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DYNAMICS OF THE VESTIBULAR SYSTEM AND THEIR RELATION TO MOTION PERCEPTION, SPATIAL DISORIENTATION, AND ILLUSIONS

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ABSTRACT

In piloting tasks, visual observation of instrument indicators and of the visual field, and sensations of motion, provide the sensible signals upon which the pilot bases his control of the aircraft. Variations of the gravitational-inertial force environment during the flight of an aircraft affect the pilot's motion sensors in his vestibular system and through them affect his control of the vehicle, his visual process, and his sense of orientation.

Through a review of the literature, a study is made of the basic physiology of the human vestibular system and its interconnection with the oculomotor system. The dynamic functions of the semicircular canals and utricles (otolith organs) and the relation between subjective perceptions of motion and the accelerations which produce them are studied. Mathematical models of the dynamic functions of the vestibular system are presented.

The visual and perceptual illusions which lead to disorientation and which are produced by motion stimulation of the vestibular system are discussed. The various illusions experienced by pilots of aircraft are related to the accelerations which produce them and to the dynamics of the vestibular sensors involved.

FOREWORD

This report is one of the results of a National Aeronautics and Space Administration program sponsored by the Biotechnology Division of Ames Research Center under Contract No. NAS2-3650. Mr. John D. Stewart served as technical monitor for Ames Research Center. The Contractor's technical director was Mr. Duane T. McRuer, and the project engineer was Mr. Robert L. Stapleford.

The work presented in this report represents the first phase of a study of the effects of motion cues in the control of manned aircraft. This report is derived from a review of the literature on the human vestibular system. Attention is centered on the derivation of a mathematical model of the vestibular system applicable to closed-loop vehicle control. Attention is also focused on the disorientation and illusions produced by motion stimulation of the vestibular system in flight and in simulators.

The author is indebted to the many researchers whose original investigations into the nature and function of the vestibular system enabled this report to be written.

The author gratefully acknowledges the fine work of the Systems Technology, Inc., publication staff in the preparation of this report.

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TABLES

SYMBOLS

a	Input linear acceleration
a_R	Acceleration of particle relative to the rotating axes
a_S	Acceleration of particle relative to the space axes
A	Cross-sectional area of endolymph ring
$[A]$	Orientation matrix expressing the orientation of the head axis system relative to an earth-fixed system
B	Viscous damping torque, at unit angular velocity of the endolymph with respect to the skull
d_{min}	Displacement of the otolith at the threshold of perception
e	The base of natural logarithms
F	Force
F	Fovea
F_{cor}	Coriolis force
F_{eff}	Effective force appearing to an observer in a rotating coordinate system to be acting on a particle moving in that system
$F(s)$	Transfer characteristic of the central nervous system, presumed to be unity
F_t	Component of Coriolis force in the plane of and tangent to the endolymph ring
g	Gravity or acceleration of gravity
G	Gravitoinertial
h_k	Altitude of aircraft in thousands of ft
I	Moment of inertia of the endolymph in a semicircular canal about its sensitive axis
I	Moment of inertia of the endolymph ring about its center
IFR	Instrument Flight Rules
K	Stiffness, torque per unit angular deflection of the cupula

K	Open-loop low frequency gain; the frequency-invariant portion of a transfer function as $s \rightarrow 0$
K_d	A constant in the expression relating otolith displacement to the subjective perception of motion at the threshold of perception
ln	Natural logarithm
m	Mass of particle or system of particles
min	Minimum
p	Roll rate of the head, angular velocity about the X_h axis, positive right ear going down
q	Pitch rate of the head, angular velocity about the Y_h axis, positive nose going up
q	Pitch rate of aircraft, angular velocity about the y axis, positive nose going up
r	Radius of the torus of the endolymph ring
r	Yaw rate of head, angular velocity about the Z_h axis, positive nose going right
r	Yaw rate of aircraft, angular velocity about the z axis, positive nose going right
R	Radius vector from origin of the rotating axes to particle
s	Laplace transform operator
t	time
t_u	Time from the onset of stimulation to the cessation of the sensation of rotation
T	Torque on the endolymph ring about its center
T_1	B/K, the long time constant of the transfer function of a semicircular canal
T_2	I/B, the short time constant of the transfer function of a semicircular canal
VFR	Visual Flight Rules
V_R	Velocity of particle relative to the rotating axes
v_s	Velocity of particle relative to the space axes

x, y, z	Stability axis system; a right-hand system of orthogonal coordinate axes, fixed with respect to the airframe, and originating at the c.g. of the airframe; the x axis is so oriented in the airplane during the steady flight condition that it is parallel to the relative wind; the z axis is perpendicular to the x axis, positive downward, and lies in the plane of symmetry of the airframe
X_h, Y_h, Z_h	A right-hand system of orthogonal coordinate axes, which is fixed with respect to the head, and which originates between the labyrinths. When the head is upright, the X_h axis is horizontal, aligned in the forward direction, and lies in the sagittal plane. The Z_h axis is directed downward along the vertical when the head is upright.
α	Angle between ω and v_R
α	Depression angle of visible horizon below sensible horizon
α_R	Instantaneous angular acceleration of the endolymph ring about its center
β	Angular displacement about the endolymph ring of a particle of endolymph relative to the tilt axis
γ	Input angular velocity about the sensitive axis of a semicircular canal
γ	Angular displacement of tilt axis from the normal to the plane of the endolymph ring
γ	Angle of counterroll of the eye
δ	Angle of counterroll of the eye
θ	Angular deflection of the cupula with respect to the skull
θ	Tilt angle of the head in pitch
θ	Pitch angle of aircraft
ρ	Mass density of endolymph
τ	Latency time, the time between onset of motion stimulation and the first sensation of motion
φ	Roll or bank angle of aircraft
φ	Tilt angle of the endolymph ring

φ	Angle between gravity vector and gravitoinertial vector. The gravitoinertial vector is the vector sum of the gravity and acceleration vectors
φ	Tilt angle of the head in roll
ψ	Heading angle of aircraft
ω	Rotation rate vector of the rotating axis system, assumed to be constant
ω_O	Undamped natural frequency of the cupula/endolymph system
ω_R	Instantaneous angular velocity of the endolymph ring about its center

Mathematical Symbols

$(\dot{\ })$	Time derivative of quantity in parentheses
	Vector cross product
$\frac{d(\ )}{dt}$	Time derivative of quantity in parentheses
$\Delta(\ )$	Incremental value

GLOSSARY*

abduct	To draw away or turn outward from the median line of the body or from a neighboring part or limb
adduct	To draw or turn inward toward the median line of the body or toward a neighboring part
afferent	Conveying toward a center (such as the brain)
aftereffect	An effect or sensation that follows at some interval after the stimulus which produces it has been withdrawn
afterimage	A visual image or other sense impression that persists after the withdrawal of the exciting stimulus
aftersensation	Aftereffect
agonist	A muscle that serves as a prime mover in a given action; a muscle opposed in action by another muscle, called the antagonist
ampulla	The dilated portion of a semicircular canal containing the cupula and crista
ampullofugal	Utriculofugal; directed away from the ampulla and utricle; used to denote a direction of flow in a semicircular canal away from the ampulla end of the canal
ampullopetal	Utriculopetal; directed toward the ampulla and utricle; used to denote a direction of flow in a semicircular canal toward the ampulla end of the canal
antagonist	A muscle that acts in opposition to the action of another muscle, its agonist
anterior	Situated in front of or in the forward part of; affecting the forward part of an organ
autokinesis	Apparent motion of a point of light or a small object when presented against a dark visual background and viewed continuously
bilateral	Pertaining to both sides

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*The majority of definitions in this glossary are taken directly or adapted from Ref. 40.

calyx	A cup-shaped organ or cavity
cochlea	The essential organ of hearing: a spiral tube which forms part of the inner ear
conjugate	Paired or equally coupled; working in unison
contralateral	Situated on or pertaining to the opposite side
Coriolis force	A hypothetical force which accounts for the apparent deflection of a particle or body moving in a rotating coordinate system (see Appendix A)
Coriolis illusion	An illusion involving a sensation of body rotation and an apparent motion of objects in the visual field which is caused by tilting the head about one axis while the head is undergoing passive rotation about another axis
counterroll	A reflex torsional movement of the eyes which tends to keep the normally vertical meridian of each eye aligned with the vertical as the head is tilted to either side
crista	A ridge or crest in the ampulla of a semicircular canal containing sensory cells and endings of the vestibular nerve
cupula	A gelatinous structure situated over and supported by the crista. The cupula forms a moving seal across the ampulla and is deflected by a flow of endolymph through the semicircular canal
cupulogram	A graph of the duration of the sensation of rotation versus the magnitude of the stimulus (a step input in angular velocity)
cuticle	A layer of more or less solid substance which covers the free surface of an epithelial cell
cytoplasm	The living substance or protoplasm of a cell exclusive of the nucleus
dextrorotator	An eye muscle which rotates the eye to the right. The primary dextrorotators are the medial rectus of the left eye and the lateral rectus of the right eye
disjugate	Not joined together in position or action; the opposite of conjugate

efferent	Conveying away from a center (such as the brain)
egocentric localization	The act of determining the direction of an object relative to oneself
elevator illusion	A visual illusion involving apparent vertical movement of objects in the visual field and which is caused by a change in the magnitude of the G vector acting vertically
endolymph	Fluid contained in the semicircular canals, utricle, and saccule
epithelium	The surface lining of the crista and of the macula which consists of sensory and supporting cells
extensor	Any muscle that extends a joint
extorsion	Tilting of the upper part of the vertical meridian of the eye away from the midline of the face
extraocular	Situated outside the eye
extrinsic	External; used in reference to the extrinsic eye muscles, meaning the oculomotor muscles
fasciculus, medial longitudinal	A well-defined fiber tract extending through the midbrain into the spinal cord and carrying vestibular fibers
fixate	To fix or make stable (the image of an object on the retina); to look at
flexor	Any muscle that flexes a joint
fovea	A small area of the retina which is the area of sharpest vision
frontal plane	A vertical (head upright) plane perpendicular to the sagittal plane which contains the lateral axis, Z_h, and the vertical axis, Y_h. The intersection of the frontal and sagittal planes defines the vertica axis which is colinear with the gravity vector when the head is upright. See figure 2.
gravitoinertial vector	The vector sum of the gravity and acceleration vectors
habituation	A gradual adaptation to a repeated stimulus. The adaptation involves a change in the response of the organ or organism stimulated.

