Vestibular Signals in Self-Orientation and Eye Movement Control

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The central vestibular system receives afferent information about head position as well as rotation and translation. This information is used to prevent blurring of the retinal image but also to control self-orientation and motion in space. Vestibular signal processing in the brain stem appears to be linked to an internal model of head motion in space.

Vertebrates possess two kinds of vestibular organs: the otolith organs, which are specialized to detect static head tilt (i.e., gravitational acceleration) or transient head displacements (i.e., linear accelerations), and the semicircular canals, which detect rotational transients (i.e., angular acceleration). During evolution, animals optimized vestibular signal processing in different ways for controlling self-orientation and motion in their habitats. Because vestibular information reaches the brain at much shorter delays than visual signals, typically in a few milliseconds, it is fundamental in the neural control of eye, head, and body posture. The evaluation of vestibular acceleration signals represents a major challenge to the brain's integrative capacity of motion processing because the otoliths, like man-made technical linear accelerometers, do not discriminate between gravitational and inertial forces. Gravitational forces displace the otoliths as a function of the head's orientation relative to gravity, whereas inertial forces oppose the motion of otoliths when the head changes its state of motion (Newton's first law). According to Einstein's General Theory of Relativity, both forces are physically equivalent (Einstein's Equivalence Principle; see Ref. 5). Thus a backward tilt of the head, which changes the head's orientation relative to gravity, can generate an afferent response pattern that the brain cannot discriminate from the afferent input due to a forward displacement of the head (Fig. 1, A and B).

When the head moves passively and vision is blurred, the central nervous system can be easily fooled about the real head motion in space, particularly if it only has access to vestibular motion signals. Obviously, ambiguous information about self-orientation and motion can have fatal consequences. At the perceptual level, illusionary tilt or heading sensations are a well-known danger in aviation. Thus jet pilots are instructed to rely on the artificial horizon rather than their tilt perception during takeoff. To minimize the risk of disorientation, the central nervous system integrates motion information from many sensory channels, including visual and somatosensory cues, a process called multisensory fusion.

Fusion of otolith and semicircular canal signals

Many mechanisms have been proposed to explain how the brain integrates diverse sensory information. The ambiguity of otolith afferent signals can be resolved within the vestibular system by correlating the otolith signals with head velocity information from the semicircular canals, a process that can be very fast. There exist rigorous mathematical algorithms that allow discrimination of the inertial and gravitational components in a signal, which represent the vector sum of gravity and inertial forces (so-called gravito-inertial signal; Fig. 1C; see Ref. 17). These algorithms work reliably provided that the graviceptive signals from the otoliths that serve as spatial reference even when they do not exactly indicate the true direction of the vertical (3). More recently, studies of the vestibuloocular reflex (VOR) have provided new insight into the central processing of otolithic and semicircular canal signals that underlie spatial orientation responses. Such responses are usually elicited by rotational head movements in a non-earth-horizontal plane (so-called off-vertical-axis rotations) that change eye, head, and body orientation relative to gravity.

Gyroscopic control mechanisms of self-orientation in space

The otolith organs provide the most important information about self-orientation relative to earth vertical. The use of this information in gaze control depends on how animals move and explore their visual environment. Animals with an almost panoramic view of the visual world, such as frogs or rabbits, can scrutinize the visual environment without significantly
The brain stem network \( N_s \) filters and transforms semicircular canal (SCC) acceleration signals by processing semicircular canal and otolith information. Before considering this issue, I shall briefly outline the orientational load for updating self-orientation relative to space would certainly become impracticable. It has been known since the last century that visually guided saccades are subject to kinematic constraints known as Listing's law (7, 16) that in fact restrict the rotational degrees of freedom of the eye. This law implies that the angular velocity of a saccade (which could be represented by a vector parallel to the axis of rotation) must lie in a particular plane, the so-called velocity plane of the eyes. Most interestingly, the orientation of this plane is not fixed for the head for a given gaze direction but rather depends on the current head orientation relative to gravity. For example, in an upright head position the velocity planes of the two eyes are approximately parallel to the frontal plane. However, when the head is moving, for example during locomotion, Listing's law is modified or superseded by strategies that are still not well understood today. An important consequence of Listing's law is that the velocity plane of the eye must systematically change.

