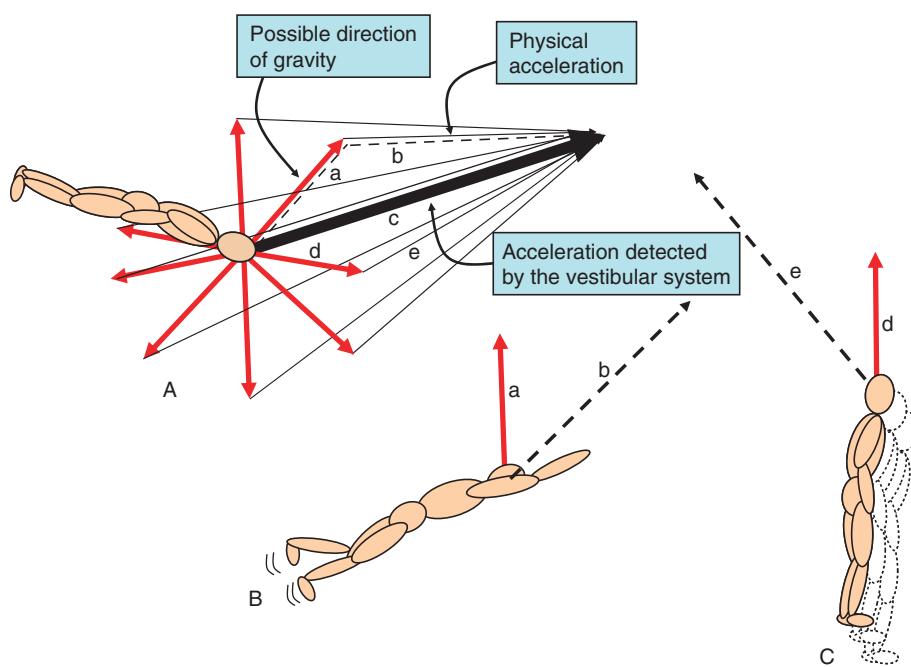


Figure 2 (A) The acceleration vector transduced by the vestibular system (thick black arrow) is the resultant of gravity (red arrows) and physical acceleration (thin black arrows). The lengths of the arrows represent the magnitudes of the accelerations. The components cannot be reconstructed unambiguously from the resultant. Several possible solutions out of an infinite, three-dimensional set are illustrated in (A). The person experiencing these accelerations is shown in a random orientation, since their orientation relative to gravity is determined by the solution of this geometry. (B, C) Show two possible solutions that are labeled by dotted lines labeled 'a' and 'd' for gravity, and 'b' and 'e' for the physical accelerations corresponding to the resultant 'c' as sensed by the vestibular system. The labeled vectors are the same (relative to the observer) in (A), (B), and (C).

illustrated in [Figure 3](#) can be distinguished by knowledge of magnitude, by detecting the preceding tilt, or by additional knowledge about the direction of gravity. By providing both rotation and direction cues, vision provides the most reliable way of solving the tilt-translation ambiguity. The fact that gravity is equivalent to acceleration thus requires visual–vestibular interactions to indicate the direction of an imposed acceleration and to indicate the pose of the head relative to gravity.

Despite these limitations to working effectively on its own, the vestibular system does have the advantage of always being available for the detection of accelerations greater than a certain minimal amount and of gravity: there is nothing equivalent to closing the eyes for the vestibular system. Also, the vestibular system is extremely fast, providing a signal to the brain in just a few milliseconds.

Visual–Vestibular Interactions for Determining the Direction of Translation

Vestibular information concerning the direction of head translation is highly ambiguous (see [Figure 2](#)). When visual and vestibular cues to direction are put in conflict (e.g., with prisms or virtual reality displays), the perceived direction of motion is dominated