hair cell	A sensory cell of the epithelium with hairlike filaments projecting from its surface
homolateral	Ipsilateral, situated on or pertaining to the same side
inferior	Situated below or directed downward
innervate	To communicate nervous energy to, stimulate through nerves; to furnish with nerves
innervation	The act of innervating; the state of being innervated; the distribution of nerves to a part
intorsion	Tilting of the upper part of the vertical meridian of the eye toward the midline of the face
invagination	The infolding of one part within another
ipsilateral	Homolateral, situated on or pertaining to the same side
kinesthesia	The sensation of movement or strain in muscles, tendons, and joints; muscle sense
kinocilium	A motile filament on the free surface of a cell; in particular a motile filament which projects from a sensory cell of the epithelia of the crista or macula. The kinocilia extend into the cupula in the ampulla and into the otolith in the utricle and saccule and appear to be involved in transmitting stimulation to the sensory cell.
labyrinth	The internal ear, consisting of a membranous portion (membranous labyrinth) suspended in a bony portion (bony labyrinth)
latency time	The time between onset of motion stimulation and the initiation of a response
lateral	Denoting a position farther from the median plane or midline of a body or structure; pertaining to a side
lateral axis	The axis lying in the frontal plane, orthogonal to the sagittal and vertical axes, and directed horizontally and to the right in the erect head. See figure 2.
levorotator	An eye muscle which rotates the eye to the left. The primary levorotators are the lateral rectus of the left eye and the medial rectus of the right eye.

macula	A thickening in the wall of the utricle or the saccule where the epithelium contains sensory cells that receive and transmit vestibular impulses
medial	Denoting a position closer to the median plane or midline of a body or structure
median	Situated in the median plane or in the midline of a body or structure
mitochondria	Small granules or rod-shaped structures found in differential staining in the cytoplasm of cells
morphology	The study of the form or structure of anything
neuron	A nerve cell with its processes, collaterals, and terminations
nystagmus	An involuntary rapid movement of the eyeball which may be horizontal, vertical, rotatory, or a combination of these varieties
oblique muscle (of the eye)	An extrinsic eye muscle producing primarily torsional movements of the eye. The superior oblique produces primarily intorsion, the inferior oblique produces primarily extorsion. See figures 17 and 18.
ocular	Of or pertaining to the eye
oculoagravic illusion	A visual illusion involving an apparent vertical movement of objects in the visual field and which is caused by a downward acceleration yielding a G vector of magnitude between 0 and 1.0; a special case of the elevator illusion
oculogravic illusion	A visual illusion involving an apparent displacement or rotation of objects in the visual field and which is caused by a rotation of the G vector relative to the observer
oculogyral illusion	A visual illusion involving an apparent movement of objects in the visual field and which is caused by angular acceleration of the head
oculomotor muscle	An extrinsic eye muscle which serves to move the eye in its orbit
optokinetic	Of or pertaining to a movement of the eye elicited by a visual stimulus as in optokinetic nystagmus
otoconia	Minute calcareous (calcium carbonate) granules within the otolith. Called also statoconia and, sometimes, otoliths.

otolith	A gelatinous membrane embedded with calcareous particles (called otoconia or statoconia) which is supported over the macula by filaments from sensory and supporting cells in the macula of the utricle and of the saccule
perilymph	The fluid between the bony and membranous labyrinths of the ear; it is entirely separate from the endolymph
posterior	Situated in back of, or in the back part of, or affecting the back part of an organ
proprioceptive	Pertaining to proprioceptors, the stimuli acting upon them, or the nerve impulses initiated by them
proprioceptor	A receptor located in subcutaneous tissues, as muscles, tendons, and joints, that responds to stimuli produced within the body
rectus muscle (of the eye)	An extrinsic eye muscle producing primarily lateral or vertical movements of the eye. The superior and inferior recti elevate and depress the eye, respectively. The medial and lateral recti adduct and abduct the eye, respectively. See figures 17 and 18.
saccule	The smaller of two sacs in the membranous labyrinth. The saccule is similar to the utricle in structure, but apparently does not serve a motion sensing function in man. See figure 1.
sagittal axis	The axis lying in the sagittal or median plane of the head and directed horizontally and forward in the erect head from its origin between the labyrinths. See figure 2.
sagittal plane	The median plane of the head; a plane dividing the head into two symmetrical halves and containing the sagittal axis, X_h, and the vertical axis, Z_h. See figure 2.
semicircular canal	Any of the three curved tubular canals in the labyrinth of the ear, associated with sensing of angular motion. See figure 1.
statoconia	Minute calcareous (calcium carbonate) granules within the otolith. Called also otoconia and, sometimes, otoliths.
stereocilia	The nonmotile filaments which project from the free surface of a cell; in particular (in this report) the nonmotile filaments which project from each sensory cell of the epithelia of the crista and macula. The stereocilia serve to support the cupula in the ampulla and the otolith in the utricle and saccule and may be involved in transmitting stimulation to the sensory cell.

superior	Situated above or directed upward; used in reference to the upper surface of a structure or to a structure occupying a higher position
synapse	The region of contact between processes of two adjacent neurons, forming the place where a nervous impulse is transmitted from one neuron to another
threshold	That value at which a stimulus just produces a sensation or comes just within the limits of perception
tonic	Producing and restoring the normal tone or degree of vigor and tension in a muscle; characterized by continuous tension
tonus	The slight continuous contraction of muscle which in skeletal muscles aids in the control of posture and the relative positions of the various parts of the body
transfer function	The mathematical expression relating the output or response of a device or organ to the motivating force, input, or stimulus producing it
trochlea	A pulley-shaped part or structure; in particular the fibrocartilaginous pulley near the internal angular process of the frontal bone through which passes the tendon of the superior oblique muscle of the eye. See figure 17.
utricle	The larger of two sacs in the membranous labyrinth. The semicircular canals communicate directly with the utricle. The utricle serves a gravity and linear acceleration sensing function. See figure 1.
utriculofugal	Ampullofugal; directed away from the utricle and ampulla; used to denote a direction of flow in a semicircular canal away from the ampulla end of the canal. The term is confusing in that both ends of each semicircular canal are connected to the utricle.
utriculopetal	Ampullopetal; directed toward the utricle and ampulla; used to denote a direction of flow in a semicircular canal toward the ampulla end of the canal. The term is confusing in that both ends of each semicircular canal are connected to the utricle.
vertical axis	The axis, in the head axis system, defined by the intersection of the frontal and sagittal planes. The vertical axis is aligned with the gravitational vertica and directed downward in an erect head.

vertigo	A feeling of dizziness associated with sensations of rotary motion of the body or surroundings. As used by pilots, vertigo means any feeling of spatial disorientation during flight, or a confusion with respect to the attitude or motion of the aircraft.
vestibular	Of or pertaining to the vestibule, in particular the motion sensing apparatus of the inner ear
vestibule	Vestibulum auris, an oval cavity in the middle of the bony labyrinth, communicating in front with the cochlea and behind with the semicircular canals, and containing the utricle and saccule

CHAPTER I

INTRODUCTION

A. BACKGROUND

In piloting tasks, visual observation of instrument indicators and of the visual field, and sensations of motion provide the sensible signals upon which the pilot bases his motor action and comment. It is known that the variations of the gravitational-inertial force environment during flight of an aircraft affect the pilot through the motion sensors of his vestibular system and through them affect the pilot's control of his vehicle, his visual process, and his sense of orientation. Effects produced on his visual system, in turn, influence the responses of his vestibular system and his sense of orientation. One of the purposes of this report is to present the results of a search of the literature on man's primary motion sensing apparatus, the vestibular system.

Until fairly recently, the role played by sensations of motion or motion cues in piloting techniques has been largely ignored. As a result, the details of how a pilot uses motion cues and which motion cues are utilized in given control situations are only vaguely understood. A clear understanding of the dynamic functions of the vestibular system and how subjective perceptions of motion are related to the accelerations which produce them are prerequisite to an understanding of how motion cues are utilized in piloting. Another purpose of this report is to present a mathematical model of the function of the vestibular system based on research reported in the literature and which is appropriate to the closed-loop control of an aircraft by a pilot.

One of the prime functions of the vestibular system is to provide signals to the oculomotor control system to permit stabilization of the retinal image as the head is moved in space. This stabilization function is served adequately for the small motions of the head encountered in everyday life. Motions of large amplitude or duration elicit various visual illusions and false perceptions of motion and orientation. Clearly, such false perceptions can have grave consequences if experienced while piloting an airplane. This report will elucidate the role played by the vestibular system is subserving the perceptual and visual illusions elicited by motion stimulation.

B. OUTLINE OF THE REPORT

Chapter II is concerned with the anatomy and physiology of the vestibular system. The structure and orientation of the vestibular sensors are related to their function, and details of the neurological system of the vestibular labyrinth are discussed. The interconnection of the vestibular and oculomotor control systems is considered. The reflexes and reactions evoked by motion stimulation of the vestibular system are enumerated in this chapter.

Chapter III considers the dynamic characteristics of the semicircular canals. A mathematical model of the function of the semicircular canals is derived which expresses the relation between the subjective perception of motion elicited by angular acceleration of the head. The experimental methods, chiefly those of Von Egmond, Groen, and Jongkees (ref. 120), utilized by various researchers to evaluate the parameters of the mathematical model are presented.

Chapter IV discusses the dynamic characteristics of the utricles. A mathematical model of the function of the utricles, chiefly the work of Meiry (ref. 97), is presented.

Chapter V discusses the visual and perceptual illusions leading to disorientation which are produced by motion stimulation of the vestibular system. Disorientation, sometimes referred to as vertigo, is responsible for a considerable percentage of aircraft accidents. The various illusions experienced by pilots of aircraft are related to the accelerations which produce them and to the dynamics of the vestibular sensors involved.

A mathematical analysis of the Coriolis illusion is presented in Appendix A.

C. HISTORICAL DEVELOPMENT

A great body of literature, perhaps as large as 10,000 papers and books, has developed since the groundwork in experimental physiology summarized by

Flourens in 1824. (ref. 44) Early work in the field concentrated on the physiology and function of the vestibular system. Considerable progress in understanding vestibular function was achieved through animal experiments. Increased recognition of disorientation as a cause of aircraft accidents spurred research on motion-induced disorientation and illusions, and on disorientation arising from disparities between visual field cues and motion cues. The development of vehicles capable of penetrating the space environment has stimulated research particularly on the effects on task performance, motion sickness, and habituation of a constantly rotating environment designed to provide a measure of artificial gravity. The literature on vestibular research has proliferated in the last few years with the massive governmental support attending the growing capability for manned space travel.

Most recently beginning to appear are studies of the effects of motion cues in closed-loop control of aircraft. In this latter category, only a handful of studies have been reported in the literature.

Table I presents some of the more notable milestones in vestibular research. This list is by no means exhaustive. In most cases, the researchers were or have been active for many years, in which cases the dates given are those of their earlier publications.

Against this brief background of research on the vestibular system, we present the following report on the literature pertinent to the derivation of mathematical models of the vestibular sensors and pertinent to an understanding of the illusions elicited by motion stimulation of the vestibular system.