moving their heads and eyes. The visual system in these species receives most of its input from a stripe of retinal ganglion cells that are close-packed along the horizontal retinal meridian (visual streak). To keep the visual streak invariant in space, the eyes must be stabilized against disturbances of head and body position in all three rotational degrees of freedom. At rest, the otolith-ocular reflexes are optimally suited for this task. They maintain ocular orientation relative to gravity in a feedforward loop, like a gyroscope that controls the artificial horizon and displays the rolling and pitching motion of the aircraft. The canaloculocerebellar reflexes supplement these basic orientation reflexes by minimizing retinal image slip during head movements. They also control the eye during eye-head saccades, which quickly redirect the center of the visual field. In addition, optokinetic reflexes minimize ocular drift velocity by processing signals from direction-selective retinal ganglion cells, which detect slippage of the visual world image over the retina with high sensitivity (14).

Vestibular control of self-orientation in space is organized differently in frontal-eyed animals with foveal vision. Although the eye's orientation is no longer under strong otolithic control (13), it is the angular eye velocity that is controlled in gravity-centered coordinates like the spinning axis of a gyroscope. Before considering this issue, I shall briefly outline the orientation strategies of foveated animals and their consequences on gaze stabilization. Animals with foveal vision typically scan their visual environment by redirecting their gaze every few hundred milliseconds by the use of saccadic eye movements. Saccades allow quick acquisition of targets of interest in the visual field. The restriction of a panoramic visual field to a small foveal area with high visual acuity in frontal-eyed animals requires new strategies for estimating the orientation of retinal coordinates relative to space. If eye orientation remained indeterminate because it could assume any of infinitely many torsional orientations after a saccade, the computational load for updating self-orientation relative to space would certainly become impracticable. It has been known since the last century that visually guided saccades are subject to kinematic constraints known as Listing's law (7, 16) that in fact restrict the rotational degrees of freedom of the eye. This law implies that the angular velocity of a saccade (which could be represented by a vector parallel to the axis of rotation) must lie in a particular plane, the so-called velocity plane of the eyes. Most interestingly, the orientation of this plane is not fixed for the head for a given gaze direction but rather depends on the current head orientation relative to gravity. For example, in an upright head position the velocity planes of the two eyes are approximately parallel to the frontal plane. However, when the head is moving, for example during locomotion, Listing's law is modified or superseded by strategies that are still not well understood today. An important consequence of Listing's law is that the velocity plane of the eye must systematically change.

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with gaze direction. The rule is simple and says that a change in gaze direction through a given angle changes the orientation of the associated ocular velocity plane in the same direction by half of that angle. How this curious constraint interferes with gaze stabilization will be explained below.

**Visual orientation vs. optimal gaze stabilization**

Although the restriction of eye velocity vectors to particular planes could facilitate self-orientation in space, it is incompatible with perfect stabilization of the retinal image against disturbances of head position. To stabilize gaze in space, the VOR must counteract disturbances in the plane of the imposed head rotation, independent of the current ocular orientation and gaze direction. Thus the commanded eye velocity must be equal and opposite to the head velocity if the VOR is to keep the orientation of the eyes perfectly invariant relative to space (Fig. 2). In contrast, if the VOR were to satisfy Listing’s law its compensatory action must be restricted to a subset of head movements, namely to those whose rotational plane does contain the current gaze vector. The worst case in such a scenario is roll (side to side) head movements, during which retinal image stabilization requires a compensatory rotation of the eye about the roll (or nasooccipital) axis. In this case, the VOR should command an eye velocity that is almost perpendicular to the admissible velocity plane according to Listing’s law. In contrast to rhesus monkeys, which perfectly stabilize their entire visual field even during roll rotations in violation of Listing’s law (Fig. 2C), the human VOR does not follow this optimal stabilization strategy (11, 12). Because of its dependence on gaze direction, in the worst case it only compensates retinal image slip in a very restricted area. The underlying strategy is to minimize retinal image slip over the fovea while maximizing compliance with Listing’s law (11, 12). Until now, Listing’s law of eye movements has not found a completely satisfactory explanation (7, 8, 15) because little is known about its role in the freely moving subject. Similarly, it is unclear why the human VOR follows a compromise strategy between optimal gaze stabilization and compliance with Listing’s law. On the other hand, one may ask why rhesus monkeys do not compromise the VOR. One reason could be that the selective stabilization of the foveal image handicaps too much simultaneous control over the peripheral visual field, which is important for survival of these animals. Indeed, the human compromise with Listing’s law results in blurring of peripheral vision. This effect is most noticeable during disturbances of head roll orientation while the subject is looking at targets to the side (11).