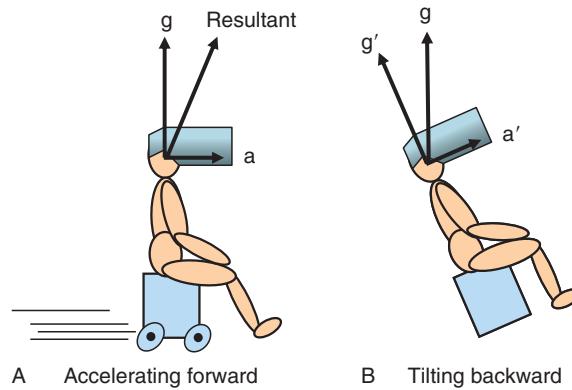


Figure 3 Tilt-translation ambiguity. Because gravity (g) is equivalent to an acceleration, when accelerating physically forward (A) a person is subject to two simultaneous stimuli that combine to produce a vector ('resultant'). A subject tilted backward (B) experiences gravity in that same direction. The only differences between the cues sensed by the otolith organs are the absolute magnitudes (always greater than g for (A) and less than g for (B)) and the history of what happened immediately leading up to these situations. However, they can be easily disambiguated by vision. The person illustrated here is wearing a virtual reality helmet in which visual environments can be simulated that attempt to encourage one or other interpretation.

by the visual cue, so much so that even if the actual physical motion (the vestibular cue) is opposite to the optic flow, the perceived direction is determined by vision. There are no significant visual–vestibular

interactions in the determination of the perceived direction of translation. This is supported by the observation that perceived motion direction (even when not generated by self-motion) is not affected by concurrent linear vestibular stimulation.

Visual-Vestibular Interactions for Determining the Magnitude and Velocity of Translation

Neither optic flow nor vestibular signals indicate either the absolute distance traveled or the velocity of self-motion, but the consortium is able to estimate distance traveled by combining information from the different sources. Vision can provide the starting position and velocity estimates that are lacking in the vestibular signal. The vestibular signals produced by active self-motion (e.g., walking) of a planned magnitude can, however, provide a rough scale. When transported passively in the dark (vestibular information only), or when motion is simulated by viewing optic flow while physically stationary (linearvection; vision only), the perceived distance of travel is generally further than the motion experienced, especially for distances further than a few meters with a low acceleration. Artificial combinations of visual and vestibular cues of different magnitude presented, for example, using virtual reality simulations, reveal an averaging of the two signals with a greater weighting of vestibular information when motion is in the operating range of the vestibular system (above about 0.1 m s^{-2}).

Attempts to influence the perceived distance of linearvection by tilting a subject, thus applying a component of gravity in the plane of optic-flow-induced movement (see [Figure 3](#)), have been unconvincing.

Visual-Vestibular Interactions for Determining Tilt

When forced to rely on the vestibular system, for example, when suspended in water with eyes closed that effectively removes somatosensory pressure cues, subjects can orient themselves either vertically or horizontally relative to gravity to within about 5° with no systematic biases. This ability to detect tilt of the body relative to gravity is a measure of the 'postural vertical.' Systematic errors appear, however, when aligning a line of light with the perceived direction of gravity to indicate the 'subjective visual vertical' while tilted in an otherwise dark room. Small tilts of the body (e.g., 10° to the left) can cause the line to be set in the opposite direction (e.g., 2° right of true vertical), a rather small and variable effect known as 'the E-effect' (for *entgegengesetzt*, German for opposite). Larger tilts, beyond about 60° , usually cause the line to be tilted away from true vertical but in the

same direction as the tilt (known as the 'Aubert or A-effect'). The 'perceptual upright,' the orientation at which visually polarized objects such as faces, animals, or letters appear correct and are most easily and speedily recognized, is also subject to an A-effect.

The perceptual vertical, subjective visual vertical, and perceptual upright are all influenced by visual cues concerning the direction of gravity, as well as by the vestibularly transduced physical direction. Subjects, especially children, can be induced to sway by moving the visual environment indicating the effect of vision on the postural vertical. How the subjective visual vertical and perceptual upright can be measured is illustrated in [Figure 4](#) and the effect of visual background and of physical tilt on these two measures is illustrated in [Figure 5](#). The A-effect exhibited by the perceptual upright is substantially larger than that induced in the subjective visual vertical. This is shown in the figure by the distance of the judgments from the 90° line (which corresponds to the veridical direction of gravity relative to the subject) when lying on one side. The effect of the visual background, indicated by the depth of modulation, is larger for the perceptual upright than the subjective visual vertical. Although compensatory rotation of the eyes in response to head tilt might play a small role in these effects, it cannot account for the differences between the two measures. Misalignments of the subjective visual vertical or the perceptual upright from the true direction of gravity indicate that the relevant perception of 'up' arises from a weighted sum of the different cues to 'up'. These cues include (1) the orientation of the body axis, which seems to be known since it can be accurately aligned with gravity in the absence of other cues; (2) visual cues to vertical (described in detail above and in [Figure 1](#)); and (3) the otoliths' gravity signal. The perceived orientation of the body is qualitatively different from the other cues as it cannot be sensed directly but is an internal representation. The representation of body orientation is often referred to as the 'idiotropic vector' or the 'M-vector' after Horst Mittelstaedt, who first developed this concept. The orientation of the subjective visual vertical and the perceptual upright can be approximated by linear weighted sums of these three vectors: vision, body axis, and gravity, as illustrated in the lower part of [Figure 5](#). The orientation of the visual and idiopathic cues has relatively little effect on the subjective visual vertical, but the perceptual upright is influenced approximately equally by all three cues.