TABLE I

SOME EARLY MILESTONES IN VESTIBULAR RESEARCH

Flourens (1824)	Sectioned semicircular canals of pigeons and rabbits and associated disturbances of head and body motions in planes corresponding to those of injured canals.
Mach (1873), Breuer (1874), Crum Brown (1874)	Propounded Hydrodynamic Theory of vestibular function whereby semicircular canals and cristae sense rotatory motion and otolith organs sense linear acceleration.
Ewald (1892)	Contributed to Hydrodynamic Theory and formulated Ewald's Laws of vestibular function. Deflected cupula of pigeon using pneumatic hammer inserted in canal.
Barany (1906)	Won Nobel Prize for work on vestibular system. Founded clinical otology, studied postrotational nystagmus in Barany chair, originated theory of caloric stimulation, studied habituation, and proposed directional balance mechanism in habituation.
Magnus and De Kleyn (1924)	Conducted extensive studies of animal physiology and identified numerous postural reflexes and reactions of vestibular origin.
Lorente de No (1926)	Studied distribution of vestibular nerve fibers and oculomotor nuclei.
Steinhausen (1931)	Observed function of cupula in vivo by injecting India ink into the endolymph of a fish (the ray). Proposed torsion pendulum analogy of function of semicircular canal and cupula.
Ross (1936)	Performed action potential experiments on frogs and concluded that semicircular canals respond to rotatory motion and that otolith organs respond to linear acceleration.
Lowenstein and Sand (1940)	Measured frequency of ampullar nerve responses (in the ray) as a function of the applied stimulus. Discovered steady-state nervous discharge with cupula at rest, increase in frequency with deflection of the cupula in one direction and decrease in frequency with the opposite deflection.
Graybiel, Clark, Guedry, and Associates (1945)	Studied effects of constantly rotating environment on nystagmus, motion sickness, task performance, habituation, disorientation. Performed numerous researches on nystagmus, illusions. Identified labyrinth functions through studies of normal and labyrinthine-defective subjects.
Van Egmond, Groen, and Jongkees (1949)	Determined constants of torsion pendulum equation of semicircular canal system.

CHAPTER II

THE VESTIBULAR SYSTEM

A. INTRODUCTION

The cochlea, which serves an auditory function, and the vestibular apparatus comprise the membranous labyrinth of the inner ear. The membranous labyrinth is suspended in a fluid, perilymph, in the bony labyrinth, a complex cavity in the temporal bone of the skull. The bony labyrinth forms the three semicircular canals and the vestibule, which contains the utricle and saccule. Figure 1 portrays the configuration of the membranous labyrinth of the right ear.

The vestibular system, or labyrinth, comprises the nonacoustic portion of the inner ear and consists of three semicircular canals, one utricle, and one saccule in each ear. The semicircular canals are three approximately circular canals whose planes are approximately orthogonal. Each canal is filled with a fluid, endolymph, which, by virtue of its inertia, flows through the canal whenever an angular acceleration in the plane of the canal is experienced by the head. Flow of the endolymph deflects the cupula, a flapper-like valve which seals an expanded portion of each duct called the ampulla. Deflection of the cupula gives rise to a sensation of rotation. The semicircular canals constitute angular accelerometers capable of sensing angular accelerations in any direction as the head is rotated.

The utricles are two in number, one being located in each inner ear. The utricle constitutes a multidirectional linear accelerometer. The utricle consists basically of two parts, the macula and the otolith. The macula is the base and receptor end of this sensory organ, providing a bed for sensory cells and the utricular branch of the vestibular nerve. The otolith, which amounts to the moving mass, is supported over the macula by strands extending from sensory cells and supporting cells in the macula. Linear acceleration of the head causes a deflection of the otolith relative to the macula. This deflection is detected by the sensory cells giving rise to a sensation of tilt or acceleration. The utricle is apparently more sensitive to components of acceleration in the plane of the macula than it is to those not in the plane of the macula. The plane of the macula is elevated (front end up) 25 to 30 deg above the horizontal in an erect head.

The saccules are two in number, one being located in each inner ear. Histologically, the saccule is identical to the utricle (ref. 97) and the two are often spoken of as the otolith organs. The plane of the saccular macula, however, is perpendicular to that of the utricular macula, suggesting that the saccule should be more sensitive to vertical accelerations than to components of acceleration in the horizontal plane. However, there is some disagreement as to whether the saccule is sensitive to motion inputs at all. Some authors (ref. 101) assume that the saccule acts as a receptor of linear acceleration, others (ref. 97) that it does not. The consensus is that in mammals the saccule is vestigial (ref. 75) and does not serve a motion sensing function. Some authors incorporate the saccule as a linear acceleration sensor because of inadequate knowledge of the stimulation process of the utricle (ref. 97). Many authors, dealing with the functions rather than the identity of the linear acceleration sensors, skirt the ambiguity of whether the saccule is included with the utricle by referring to their common designation, the otolith organs.

The orientation of the sensors with respect to the head is of particular importance in determining the accelerations to which the sensors are sensitive. The axis system to be used and the nominal orientation of the sensors are discussed in section B. The physiological structure of the sensors is discussed in section C. Their innervation and interconnection with the eye motor control system is treated in section D. Section E considers the functions served by the vestibular system, functions which have been identified by the reflexes or reactions produced by stimulation of the vestibular system.

B. THE AXIS SYSTEM

The vestibular sensors are fixed with respect to the head, so that motions of the head constitute motion inputs to the vestibular system. An axis system, fixed with respect to the head, is thus an appropriate reference coordinate system.

The head axis system, X_h, Y_h, Z_h, is shown in figure 2 as a right-hand system of orthogonal coordinate axes which is fixed with respect to the head and which originates between the labyrinths. When the head is upright the X_h axis is horizontal, aligned in the forward direction, and lies in the sagittal plane. The Z_h axis is directed downward along the vertical when the head is upright, and lies in the sagittal plane. The Y_h axis extends to the right and lies in the frontal plane.

Two vertical perpendicular planes are defined for the head. The sagittal plane divides the head into two symmetrical halves and contains the sagittal (fore and aft) axis, X_h, and the vertical axis, Z_h. The frontal plane is a vertical plane (head upright) perpendicular to the sagittal plane. The intersection of the frontal and sagittal planes defines the vertical axis which is colinear with the gravity vector when the head is upright.

Before discussing the orientation of the vestibular sensors relative to the head, it will be well to clarify the nomenclature of the three semicircular canals. In this report the terms used for the canals are: horizontal, superior, and posterior. The superior and posterior canals together are referred to as the vertical canals. Some other names by which the canals are known are listed below:

HORIZONTAL	SUPERIOR	POSTERIOR
lateral	superior vertical	inferior vertical
external	upper vertical	inferior lower vertical
medial	anterior	
	sagittal	sagittal
	frontal	

The approximate orientation with respect to the head of the semicircular canals is shown in figure 3. The plane of the horizontal canals is elevated 23 to 25 deg from the horizontal plane when the head is erect. Tilting the head forward about 25 deg brings the horizontal canals into the horizontal plane. The planes of the right superior and left posterior canals are nearly parallel to each other as are those of the left superior and right posterior canals.

The three semicircular canals of each inner ear are not quite orthogonal to one another (ref. 44). The planes of the superior and posterior canals of each ear are separated on the average by an angle of 83 to 85 deg. The average separation between the planes of the posterior and horizontal canals is 80 to 92 deg.

Experiments described in Chapter IV indicate that the utricle is most sensitive to components of acceleration in the mean plane of the macula which, as mentioned in Section A, is elevated between 25 and 30 deg above the horizontal plane.

C. STRUCTURE OF THE SENSORS

1. Semicircular Canal System

Each semicircular canal forms about two-thirds of a circle with an outer diameter of from 4 to 7 mm. The utricle completes the circuit of each canal. A cross section of the horizontal canal and utricle is shown in figure 4. The canals have five orifices to the utricle, the superior and posterior canals sharing a common duct along the intersection of their respective planes. The inside diameter of the duct of each canal is about 0.3 mm. Reference 76 presents the results of a detailed dimensional study of the vestibular sensors. Near one "end" of each canal is a dilatation called the ampulla, a cross section of which is shown in figure 5. The sensory epithelium of each canal lies within the ampulla and is heaped up to form a ridge called the crista. The crista supports sensory cells, each of which has many hair-like projections which pass into and support the cupula. The cupula acts as a spring-restrained flapper-like valve which, together with the crista, forms a seal across the ampulla. A fluid, endolymph, fills each canal. Angular accelerations of the head in the plane of the canal cause the endolymph, due to its inertia, to flow through the canal, deflecting the cupula from its rest position. Deflection of the cupula gives rise to a sensation of turning. The semicircular canal/endolymph/cupula system acts as a heavily damped angular accelerometer, responding to angular accelerations in its own plane and yielding sensations of angular rate. The semicircular canal system is ideally adapted to sense the motions which are likely to be experienced by the head in the normal course of daily life. If, for instance, the head is moved and then stopped, acceleration is followed almost immediately by deceleration, the inertia of the endolymph causes the cupula to be displaced only momentarily, and the effects of its displacement are short-lived. If, however, acceleration is followed by rotation at a constant rate, the endolymph catches up with the rotating canal, and the deflected cupula is restored to its rest position very slowly only by virtue of its own elasticity (ref. 54). This action gives rise to an erroneous perception of motion, i.e., the subject thinks that he has stopped, presuming he is deprived of other cues such as those provided by vision and audition. On cessation of rotation the inertial reaction of the endolymph tends to keep it moving, thus deflecting the cupula in the direction opposite to its initial deflection. This gives rise to a sensation of rotation in a direction opposite to that of the physical rotation. The post-rotatory sensation persists until the cupula is again restored to its rest position by its elasticity. Such prolonged turning is not commonly experienced unless we become passengers in some man-made conveyance.

It is argued whether or not the semicircular canals are stimulated by linear acceleration. While some authors admit this possibility (ref. 84), others deny it (ref. 77). Recent research (ref. 36) into the response of the ampullar sensory cells of the cat when subjected to various orientations of acceleration with respect to its head indicates that the semicircular canals are not stimulated by linear acceleration.

2. Utricle and Saccule

The utricle is a large, oblong sac located beneath and connecting with the semicircular canals. The utricle is filled with the endolymph which also fills the semicircular canals. The basic component parts of the utricle are the macula and the otolith. The macula is about 2 mm by 3 mm, and provides a bed for sensory cells and the utricular branch of the vestibular nerve. The otolith is a gelatinous membrane embedded with calcareous particles or statoconia, which sometimes are called otoliths themselves. The otolith has a higher density, 2.95, than the endolymph, 1.02, and is supported over the macula by hair-like strands extending into the otolith from sensory and supporting cells in the macula. Figure 5 portrays a sectional view of the utricle. Linear acceleration in the plane of the macula causes a sliding displacement of the otolith relative to the macula, which produces a sensation of tilt or acceleration. Electrophysiological studies have shown that the utricle responds only to linear acceleration (ref. 7).

Histologically, the saccule is identical to the utricle (ref. 97), but, as discussed in section A, apparently has not been identified as serving a motion sensing function.

D. NEUROLOGICAL SYSTEM OF THE VESTIBULAR LABYRINTH AND INTERCONNECTION WITH THE OCULOMOTOR CONTROL SYSTEM

There is a wealth of literature on the nervous structure of the vestibular system, only a small portion of which was covered in this study. References 1, 7, 12, 42, 86, 110, 111, 127, and 128 present results of studies of the ultrastructure and innervation of the sensory epithelia of the vestibular system. Their bibliographies suggest additional sources. Of particular interest in the following discussion is the relation of structure to function with especial reference to directional sensitivity of the sensors.