**Neural representation of vestibular self-orientation signals**

In neural control of balance and posture, the ubiquitous gravitational field provides a crucial reference. Such reference can be updated in the vestibular system very rapidly to follow changes of the subject’s self-orientation relative to earth vertical. For this, only two angular parameters are required, one parameter to specify the azimuth of the tilt plane relative to the head (for example, relative to the head’s midsagittal plane) and another parameter to specify the angle of head tilt in this plane. A similar set of parameters would be needed to represent head position and angular head velocity signals relative to gravity. Recent work on the optokinetic reflexes and VOR suggests that this is true for the internal representation of postrotatory eye velocity, which orients toward gravity (1, 4, 9). The issue of a space-referenced vs. head-fixed coding of vestibular signals...
was first addressed by Purkinje in his pioneering experiments on vertigo more than 150 years ago (for a review of these experiments, see Ref. 6). With the advent of precise three-dimensional eye movement recording techniques, this question has been quantitatively studied in the VOR. An example of a postrotatory response is illustrated in Fig. 3, A and B, for a VOR elicited by constant-velocity rotation (at 60°/s) around the head vertical axis, which had been tilted by 24° off earth vertical. When head rotation was stopped (Fig. 3A), not only a horizontal but also smaller torsional and vertical response components emerged, indicating that the canal-induced eye velocity signals are referenced to space rather than to the head. Clearly, if head motion were coded in a head-fixed reference, eye velocity would align with the head vertical axis independently of final head orientation. The alternative assumption that head velocity is coded relative to space (i.e., in gravity-centered coordinates) predicts that at stop of rotation the VOR breaks up into components that reflect the final head orientation relative to gravity. In the illustrated example, the head had been stopped at a position between nose down and left side down. In pure nose-down orientation the VOR should brake up into a horizontal and torsional component (see Fig. 3B, top), whereas in side-down position it should resolve into a horizontal and a vertical component (Fig. 3B, middle). Because the head came to a stop in between these two orientations, the postrotatory VOR slow phase velocity exhibits three components, as illustrated in the three different views in Fig. 3B. The ratio between these components determines the spatial orientation of eye velocity. A systematic comparison of such responses with the actual direction of gravity reveals a close alignment of postrotatory velocity with the direction of gravity (Fig. 3B). The experiments also reveal that it is the tilt plane that is reflected with remarkable precision (Fig. 4A), whereas the angle of head tilt is often underestimated (Fig. 4B; see also Ref. 4).
brain stem extracts head velocity information from dynamic otolith signals to back up the response of semicircular canal afferents whose modulation eventually subsides during constant-velocity rotation. Consistent with experimental findings, these signals are low-pass filtered before contributing to total eye velocity in the postrotatory response (Fig. 4C).

A closer look at the postrotatory VOR reveals interesting details about vestibular signal processing. It shows that the postrotatory VOR results in general from a superimposition of three different signals: a direct-velocity signal originating from the semicircular canals in response to head deceleration, a decaying otolith-born head velocity signal reflecting the previous head rotation in space, and a low-pass filtered canal-born velocity signal reflecting a space-referenced head velocity signal.

**Conclusion**

Recent work on vestibular signals in eye movement control has shown that the VOR not only keeps the eyes’ orientation invariant in space to avoid blurring of the retinal image of the world but also supports self-orientation in space. To facilitate locomotion, head acceleration and velocity signals are centrally represented in a network that is organized in space coordinates and provides a common reference for multisensory integration.

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**References**

3. Brindley GS. How does an animal that is dropped in a non-upright posture know the angle through which it must turn in air so that its feet point to the ground? (Abstract). *J Physiol (Lond)* 180: 20P, 1965.