If a subject is tilted relative to gravity with an acceleration below the semicircular canals' detection threshold (no vestibular cues to the reorientation) and the visual cues to orientation are moved along

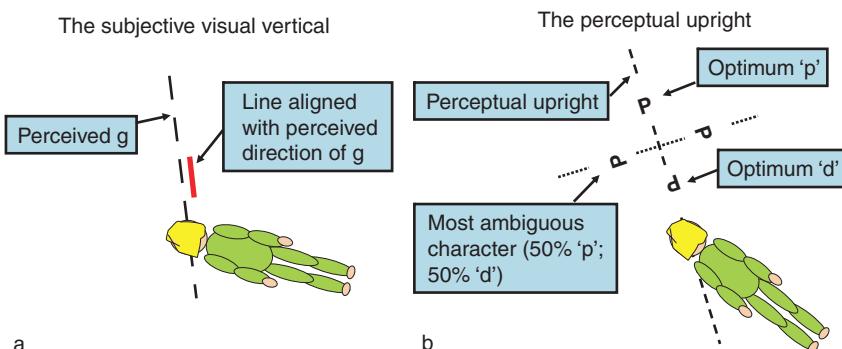


Figure 4 The subjective visual vertical (a) and the perceptual upright (b). These two measures can be used to assess the effect of visual and vestibular cues on perceived orientation. To assess the subjective visual vertical, subjects align a line with the perceived orientation of gravity. Performing this task requires introspection and estimation. The perceptual upright can be assessed by having subjects identify a character or shape the identity of which depends on its orientation. The direction between the orientations of maximum ambiguity (most easily detected psychophysically as the 50% correct identification point) indicates the perceptual upright: the orientation at which objects are most easily recognized

with the subject (visual cues indicate no tilt), then the direction of gravity is not perceived to move during the tilt. This is most easily arranged in a rotating room. For subjects who have been tilted onto their backs, objects hanging from the wall in front of them now appear to levitate as they hang under the influence of gravity, giving the illusion its name, the 'levitation illusion.' The levitation illusion demonstrates the importance of visual and semicircular canal cues for updating the internal representation of gravity. If those cues are absent, even in the presence of a 90° change in the direction of gravity, the perceived direction of gravity can remain unchanged.

When a textured background lacking visual cues to gravity is rotated around the line of sight of an upright observer, it produces a paradoxical perceptual effect in which subjects feel they are rotating constantly, but at the same time statically tilted. This is because of an anchoring effect of gravity (which indicates no tilt). When the same background motion is around an axis aligned with gravity, or when the strength of the visual cues is increased by using a scene rich in frame, horizon, lighting, polarity, and support relationship cues, continuousvection is often experienced.

(undetected) constant velocity axis produces illusory rotation about an axis orthogonal to both of them. Curiously, tilting one's head (or moving the visual stimulus) during constant velocity circularvection can also evoke complementary complex effects, known as 'pseudocoriolis illusions.'

Visual–Vestibular Interactions for Determining the Amplitude of Rotation

The sensation of rotation from vision alone, circularvection, takes several seconds to build up, but it increases at the same rate that the vestibular response to an actual body rotation decreases. Thus, when rotating in the light a relatively accurate response made up of visual and vestibular components is maintained. This complementarity is reflected in the visual and vestibular responses of cells in the vestibular nucleus. Spinning people around is a classic way of disorienting them: children are intuitively aware that the vestibular system cannot signal position. However, for short-duration rotations, such as natural head movements, the vestibular system is capable of deriving the size and direction of the movement. Even this feat, however, may need help from higher cognitive centers since, when head movements are performed in the dark, only if an Earth-stationary target is imagined can appropriate eye movements be generated. If a small, subject-stationary target is provided as a subject accelerates angularly, the target appears paradoxically to be both moving in orbit around the subject's head, and at the same time not to be advancing from the straight ahead position. This is the 'oculogyral' illusion and might be connected to failures of the process involved in deducing the linear speed of an object under such unnatural conditions.