1. Sensory Epithelia of the Crista and Utricular Macula

The vestibular sensory cells are contained in five areas in each ear. These areas are the three cristae, one in each ampulla of the three semicircular canals, and the two maculae, one each in the utricle and the saccule. The sensory cells of the cristae ampullares are similar in structure and function to those of the maculae of the utricle and saccule. It is generally accepted (ref. 1) that there are two basic types of sensory cells in the vestibular sensory epithelia. The gross features of these cells are illustrated in figure 6 (ref. 7). Type I cells are bottle-shaped and nearly surrounded by a nerve chalice or calyx (cup). Type II cells are more nearly cylindrical in shape and lack the nerve calyx. There also appear cells of intermediate type and groups of cells enclosed in a single nerve calyx as shown in figure 7.

Each sensory cell, also called a hair cell, is equipped with sensory hairs which project, in the case of the cristae, into the cupula, or in the case of the maculae, into the otolith. The sensory hairs are of two types: stereocilia and kinocilia as shown in figure 8. Typically, each sensory cell has a single kinocilium and about 30 to 100 stereocilia. The stereocilia are bundled together in a closely packed hexagonal pattern (ref. 110) with the kinocilium always situated on the periphery of the bundle (fig. 9). The stereocilia vary in length in a systematic way. The stereocilia closest to the kinocilium are longest, the remainder progressively decreasing in length with increasing distance from the kinocilium, so that the shortest are only about 1 micron long (ref. 128).

The kinocilia are distinguished by a structure (discernable in figure 9b) consisting of nine peripherally arranged double tubular filaments and two centrally located single tubular filaments (ref. 110). This structure is typical of kinocilia found in a variety of different tissues in all animals, such as in the ciliated cells of the epithelium of the lung, in the rod cells of the retina, and in the olfactory sensory epithelium. The filaments of the kinocilium extend into the basal body forming a short cylinder with the nine filaments each transformed into a triplet and arranged in a spiral as shown in the sketch of figure 9c. The structural similarity of the basal body to other functionally important components of living cells suggests an important role played by the kinociliar basal body which may be related to the functional polarization of the sensory cell.

2. Organization of the Sensory Cells

When large surface sections of the sensory epithelium are examined, a regular pattern of orientation of the sensory cells is apparent (ref. 128). Over large areas of the sensory epithelium, the sensory cells are oriented in the same direction with regard to the location of the kinocilia relative to their respective stereocilia bundles (fig. 10). The most regular organization occurs in the cristae where the vast majority of sensory cells are oriented in the same direction. The direction of orientation is considered to be from the hair bundle to the kinocilium. On the cristae of the horizontal semicircular canals the kinocilia are on the sides of the cells nearest the utricle. On the cristae of the vertical canals the kinocilia are on the sides of the cells farthest from the utricle or facing the canal.

The orientation of sensory cells in the maculae is more complex. The sensory hairs are shorter in the maculae than in the cristae, but otherwise their structure is identical (ref. 110). The sensory cells are uniformly oriented or polarized over large areas, but the direction of polarization varies gradually over the surface of the macula as exemplified in figure 11 for the utricular and saccular maculae of the guinea pig. The maculae are characterized by having a curving line of demarcation which divides the area of the macula roughly in half and across which the sensory cells are oppositely polarized. Typically, in utricular maculae the sensory cells are polarized towards each other across this line of demarcation, and in saccular maculae the sensory cells are polarized away from each other across this line (ref. 110). These features are shown in figure 11 for the guinea pig and in figure 12 for the squirrel monkey. In figures 11a and 12, it is apparent that all possible directions of polarization are represented in the utricular macula (ref. 110). Figure 11b shows that this is not true of the saccular macula, the main polarization being about equally divided between the antero-inferior and the postero-superior directions.

Microscopic examinations of the sensory epithelia of numerous animals, including fish, frogs, birds, mammals, and man, have shown that the major structure and pattern of organization of sensory cells is the same. The question naturally arises: Are the physical polarization patterns of hair cells, which are a common characteristic of a large number of vertebrates, associated with patterns of functional polarization? Evidence presented in the following subsection points to an affirmative answer.

3. Significance of the Sensory Cell Polarization

According to Wersäll and Lundquist (ref. 128), "The asymmetry of the sensory cell is considered to reflect an asymmetrical organization of the hair-bearing end of the sensory cells at the molecular level, forming a direction-sensitive transducer mechanism. It is suggested that the main orientation of the sensory cells, within a certain area of the sensory epithelium, reflects the directional sensitivity of that area, which allows a charting of each part of the inner ear with regard to its function."

Wersäll and Lundquist (ref. 128) report that Lowenstein and Wersäll (ref. 90) were the first to identify and associate the morphological polarization of the vestibular epithelia (in the crista ampullaris of the ray) with the previously discovered (Lowenstein and Sand, ref. 89) directional asymmetry in the response of the semicircular canal. Lowenstein and Wersäll showed that the sensory cells were aligned in the direction of cupular displacement. Previously, Lowenstein and Sand had learned that deflection of the cupula toward the kinocilia increased the discharge rate of the innervating nerve fibers and that deflection of the cupula in the opposite direction decreased the discharge rate (fig. 13). The correlation between the morphological polarization of the sensory cells and their directional sensitivity has been corroborated by other researchers working with various animals. (See ref. 128.) The word correlation is used because the importance of the kinocilium to the stimulation of the sensory cell has not been established (ref. 128). The phenomenon linking morphological and functional polarization is observed, but the mechanism by which it operates is unexplained.

If the same correlation of morphological and functional polarization is assumed for the macula, then the macula should be sensitive to linear accelerations in all four quadrants of the macular plane, because all four directions of polarization of the sensory cells are represented in the utricular macula. This conclusion is in accord with the findings of Lowenstein and Roberts (ref. 88) who obtained responses from a single utricular macula to tilting about all horizontal axes.

As long ago as 1892, Ewald (ref. 43), experimenting with pigeons, observed that endolymph flow through the horizontal canal toward the ampulla and utricle (termed ampullopetal or utriculopetal flow) elicited a stronger nystagmus reaction than did equal flow in the opposite direction (termed ampullofugal or utriculofugal flow). The effects were reversed in the vertical canals; that is, ampullofugal flow was the more effective stimulus. These observations have become known as Ewald's Second Law of Directional Preponderance, describing behavior characteristic of the semicircular canals. Ewald's Second Law is certainly valid under the experimental conditions which led to its formulation, but its applicability to humans under normal conditions is questioned. A discussion of the pros and cons is given in reference 75, pp. 118-120.

Two basic functional characteristics of the semicircular canals are expressed in Ewald's Second Law (ref. 110):

- The receptors of the semicircular canals are direction specific.
- There is a quantitative difference in the response to equal ampullopetal and ampullofugal stimulation.

The directional specificity has already been associated with the morphological polarization of the sensory cells. The second feature of Ewald's law, the quantitative difference in response to stimulation of opposite signs, is more difficult to explain on the basis of structural asymmetry. As described in reference 110, Lowenstein and his colleagues (ref. 85) found an explanation based on electrophysiological grounds.

They found two types of sensory units, one having a steady-state firing rate at rest, the other being quiescent at rest. Positive stimulation (i.e., stimulation in the direction of polarization of the sensory cells) increases the firing rate of the spontaneously active cells and activates the quiescent cells. Negative stimulation decreases the firing rate of the spontaneously active cells, but does not activate the quiescent cells. The net result, depicted in Table II, is a greater overall change in firing rate for positive stimulation than for negative stimulation.

TABLE II

DIRECTIONAL ASYMMETRY OF SENSORY CELL RESPONSE TO STIMULATION OF OPPOSITE SIGNS

SENSORY CELL TYPE	REST RATE PULSES/SEC	RATE FOR POSITIVE STIMULATION		RATE FOR NEGATIVE STIMULATION	
		RATE	CHANGE FROM REST	RATE	CHANGE FROM REST
Spontaneously Active	10	15	+10	5	-5
Spontaneously Quiescent	0	5		0	

Table II suggests that the active and quiescent cells contribute equally to the total firing rate, but actually the spontaneously active cells are in the majority, and in addition, the quiescent cells appear to have a higher threshold. The two types of sensory cells, active and quiescent, cannot be correlated with the two structural types I and II discussed in subsection D.1., because electrophysiological studies of the labyrinth of fishes have shown both active and quiescent cells to be present in a population of only the morphological Type I cells.

The distinctive functional difference between the active and quiescent cells may lie in their innervation.

4. Innervation of the Sensory Epithelia

The general structural features distinguishing Type I and Type II sensory cells were discussed in subsection D.1. Figures 14 and 15 present the structural details of the two basic cell types, and distinguish two types of innervation of the cells. The Type I cells are nearly surrounded by a single nerve chalice or calyx constituting the ending of a single large nerve fiber (ref. 111). The Type II cells are innervated by at least two different kinds of nerve endings (ref. 1). The Type 1 ending is sparsely granulated and considered to be an afferent ending. The membranes joining the nerve ending and sensory cell are differentiated in various ways which are characteristic of synapses elsewhere. The Type 2 nerve ending is densely granulated and considered to be an efferent ending. The granulated endings are in direct contact with the sensory cell surface and can also contact and form synapses with nerve fibers of Type 1, as shown in figures 14 and 16. The same type of granulated nerve ending is found in contact with the nerve calyces of the Type I sensory cells.

The Type I sensory cell is nearly surrounded by a sparsely granulated nerve calyx. Several areas within the calyx apparently form synaptic junctions with the cell, some with an indentation or invagination into the cell.

Details of the sensory cell and nerve ending structures are discussed in references 1, 42, 86, 110, 111, 126, 127, and 128.

The structural features of the vestibular epithelia and innervation of the sensory cells which may be responsible for some of the observed complexities of vestibular function are summarized as follows (ref. 42):

- The mammalian vestibular epithelia all contain two structural types of sensory cells which differ from each other in form and in the exact pattern of nerve endings.

- The sensory cells of the vestibular epithelia are further differentiated into two so-called activity types, one type showing a spontaneous nervous activity when unstimulated, and the other being quiescent when unstimulated. This activity differentiation is pertinent to the directional sensitivity of the vestibular sensors.

- There are at least two morphologically distinguishable types of synaptic connections which may be also functionally distinguishable.

- The sensory cells have both afferent and efferent endings, the functional significance of the latter being as yet little known.

- The polarization and orientation of the vestibular sensory cells, as indicated by position of the kinocilia, follow definite patterns in each of the cristae and maculae and have important implications bearing on the directional sensitivity in the macula especially.

5. Interconnections with the Oculomotor System

a. The Extrinsic Eye Muscles

The extraocular or extrinsic eye muscles control the position of the eye in its socket. In each eye there are three pairs of antagonistic muscles: the superior and inferior rectus muscles, the lateral and medial rectus muscles, and the superior and inferior oblique muscles. Several views of these muscles are given in figure 17. In general, the superior and inferior recti move the eye up and down (elevation and depression, respectively), the lateral and medial recti move the eye toward the side of the head or toward the nose (abduction and adduction, respectively), and the superior and inferior oblique muscles roll or rotate the eye about its visual axis toward or away from the nose (intorsion and extorsion, respectively). Due to the orientation of the eye muscles (most clearly seen in the top view of fig. 17), their contraction does not produce the pure motions indicated above. Contraction of the superior rectus, for instance, produces a strong elevation of the eye and weaker amounts of adduction and intorsion. Movements of the eye which result from contractions of each of the six eye muscles are shown in figure 18 (ref. 2).

b. Functional Pattern of Interconnection Between the Semicircular Canals and the Oculomotor System

The exact anatomic pathways interconnecting the vestibular and oculomotor systems are still in dispute (ref. 44). Howard and Templeton (ref. 75) report that Szentágothai (ref. 115) found electrophysiological evidence suggesting that the main route from the vestibular apparatus to the eye muscles involves a three-neuron chain running via the medial longitudinal fasciculus, but that other more complex pathways also exist. Szentágothai stimulated the semicircular canal cupullae individually and elicited contractions in pairs of eye muscles as follows:

Horizontal canal	homolateral (same side) medial rectus contralateral (opposite side) lateral rectus
Superior canal	homolateral superior rectus contralateral inferior oblique
Posterior canal	contralateral inferior rectus homolateral superior oblique

Transection of the medial longitudinal fasciculus abolished these reactions (ref. 13). Figure 17 shows the locations of the extrinsic ocular muscles.

Cohen, et al. (ref. 34), describe the oculomotor activity induced by stimulating single ampullary nerves of the cat by a train of electrical impulses. Their findings support those of Szentágothai. Stimulation of single nerves produces strong contractions in one pair of ocular muscles and weak contractions in a second pair as shown in Table III. Simultaneously, the antagonists of each of the muscles involved in these reactions relax. The pattern of excitation and inhibition in the eye muscles evoked by stimulation of individual ampullary nerves of the vertical canals is shown in Table IV.

TABLE III

OCULOMOTOR RESPONSES INDUCED BY ELECTRICAL STIMULATION OF SINGLE AMPULLARY NERVES (REF. 34)

SEMICIRCULAR CANAL STIMULATED	OCULOMOTOR RESPONSE	
	STRONG CONTRACTIONS	WEAK CONTRACTIONS
Horizontal	Homolateral medial rectus Contralateral lateral rectus	None
Superior	Homolateral superior rectus Contralateral inferior oblique	Contralateral superior rectus Homolateral superior oblique
Posterior	Contralateral inferior rectus Homolateral superior oblique	Homolateral inferior rectus Contralateral inferior oblique

TABLE IV

EYE MUSCLE EXCITATION/INHIBITION REACTIONS
TO ELECTRICAL STIMULATION OF SINGLE AMPULLARY NERVES
OF THE VERTICAL CANALS (REF. 34)

LEFT EYE MUSCLE	SEMICIRCULAR CANAL STIMULATED			
	LEFT SUPERIOR	RIGHT SUPERIOR	LEFT POSTERIOR	RIGHT POSTERIOR
Superior rectus	strong excit.	weak excit.	inhibition	inhibition
Inferior rectus	inhibition	inhibition	weak excit.	strong excit.
Superior oblique	weak excit.	inhibition	strong excit.	inhibition
Inferior oblique	inhibition	strong excit.	inhibition	weak excit.
RIGHT EYE MUSCLE	LEFT SUPERIOR	RIGHT SUPERIOR	LEFT POSTERIOR	RIGHT POSTERIOR
Superior rectus	weak excit.	strong excit.	inhibition	inhibition
Inferior rectus	inhibition	inhibition	strong excit.	weak excit.
Superior oblique	inhibition	weak excit.	inhibition	strong excit.
Inferior oblique	strong excit.	inhibition	weak excit.	inhibition

The muscle contractions elicited by single ampullary nerve stimulation produce the eye movements shown in Table V. Stimulation of the vertical canals singly produces disjugate eye movements, that is, the eyes move in different directions. Stimulation of either horizontal canal produces conjugate eye movements. Rolling of the eyes denotes a rotatory movement of the eye more or less about its optical axis. (We say "more or less" because the axes of rotation of the eye are not fixed, but depend on the position of the eye and other factors. A discussion of this problem is given in ref. 75.) For instance, stimulation of the ampullary nerve of the left superior canal causes the left eye to move up with a weaker rolling movement to the right and causes the right eye to roll to the right with a weaker upward movement.

Cohen and his coworkers also stimulated the ampullary nerves in various combinations and observed the eye movements tabulated

TABLE V

EYE MOVEMENTS INDUCED BY ELECTRICAL STIMULATION OF SINGLE AMPULLARY NERVES (REF. 34)

SEMICIRCULAR CANAL STIMULATED	EYE MOVEMENT RESPONSE			
	LEFT EYE		RIGHT EYE	
	STRONG	WEAK	STRONG	WEAK
Left Horizontal	right	none	right	none
Right Horizontal	left	none	left	none
Left Superior	up	right roll	right roll	up
Right Superior	left roll	up	up	left roll
Left Posterior	right roll	down	down	right roll
Right Posterior	down	left roll	left roll	down

in Table VI. The disjugate eye movements elicited by stimulation of single ampullary nerves of the vertical canals are no longer seen, the eyes moving conjugately (together) or not at all. For instance, simultaneous stimulation of the left and right superior canals evokes a strong upward movement of both eyes, and the rotatory movements visible in the contralateral eye during single superior canal stimulation disappear. This behavior can be inferred from the pattern shown in Table IV. Simultaneous stimulation of the superior canals produces excitation of the left and right superior rectus muscles and inhibition of the oblique muscles and inferior rectus muscles of both eyes. Tension recordings made by Cohen and his coworkers show that inhibition generated in antagonists during stimulation is stronger and predominates over the excitation produced by stimulation of another canal.

Cohen and his associates also demonstrated oblique eye movements resulting from simultaneous stimulation of both superior canals and either horizontal canal and from simultaneous stimulation of both posterior canals and either horizontal canal. The

TABLE VI

EYE MOVEMENT RESPONSES TO STIMULATION OF AMPULLARY NERVES IN PAIRS (REF. 34)

SEMICIRCULAR CANALS STIMULATED	EYE MOVEMENT RESPONSE	
	LEFT EYE	RIGHT EYE
Left and right horizontal	none	none
Left superior, right superior	up	up
Left superior, left posterior	right roll	right roll
Left superior, right posterior	none	none
Right superior, right posterior	left roll	left roll
Right superior, left posterior	none	none
Left posterior, right posterior	down	down

angle of obliqueness depended upon the relative intensities of stimuli sent to the vertical and horizontal canals.

These data indicate that a highly ordered pattern of excitation and inhibition is dominant in the intact animal. This pattern is indispensable to an understanding of the results of combined canal stimulation. It may be recalled from subsection D.3. that ampullopetal endolymph flow in the horizontal canals and ampullofugal flow in the vertical canals increases the firing rate of the sensory cells of the ampullary cristae. Flow in the opposite direction decreases the firing rate, but not to as great an extent. Thus, according to Ewald's Second Law of Directional Preponderance, the angular accelerations to which the canals are most responsive are those which produce ampullopetal flow in the horizontal canals and ampullofugal flow in the vertical canals.

The directions of angular acceleration effective in stimulating the canals are represented by vectors (using the right-hand screw rule) in figure 19. The vector for the right horizontal canal is directed downward through the paper and is indicated by a small circle with a cross in it. The vector for the left horizontal canal is directed upward through the paper and is indicated by a small circle with a dot in it. The table in figure 19 shows the canals which are stimulated by accelerations about the principal axes of the head and the compensatory eye movements evoked. The compensatory eye movements of figure 19 agree with the eye movement responses to electrical stimulation of the appropriate canals as shown in Table VI.

It is apparent that the movements elicited by electrical stimulation simulate the types of reflex eye movements which occur with head turning. It is also clear that movements of the head stimulate the canals in pairs, thus producing conjunctive movements of the eyes. The neural interconnections between the vestibular and oculomotor systems are coded so that:

- Vertical canals on either side provide compensatory eye movements for rolling accelerations to that side.
- Bilateral superior canals provide compensatory eye movements for pitching down.
- Bilateral posterior canals provide compensatory eye movements for pitching up.
- Either horizontal canal provides compensatory eye movements for yawing to that side.
- Oblique movements of the head stimulate the lateral and vertical canals in combination, yielding oblique compensatory eye movements.

c. The Quadrant Theory of Interconnection Between the Utricles and the Oculomotor System

Szentágothai (ref. 116) and his associates studied the pattern of reflexes in the extraocular muscles of the dog to artificially induced movement of the utricular otolith. Their findings agreed in essence with the classical theory of Breuer, which asserts that the effective stimulus of the utricle is a displacement of the otolith in the plane of the macula.

The ocular muscles respond as would be expected if the head were tilted; that is, when the otolith is moved laterally the appropriate eye muscles tend to counterroll the eyes, and when the otolith is moved forward the appropriate eye muscles tend to elevate the eyes. These reflexes develop extremely slowly compared to those elicited by stimulation of the semicircular canals, indicating more complex and devious pathways interconnecting the utricular maculae and ocular muscles.

Noting that the pattern of ocular muscle responses varied with the direction of force applied to the otolith, Szentágothai and his associates developed a mosaic quadrant theory of macular function. According to this theory the sensory cells of each quadrant of the maculae activate a different pair of ocular muscles as shown in figure 20. They assumed that whenever the otolith moves, bending of the hairs of the macula toward the center or opposite margin of the macula increases the discharge rates of their sensory cells, thus causing the muscles indicated in figure 20 to contract. Simultaneously, the antagonists of the contracting muscles are caused to relax or are inhibited. The pattern of excitation and inhibition of ocular muscles versus quadrant stimulated is tabulated in Table VII. The eye muscle response to stimulation of either the left or right macula is the same for corresponding (1 to 1, 2 to 2, etc.) quadrants.

According to Table VII, if the head is tilted forward, i.e., pitched down, thus stimulating quadrants 1 and 2 of each macula, the superior rectus and inferior oblique muscles of each eye contract. This would appear to cause both eyes to elevate, the left eye to roll left, and the right eye to roll right. Elevation of both eyes is compensatory and the reflex to be expected, but disjugate rolling of the eyes is neither (unless the eyes are mounted on either side of the head). However, recalling the discussion of subsection D.5.a. and figure 18, it may be that the contractions of the inferior obliques are just sufficient to counteract the tendency of the contracting superior recti to produce intorsion of the eyes. If this were so, a pure compensatory motion of the eyes would result. Similar, but oppositely directed,

TABLE VII

QUADRANT THEORY OF EYE MUSCLE EXCITATION/INHIBITION REACTIONS TO STIMULATION OF INDIVIDUAL QUADRANTS OF THE UTRICULAR MACULA (REF. 116)

LEFT EYE MUSCLE	QUADRANT STIMULATED*			
	1	2	3	4
Superior rectus		excitation		inhibition
Inferior rectus		inhibition		excitation
Superior oblique	inhibition		excitation	
Inferior oblique	excitation		inhibition	
RIGHT EYE MUSCLE	1	2	3	4
Superior rectus	excitation		inhibition	
Inferior rectus	inhibition		excitation	
Superior oblique		inhibition		excitation
Inferior oblique		excitation		inhibition

*Responses to stimulation of the left and right utricles are the same.

reflexes follow tilting the head back, and a similar explanation is offered regarding the action of the obliques.