Visual–Vestibular Interactions for Determining the Axis of Self-Rotation

Determining the axis of self-rotation from vestibular cues alone is also complicated by the vestibular systems' exclusive sensitivity to acceleration: constant velocity rotations are not sensed after the response to the initial acceleration has died away (after about 20–30 s). Subsequent rotations around other axes can then produce complex 'Coriolis effects,' in which, predictable from the laws of conservation of angular momentum, rotation about an axis orthogonal to the

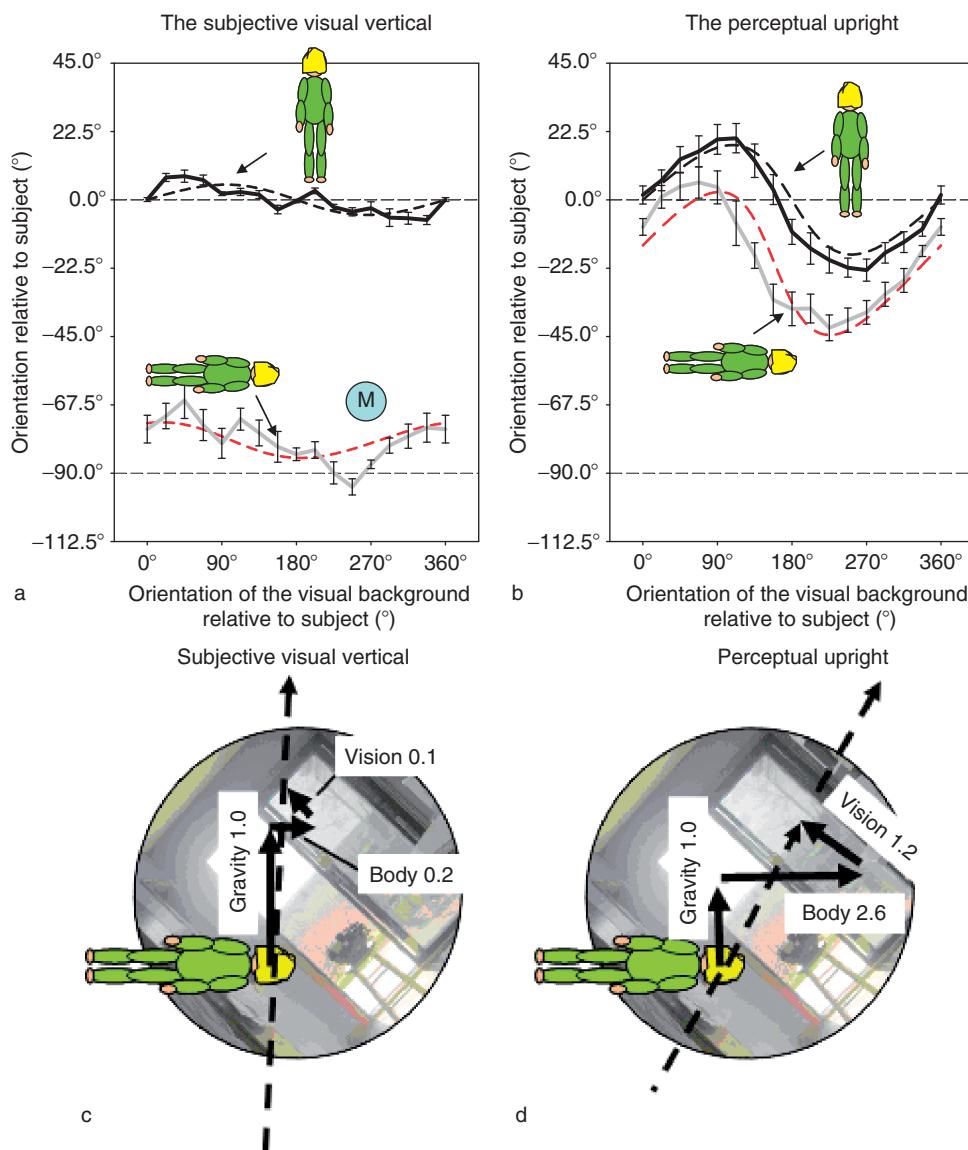


Figure 5 How the perceptual upright and the subjective visual vertical vary with visual and vestibular cues. The graphs plot the orientation of the subjective visual vertical (a) and the perceptual upright (b), relative to the subject, as a function of the visual background for two body orientations, upright and right side down. The subjective visual vertical is less influenced by vision and more influenced by gravity than the perceptual upright. Fitted through the data is the output of a simple, weighted, linear model illustrated in panels (c) and (d) where the lengths of the three vectors are weighted as shown. Data from Dyde RT, Jenkin MR, and Harris LR (2006) The subjective vertical as a function of visual and extraretinal cues. *Acta Psychologica* 63: 63–85 where subjects lay in a room oriented earth vertically.

Suppression of Visual Responses by Vestibular Signals

Perception of visual motion in general is suppressed by concomitant angular or linear vestibular stimulation. This may be related to the use of optic flow resulting from the visual background motion to inform about self-motion. The suppression may be related to mutual inhibitory pathways between vestibular and visual cortical areas. Motion thresholds are increased during rotation but curiously seem to be

elevated most during motion in the direction opposite to that of the associated optic flow. For example, when moving to the left, visual motion to the left is more suppressed.

Suppression of Vestibular Responses by Visual Signals

Although under natural circumstances visual and vestibular cues to motion are usually complementary and, within the constraints described above,

redundant, they can also frequently be opposed to each other. For example, reading a newspaper in a moving vehicle or while walking requires fixation on the paper, not on Earth-stationary features. Visually controlled eye movements, including those involved in stabilizing the image, now work on the subject-stationary image of the paper, whereas the vestibular system is simultaneously required to guide locomotion and to maintain balance. This feat of suppressing vestibular cues for some aspects of perception while simultaneously using it for others can only be successfully carried out at frequencies below about 0.5 Hz and probably only by primates with well-developed smooth pursuit capability. At higher frequencies of movement, eye movements of vestibular origin cannot be suppressed by vision and attempts to fixate on near objects will generate large compensatory eye movements appropriate for maintaining gaze on something that remains Earth stationary, even in the presence of subject-stationary objects.