In the case of lateral tilting or rolling of the head, say, to the left, quadrants 2 and 3 of the maculae are stimulated. This causes the superior rectus and superior oblique muscles of the left eye and the inferior rectus and inferior oblique muscles of the right eye to contract. These reflexes tend to produce the desired compensatory counterrolling of both eyes to the right, but also tend to produce elevation of the left eye and depression of the right eye. These eye motions are not desired unless the eyes are located on either side of the head. It may be, however, that the contractions of the rectus muscles are just sufficient to counteract the tendency of (1) the contracting superior oblique to depress the left eye, and (2) the contracting inferior oblique to elevate the right eye. Again, if this were so, pure compensatory motion of the eyes would result. Since observations of normal animals and human subjects show that pure compensatory eye motions do take place, it is likely that either the proposed explanation is valid or that patterns of inhibition exist outside the quadrant theory which act to suppress the disjugate eye movement reflexes.

Szentágothai and his co-workers tested their hypothesis by electrically stimulating various parts of the utricular macula in the dog. These tests supported the hypothesis, but were restricted only to posterior portions of the macula. Later research (refs. 110 and 128, discussed in subsections D.2. and D.3.) has shown that all four quadrants of sensory cell polarization are indeed represented in the utricular macula, but are not necessarily disposed as suggested in the quadrant theory and indicated in figure 20. Still, the quadrant theory may correctly represent the functional organization of innervation between the maculae and ocular muscles, even though the mosaic of sensory cell polarization may be quite different than assumed, and, as suggested by a comparison of figures 11 and 12, may vary from animal to animal.

E. FUNCTIONS OF THE VESTIBULAR SYSTEM — TONIC REFLEXES AND EYE MOVEMENT REFLEXES

The properly functioning vestibular system is responsible for a number of reflexes and reactions. The reflexes and reactions are of two types: those involving body posture and muscle tonus and those involving compensatory movement of the eyes. Muscle tonus refers to a state of tension of the body musculature which is maintained without voluntary innervation and which serves to control body posture and the relative positions of the various parts of the body (ref. 44). Compensatory eye movements elicited by the vestibular system serve to maintain a stable image on the retina as the head is moved.

According to Fischer (ref. 44), Ewald demonstrated the tonic influence of the labyrinth on the entire musculature and proved experimentally that each labyrinth is concerned with the tonus of the homolateral extensors and abductors and the contralateral flexors and adductors. Ewald's findings have been corroborated by electrophysiological studies.

The involuntary contractions of muscles involved in the maintenance of normal tonus are masked by voluntary movements. Elimination of these voluntary movements through resection of various nervous pathways has facilitated the study of tonus in animals. Such drastic procedures cannot be applied to humans, and as a result, knowledge of the tonus problem is further advanced in animals than in man. While the results of animal experiments have contributed greatly to the knowledge of the tonic function of the vestibular system, they cannot be applied indiscriminately to man. Despite these objections, the investigation of the tonic reflexes has helped elucidate the role of the vestibular system as the predominant motion sensing system in animals and man.

The tonic reflexes and eye movement reflexes can be classified into two groups: those elicited by stimulation of the otolith organs and those elicited by stimulation of the semicircular canals.

1. Otolith reflexes
    a. Tonic labyrinthine reflexes
    b. Labyrinthine righting reflexes
    c. Compensatory eye movements
2. Semicircular canal reflexes
    a. Angular movement reflexes
    b. Reflexes upon thermic stimuli

These reflexes are now discussed on the basis of this classification.

1. Otolith Reflexes

These reflexes are elicited by stimulation of the otolith organs: the utricle and, in lower animals, the saccule. These reflexes occur in animals even when the cerebrum has been completely removed, and hence are independent of conscious sensations.

a. Tonic Labyrinthine Reflexes

The labyrinths directly influence the tonus of the muscles of the neck, trunk, and extremities. The neck muscles exert a secondary influence (neck reflex) on the muscles of the extremities. In studying the tonic labyrinthine reflexes, the neck reflexes are eliminated by severing appropriate nerves or by physically restricting relative motion between the head and body. The tonic labyrinthine reflexes consist of flexions and extensions of the extremities in response to changes in the position of the head with respect to inertial space. The neck reflexes are elicited by changes in the position of the head relative to the body.

b. Labyrinthine Righting Reflexes

The labyrinthine righting reflexes are related to the tonic reflexes, but refer specifically to those reflexes which enable the individual to restore himself to an upright position (with respect to the gravity vector) when disturbed, or to restore his head to an upright position if his body is restrained. These reflexes cease to occur when both labyrinths are destroyed.

c. Compensatory Eye Movements

In humans the utricles are responsible for two types of compensatory eye movements: the so-called doll eye movement and counterrolling or countertorsion. The doll eye movement is the tendency of the eyes to remain horizontal as the head is tilted forward or backward about the lateral axis. According to Howard and Templeton (ref. 75), the doll eye movement is present only in newborn infants for a few days after birth. Miller and Graybiel (ref. 101), however, cite evidence to the effect that the otolith organs do elicit compensatory vertical eye motions when the head is tilted in the sagittal plane. They do not say how these reactions are distinguished from those elicited by stimulation of the semicircular canals when the head is tilted in the sagittal plane.

Compensatory vertical eye motions have been recorded during sudden changes in magnitude of gravitoinertial force (ref. 103) and during changes in direction of gravitoinertial force in the sagittal plane (ref. 129). (See Chapter V, section B.) The existence of a compensatory vertical eye motion originating in the utricle is supported by the experiments on ocular muscle responses to stimulation of the utricle, which were discussed in subsection D.5.c.

Counterrolling is the tendency of the normally vertical meridian of the eye to remain vertical as the head is rotated to the right or left about the sagittal axis. Counterrolling is the only well-defined, entirely involuntary utricular reflex in man (ref. 75). The semicircular canals may contribute both to vertical eye movements and counterrolling (as described in subsection D.5.b.) during initial movement of the head, but since neither reflex decreases significantly with time, their steady-state component can be due only to utricular stimuli. Counterrolling is readily observed in any normal subject with markings on his iris to serve as a reference. As the subject's head rotates about the sagittal axis from upright to 90 deg, his eyes will rotate from their normal position about 6 to 8 deg in the opposite direction about their visual axes. Counterrolling does not occur in labyrinthine defective individuals, and does not occur in normal individuals in a "gravity-free" or weightless state. Details of eye movement reflexes to utricular stimulation were given in subsection D.5.c.

2. Semicircular Canal Reflexes

These reflexes are elicited by stimulation of the semicircular canals producing endolymph flow which causes a deflection of the cupula. The normal stimulus is angular acceleration in the plane of one or more of the canals, but endolymph flow and consequent cupula deflection can be induced by temperature gradients in the endolymph brought about by irrigation of the ear with hot or cold water or other fluids (caloric stimulation). The semicircular canal reflexes can be simulated by electrical stimulation of the ampullary nerves, as described in subsection D.5.b. These simulated reflexes are not complete, however, it being impossible to duplicate electrically the nervous stimulation evoked by movements of the head.

a. Angular Movement Reflexes

Some postural reflexes are produced by angular accelerations of animal subjects. These reflexes are generally suppressed in humans due probably to the inhibiting influence of the cerebrum.

The eye movement reflexes produced by angular accelerations of the head are of particular importance because they are readily observed in animals and man and provide valuable clues, both qualitative and quantitative, to the function of the vestibular system and its interconnection with the oculomotor system.

The general nature of the eye movement reflexes is as follows: When an animal or human subject with head erect is rotated about a vertical axis, each eyeball will rotate in the opposite direction. This action is clearly directed toward maintaining a steady image on the retina. If the rotation persists, nystagmus will occur, wherein the eyes, upon nearing the limit of their travel, will rapidly flick in the direction of rotation and then resume their compensatory motion in the direction opposite to that of the imposed rotation of the head. The compensatory portion of the eye movement is termed the slow phase of nystagmus, and the quick motion of the eyes in the direction of rotation of the head is termed the fast phase of nystagmus. Nystagmus is said to have the direction of the fast phase. If the rotation persists for several seconds and then stops, the reflex reverses and nystagmus in the opposite direction occurs. Even precluding other modalities (i.e., vision and hearing) of sensing angular motion, the subject has a sensation of angular velocity when he is accelerated. Upon cessation of rotation, his sense of angular velocity reverses along with the nystagmus, both conditions persisting for as long as 30 sec or more. The explanation for the prolonged aftersensation of turning and the reversed nystagmus is considered briefly in subsection C.1. and in greater detail in Chapter III.

Motion-induced nystagmus can be evoked about any axis, including a rotatory nystagmus about the visual axis. Some of the details of how stimulation of the vestibular system produces compensatory eye movements is discussed in subsection D.5.b.

The nystagmic reflex occurs even when the subject is in the dark, so it is not dependent on vision. In the dark, however, the speed of the slow phase is less than that of the head. Over the frequency range 0.2 to 15 rad/sec, Meiry (ref. 97) found the compensatory eye velocity to be about 40 percent of that of the head for rotations about the vertical axis. When a visual field is provided, the nystagmus is more precisely geared to the speed of rotation of the head. It is believed that the vestibular system initiates nystagmus, and that optokinetic or visually induced nystagmus takes command when a visual field exists. Optokinetic nystagmus is apparently dominant over vestibular nystagmus (ref. 75). The dominance of vision over vestibular nystagmus is demonstrated by the nearly complete inhibition of nystagmus if the subject fixates on a visual target rotating with him.

The word "dominance" perhaps does not express the proper relationship between visual and vestibular feedback signals in the control of nystagmus. It has already been stated (subsection C.1.) that each semicircular canal acts as a heavily damped angular accelerometer. As such it can provide an appropriate feedback signal to the oculomotor system for motions of short duration, as are normally encountered. During prolonged rotation, however, the signal output of the semicircular canal diminishes due to the elastic restoration of the cupula. Some other modality must take over if stabilization of the retinal image is to be achieved. Vision can and does serve this function, providing at least position error information. Teleologically speaking, one of the functions for which the vestibular system appears to be designed is to provide stabilization of the retinal image for movements of the head of limited amplitude and duration, i.e., movements of the head normally encountered in everyday life.

b. Reflexes Upon Caloric Stimuli

The semicircular canals may be stimulated by temperature changes introduced, usually, by irrigating the outer ear and auditory canal with either hot or cold water or air. The temperature change is conducted first to the lateral part of the horizontal canal and then to the lateral parts of the vertical canals. The change in temperature introduces temperature gradients and hence density gradients in the endolymph. Convection currents will thus be produced in any canal not lying in the horizontal plane, and the associated cupula will be deflected. Reversing the temperature gradient by using cold instead of hot water reverses the direction of convection currents and reverses the deflection of the cupula.