The Detection of Conflict in Visual–Vestibular Interactions

In many documented instances, information that arises from different senses is combined linearly using a weighted average where the weights are assigned according to the reliability of the contributing sources. This is true for visual–vestibular combinations for both the distance traveled and the perception of orientation (as described above). A linear combination does involve an interaction since the response to both cues can be predicted from the responses to either of the two cues alone. However, conflict between visual and vestibular signals can be independently detected, leading to long-term adaptive changes, especially significant for calibrating vestibular responses as measured subsequently in the dark and, in the short term, to the too-well-known symptoms of motion sickness. Conflict detection is a nonlinear process with its own detection threshold. The nonlinear conflict detection process is a process parallel to the examples of visual–vestibular cooperation described above.

Conclusions

For the detection of self-motion, either rotational or translational, both the visual and the vestibular systems have their weaknesses, which are largely

overcome when both signals are present. However, even when both systems are present, systematic errors in assessing velocity and displacement are still found. It may be necessary to include additional sensory and extrasensory information, such as anticipation, prediction, and ‘efference copy’ of active motor commands to reach natural performance levels.

In assessing orientation, neither visual nor vestibular systems are directly sensitive to gravity. Both must rely on observing the effects of gravity on objects: either on the stones within the inner ear’s labyrinth (detected by the hair cells of the vestibular system) or on objects in the environment (detected by the visual system). There is a weighted average of the cues involved in which more weight is placed on the more reliable cues.

The visual–vestibular consortium provides a best estimate of self-motion and orientation cues that enable us to interact effectively with our environment.

See also: Canal–Otolith Interactions; Optokinetic Eye Movements; Sensorimotor Integration: Models; Spatial Orientation: Our Whole-Body Motion and Orientation Sense; Vestibular Influences on Cognition; Vestibular System; Vestibulo-Ocular Reflex; Vision: Mechanisms of Orientation, Direction and Depth.

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