Nystagmus, of course, accompanies deflection of the cupula. The canal stimulated and the direction of nystagmus evoked depends upon the orientation of the head during the test and whether hot or cold water is used. Thus it is possible, with this method, to stimulate the vestibular system on either side of the head and any single canal in either direction. The intensity of the evoked responses can be varied by changing the temperature and/or duration of the irrigation and by changing the ambient gravitational or gravito-inertial field. The convection currents and the resultant nystagmic reflexes are increased by centrifugally increasing the gravitational field and can be eliminated completely by eliminating the effective gravitational field as in a zero-g parabolic flight path. The convection current theory of caloric stimulation is thus supported by the results of such tests of the effects of the gravitational field. If thermic stimuli acted directly on the ampullary or oculomotor nerves, as suggested by some researchers, variations in the gravitational field would have no effect.

3. Summary

This brief review of reflexes evoked by stimulation of the vestibular system should serve to underline the importance of the vestibular system as the predominant motion sensing system in animals and man. Destruction of the labyrinths reduces severely or completely eliminates these reflexes. Certainly other modalities such as vision, hearing, and proprioception serve motion sensing roles, but not to the extent served by the vestibular system. It is predominantly the signals generated by motion stimulation of the vestibular system which are used to achieve and maintain equilibrium of the body and stabilization of images on the retina as the head and body are moved.

CHAPTER III

CHARACTERISTICS OF THE SEMICIRCULAR CANALS — THE CUPULAR MODEL

A. INTRODUCTION

The semicircular canals are man's angular accelerometers. In Chapter II it was shown that stimulation of the semicircular canals evokes sensations of rotation, discrete compensatory motions of the eyes, and nystagmus. The latter two reactions serve the purpose of stabilizing the retinal image as the head is moved.

Anatomically, the semicircular canals consist of three approximately orthogonal ducts in each inner ear. Each duct is filled with a fluid, endolymph, which flows through the duct whenever an angular acceleration in the plane of the duct is experienced by the head. Flow of the endolymph deflects the cupula, a flapper-like valve which seals an expanded portion of each duct called the ampulla. Deflection of the cupula gives rise to a sensation of rotation. The semicircular canals constitute angular accelerometers capable of sensing angular accelerations in any direction as the head is rotated.

As described in Chapter II, subsections C.1. and E.2., the semicircular canals are ideally adapted to sense the short rotations normally experienced by the head and to provide the signals which control compensatory motion of the eyes. If, however, the rotation of the head persists for several seconds, the signal output of the semicircular canals gradually declines, the sensation of rotation vanishes, and compensatory eye motions are no longer elicited. Furthermore, when the rotation stops, the sensation of rotation and compensatory eye motion reverse polarity and persist for 30 sec or more. If the changes in rotation rate are large enough and sufficiently abrupt, disorientation results as the reactions evoked cannot be suppressed by other modalities such as vision. Clearly, such a situation would have important consequences in a piloted aircraft.

It is the purpose of this chapter to explain the dynamics of the semicircular canals and to relate analytically the subjective perception of motion to the acceleration experienced by the head.

The prolonged aftersensations of turning, which may persist for 30 sec or more following unidirectional rotation of the head, cannot be explained on the basis of the fluid-mechanical properties of the semicircular canal alone. This is because frictional damping stops flow of the endolymph relative to the semicircular canal in about 0.5 sec following a change in angular velocity of the canal. However, the cupula forms a movable seal across the ampulla and is made to bend as the endolymph flows "through" the ampulla. When deflected the cupula tends to restore itself to its neutral position, the process taking up to 60 sec or so, depending upon the magnitude of the deflection. So long as the cupula is deflected, the sensation of turning persits. Other manifestations of the cupular deflection, such as the oculogyral illusion (see Chapter V) and nystagmus, may occur.

B. THE TORSION PENDULUM ANALOGY

Steinhausen in 1931 proposed that the function of the semicircular canal/cupula/endolymph system could be represented analytically by that of a heavily damped torsion pendulum. The inertia, spring restoring torque, and damping of the pendulum are analogous, respectively, to the inertia of the endolymph ring, the elastic restoring force of the cupula, and the viscous damping of the endolymph in the canal.

The differential equation describing the system behavior is thus second order, and a number of researchers have attempted to evaluate the constants of the equation. Van Egmond, et al., (ref. 120) describe the method by which the constants of the torsion pendulum model of the cupula/endolymph system were determined. The governing equation is

$$I\ddot{\theta} + B\dot{\theta} - K\theta = I\alpha \qquad (1)$$

or, in Laplace transform form,

$$\left(s^2 + \frac{B}{I}s + \frac{K}{I}\right)\theta = \alpha \qquad (2)$$

where I = moment of inertia of the endolymph in the canal about the sensitive axis of the canal

B = viscous damping torque, at unit angular velocity of the endolymph with respect to the skull

K = stiffness, torque per unit angular deflection of the cupula

θ = angular deflection of the cupula with respect to the skull

α = input angular acceleration about the sensitive axis of the canal

Since the viscous torque is very high compared to the elastic torque, the assumption is made that

$$\frac{K}{B} \ll \frac{B}{I} \tag{3}$$

Equation 2 can then be solved, yielding two real roots. The transfer function expressing cupula deflection, θ, per unit angular acceleration of the head in the plane of the corresponding semicircular canal is

$$\frac{\theta}{\alpha} \doteq \frac{1}{\left(s + \frac{K}{B}\right)\left(s + \frac{B}{I}\right)} = \frac{1}{\left(s + \frac{1}{T_1}\right)\left(s + \frac{1}{T_2}\right)} \tag{4}$$

where

$$\frac{1}{T_1} = \frac{K}{B} \quad ; \quad \frac{1}{T_2} = \frac{B}{I}$$

Using inequality 3, the approximate solution of equation 4 for a velocity step input, γ, is given by

$$\theta \doteq \gamma \frac{I}{B}\left(e^{-Kt/B} - e^{-Bt/I}\right) \tag{5}$$

Again using inequality 3, the approximate solution of equation 4 for an acceleration step input, α, is given by

$$\theta \doteq \alpha \frac{I}{K}\left[1 - \frac{K}{B}\left(\frac{B}{K} e^{-Kt/B} - \frac{I}{B} e^{-Bt/I}\right)\right] \tag{6}$$

1. Determination of B/K

The method used by Van Egmond, et al., to determine the constant B/K is described as follows: The subject is placed in a rotatable chair. For testing the characteristics of the horizontal semicircular canal, the subject's head is tilted forward 30 deg so that the plane of the canal is perpendicular to the axis of rotation of the chair. (This procedure of tilting the subject's head forward has not been followed by all investigators in their efforts to evaluate this same time constant.) The chair is given a subthreshold acceleration until the desired angular velocity is reached. At this point the chair is stopped suddenly in 1 to 3 sec, depending on the velocity. The subject then has a sensation of rotation in the opposite direction to that of the chair. This sensation persists for a period of time dependent upon the "step" change in velocity. The duration of sensation plotted versus, usually, the natural logarithm of the angular velocity step input is called a cupulogram.

The test is performed in darkness. Measurements may also be made of the duration of nystagmus. A plot of the duration of nystagmus versus the log of the input step velocity is the nystagmus cupulogram. Some investigators have presented the subject with a target light, usually a collimated line or star, in an otherwise dark enclosure. The target rotates with the subject, so there is no relative motion between target and subject. In this situation, the subject perceives motion of the target relative to himself which is termed the oculogyral illusion. This illusion is described in Chapter V. The duration of the oculogyral illusion plotted versus the log of the input velocity step is termed the oculogyral cupulogram.

The angular velocities used in the experiments lie between 1 and 60 deg/sec. Larger values have been reported by Van Egmond, et al. (ref. 120) to cause deformation of the cupula resulting in a leak of endolymph past the seal formed between the cupula and ampulla. This leak produces changes in the cupulogram. If the deformation of the cupula is severe, its effects may endure for months.

After the chair stops rotating, the cupula deflects according to equation 5. Figure 21 shows the natural logarithm of cupular deflection versus time for the step change in velocity. The transient associated with the second exponential term in equation 5 dies out quickly and is followed by the slowly decaying exponential $e^{-Kt/B}$. Neglecting the quick transient, $e^{-Bt/I}$, we may write

$$\theta \doteq \frac{\gamma I}{B} e^{-Kt/B} \tag{7}$$

or

$$\ln \theta = \ln \frac{\gamma I}{B} - \frac{Kt}{B} \tag{8}$$

Since the ordinate of figure 21 is $\ln \theta$, the slope of the decaying curve gives the value of K/B. The subject has a sensation of declining angular velocity as the cupula deflection decreases to its neutral position. At some minimum deflection (the threshold deflection, θ_{min}) the sensation of rotation ceases. This threshold deflection differs for either nystagmus or perception of the oculogyral illusion. The time from the onset of stimulation to the cessation of the sensation of rotation is indicated in figure 21 as t_u. Manipulating equation 7 and letting $\theta = \theta_{min}$, gives

$$t_u \doteq \frac{B}{K} \ln \frac{\gamma I}{\theta_{min} B} \tag{9}$$

A plot of the duration of sensation versus the natural logarithm of the magnitude of the step change in angular velocity should be a straight line with a slope of B/K as indicated by equation 9. This relation was first determined by Van Egmond, et al., (ref. 120). The best straight line through the data points of figure 22 gives a value of $B/K = 10$ sec. The data were obtained from a normal sensitive subject. The data from other normal sensitive subjects were similar. The average values for all normal subjects tested gave $B/K = 8$ sec.

Data obtained for B/K by other researchers is presented in section C.

2. Determination of I/B

A torsion swing was utilized by Van Egmond, et al., to determine the constant I/B. Harmonic oscillations about the subject's vertical axis were imposed by placing him in a torsion swing. The resultant stimulation of the horizontal semicircular canals produces a subjective perception of harmonic motion. A specific input/output relationship exists at the undamped natural frequency of the cupula/endolymph system. From equations 2 and 4, the undamped natural frequency of the cupula/endolymph system is

$$\omega_o = \sqrt{\frac{K}{I}} = \sqrt{\frac{K}{B} \cdot \frac{B}{I}} = \sqrt{\frac{1}{T_1} \cdot \frac{1}{T_2}} \tag{10}$$

When the frequency of the swing is equal to the undamped natural frequency of the cupula/endolymph system, the deflection of the cupula (and hence the sensation of rotation) lags the deflection of the swing by 90 deg as illustrated in figure 23. When the swing is at its maximum deflection, the cupula deflection is zero and there is no sensation of turning. When the swing is at zero deflection, the cupula is at maximum deflection and the sensation of the rate of rotation is a maximum. If the frequency of the swing is greater than the undamped natural frequency of the cupula/endolymph system (or canal to be brief), the sensation of rotation lags the swing deflection by more than 90 deg, and if the swing frequency is less than that of the cupula/endolymph system, the sensation of rotation lags the swing deflection by less than 90 deg. By comparing the phase relationship between the sensation of motion and the deflection of the swing, it is possible to determine the frequency of resonance and, hence, the natural frequency, ω_o, of the canal. This determination, possible only for sensitive subjects, was found by Van Egmond to be: $\omega_o = 1.0$ rad/sec. Utilizing equation 10 and the previous determination that B/K = 10 sec, we can show that

$$\frac{I}{B} = \frac{1}{\frac{B}{K}\omega_o^2} = 0.10 \text{ sec} \tag{11}$$

Inserting these values for I/B and B/K into equation 4, the transfer function expressing cupula deflection, θ, per unit angular acceleration, gives

$$\frac{\theta}{\alpha} = \frac{1}{\left(s + \frac{K}{B}\right)\left(s + \frac{B}{I}\right)} = \frac{1}{\left(s + \frac{1}{T_1}\right)\left(s + \frac{1}{T_2}\right)} = \frac{1}{(s + 0.1)(s + 10)} \qquad (12)$$

This transfer function is valid for an input angular acceleration, α, the vector of which is perpendicular to the plane of the horizontal semicircular canal. Transfer function parameters for the superior and posterior canals are presented in the next subsection.

3. The Subjective Perception Transfer Function

The cupular deflection transfer function of equation 12 is related to the subjective perception transfer function as follows. Some subjects are able to estimate the angle through which they feel they have turned due to the sensation of angular velocity after the turning test. By timing, say, the revolutions perceived by the subject, the mean subjective angular velocity can be determined. As reported in reference 120, Groen and Jongkees (ref. 69) performed such an experiment and obtained good agreement between the actual step input velocity and subjective velocity estimates extrapolated to t = 0.

Reference 75 illustrates an example of this type of experiment as shown in figure 24. The subjective angular velocity following a step input of 40 deg/sec is extrapolated to t = 0 giving 40 deg/sec, perfect agreement for this particular example. If the rapidly decaying transient term, $e^{-Bt/I}$, in equation 5 is neglected, the cupula deflection, θ, in response to a step input velocity, γ, is given by

$$\theta \doteq \frac{\gamma I}{B} e^{-Kt/B} \qquad (13)$$

Extrapolating to t = 0,

$$\theta \doteq \frac{\gamma I}{B} = 0.1\gamma \text{ sec} \qquad (14)$$

The subjective perception of angular velocity is equal to the objective velocity step input or is equal, numerically, to ten times the cupula deviation, θ. The subjective perception transfer function, therefore, has a gain ten times that of the cupular transfer function. Thus for the lateral semicircular canal we have

$$\frac{\text{subjective angular velocity}}{\text{input angular acceleration}} = \frac{10}{(s + 0.1)(s + 10)} \qquad (15)$$

or

$$\frac{\text{subjective angular velocity}}{\text{input angular velocity}} = \frac{10s}{(s + 0.1)(s + 10)} \qquad (16)$$

4. Accuracy of Results

Van Egmond (ref. 120) states that the probable error in measuring K/I is about 20 percent, and the probable error in measuring B/I is about 25 percent. The probable errors in T_1 and T_2 are therefore about 25 percent.

C. COMPARISON OF DATA OBTAINED BY VARIOUS RESEARCHERS FOR MOTIONS ABOUT THE YAW, PITCH, AND ROLL AXES

Numerous researchers have, in essence, repeated the rotation test experiments of Van Egmond, et al., to determine the value and variability among subjects of the long time constant, B/K. The results of a number of these efforts are tabulated in Table VIII. Most of the studies treat motions about the vertical (yaw) axis of the head. Additionally, Jones, Barry, and Kowalsky (ref. 81), and Benson and Bodin (ref. 8) treat motions about the lateral (pitch) axis, and Jones, Barry, and Kowalsky (ref. 81), and Meiry (ref. 97) treat motions about the sagittal (roll) axis.

For yawing motions, Table VIII shows that values of the cupulogram slope, B/K, average to be 7–8 sec for perception of the oculogyral illusion, 6–10 sec for subjective perception of motion, and 8–16.5 sec for nystagmus. Representative cupulograms of the three phenomena are shown in figure 25. Experimental methods of the various investigators differed in detail and in the degree of vestibular training of the subjects. The

TABLE VIII

EVALUATION OF THE LONG TIME CONSTANT, B/K, BY VARIOUS RESEARCHERS

RESEARCHER, YEAR, AND REFERENCE	CHANNEL	AVERAGE VALUE OF B/K OBTAINED BY EACH OF THREE METHODS			NUMBER AND EXPERIENCE OF SUBJECTS	EXPERIMENTAL METHOD
		SUBJECTIVE CUPULOGRAM	NYSTAGMUS CUPULOGRAM	OCULOGYRAL CUPULOGRAM		
Van Egmond, Groen, and Jongkees, 1949, ref. 120	Yaw	8 sec normal subjects 10 sec sensitive subjects			Not specified	Subject seated in rotating chair with head inclined forward about 30 deg. Acceleration subliminal (inferred 1/3 deg/sec^2) to angular velocity of 1 – 60 deg/sec. Braking time: 1 – 3 sec. Subject in darkness.
Groen, 1960, ref. 67	Yaw	8 sec normal subjects 6 sec 18 experienced aviators	16 sec normal subjects 8 sec 18 experienced aviators		18 experienced aviators plus an unknown number of ordinary normal subjects	Not known
Jones, Barry, and Kowalsky, 1964, ref. 81	Yaw Pitch Roll	10.2 ± 1.8 sec 5.3 ± 0.7 sec 6.1 ± 1.2 sec	15.6 ± 1.2 sec 6.6 ± 0.7 sec 4.0 ± 0.4 sec		7–8 normal subjects	Subject seated erect on platform rotated about a vertical axis. Head fixed in appropriate orientation by means of a dental bite which itself was fixed to turntable via a universal joint. Apparently, normal head/neck posture not maintained for pitch and roll tests. Angular velocity stimuli of 5, 10, 20, 40, 60°/sec. Acceleration unspecified. Braking time unspecified.
Meiry, 1965, ref. 97	Roll	7 sec			3 normal subjects	Subject seated and bent forward at waist (to retain normal head/neck posture) facing downward with head on a rest. Rotation about vertical axis in a darkened, hooded cab. Acceleration, angular rates, and braking time unspecified.
Benson and Bodin, 1965, ref. 8	Yaw Pitch		8.5 sec* 14 normal subjects 16.5 sec** 8 normal subjects 7.5 sec** 8 normal subjects		8–14 normal subjects	*Subject strapped in a rigid stretcher and rotated about a horizontal axis passing through the subject's longitudinal axis. Subject rotated with eyes closed at 60 deg/sec for 6 complete revolutions and stopped in one of four positions: face up or down, or right side up or down. B/K appeared to be independent of stopping position. Acceleration and braking times not specified. Measurements of eye movement made by a dc oculographic technique. **Subject seated in a tiltable chair which rotated about a vertical axis. Subject accelerated at 1 deg/sec^2 to 60 deg/sec. Subject stopped after one minute (10 revolutions) in less than 2 sec.
Dobie, 1965, ref. 39	Yaw			7.2 sec.. 7.73 sec.. 7.14 sec..	158 student pilots 31 student pilots with 50-300 hr previous in-flight training (average 170 hr) 127 student pilots without previous inflight training	Subject seated erect in a chair which is rotated about a vertical axis. Acceleration at 1/3 deg/sec^2 to ±60, ±40, ±20, ±10, ±5 deg/sec. Rotation at constant velocity for 60 sec. Braking time: 1.5 sec.

effects of vestibular training (habituation) are discussed in section F. In the yaw channel experiments, Van Egmond, et al., tilted the subject's head forward 30 deg so that the axis of rotation (vertical) was perpendicular to the plane of the lateral semicircular canals. The other researchers of Table VIII neglected this refinement and rotated their subjects about the head vertical axis. Apparently little difference was produced in the data.

Benson and Bodin (ref. 8) show the very low value of B/K = 8.5 sec for the nystagmus cupulogram in yaw when a reclining subject is rotated about a horizontal axis aligned with the subject's longitudinal axis. The researchers' object was to show how the orientation of the subject with respect to the gravity vector affected the cupulogram. Such orientation does affect the cupulogram slope, B/K, and must be taken into account when interpreting data. To compare with flight experience, the nominal orientation of the subject should be that of a person seated upright with his head erect, and the turning test should terminate with the subject in this position. It is also desired to minimize stimulation of the utricles so as to minimize whatever influence they assert on responses of the semicircular canals.

The findings of the various investigators of Table VIII are in fairly good agreement with one another considering the high degree of variability among subjects. The largest number of subjects were tested by Dobie (ref. 39). An idea of the spread in evaluations of B/K determined from the perception of the oculogyral illusion in yaw is given by figure 26. While the 158 student pilot subjects averaged 7.2 sec for B/K, there is a broad spread of data between 4 and 12 sec. A similar spread can be expected in B/K for the subjective perception of motion.

In the pitch channel the only evaluation uncovered for subjective perception was that of Jones, Barry, and Kowalsky (ref. 81) which gives B/K = 5.3 ± 0.7 sec. This value compares with 6.6 ± 0.7 sec obtained by the same investigators for the observation of nystagmus and 7.5 sec obtained by Benson and Bodin (ref. 8) for nystagmus. It should be noted that in the experiments of Jones, et al., normal head/neck posture was not retained, and in the experiments of Benson and Bodin the subjects were rotated about a vertical axis while seated with either their right or left sides down, a situation not generally encountered in flight.

In the roll channel, Jones, et al., obtained a value of B/K = 6.1 ± 1.2 sec for subjective perception compared to B/K = 7 sec obtained by Meiry. Again, normal head/neck posture was not retained in the experiments of Jones, et al., but was in Meiry's work.

No other researchers were found to have corroborated the evaluation of I/B = 0.1 sec by Van Egmond, et al. Hallpike and Hood (ref. 73) claim to have done so, but in actual fact they did not; their evaluation was independent of I/B.

D. THRESHOLD OF PERCEPTION

The threshold level of acceleration required to elicit a noticeable response has been determined by observing the three separate indicators of semicircular canal activity. These are: (1) subjective perception of motion, (2) nystagmus, and (3) the oculogyral illusion (an apparent movement of a target light in the dark). In general, researchers have found that the threshold for the first occurrence of nystagmus exceeds that of the subjective perception of motion which, itself, is nearly the same as that for the first appearance of the oculogyral illusion. Table IX (adapted from ref. 75) shows some of the determinations made of the three thresholds. The thresholds listed are for rotation about the vertical axis with the head erect.

The wide variation in results even in determination of the same threshold can be attributed to a number of factors. First among these is probably the variability among the subjects tested. Many of the experimenters tested only a small number of subjects (as few as three). Second, the conditions under which the experiments were made affect the results. It is difficult to accelerate a subject smoothly and to exclude extraneous sources of information such as sound. Third, procedure in the conduct of the experiment and the evaluation of the results differ among investigators. For instance, in determining the subjective perception threshold, a widely used method is to apply a known constant angular

TABLE IX

THRESHOLDS FOR ROTATION ABOUT THE VERTICAL AXIS
(ADAPTED FROM REF. 75)

METHOD	INVESTIGATOR (YEAR)	THRESHOLD VALUE deg/sec^2
Subjective Perception of Motion	Mach (1875)	2.0
	Dodge (1923)	2.0
	Tumarkin (1937)	0.2
	Hilding (1953)	< 1.0
	Mann and Ray (1956)	0.035
	Clark and Stewart (1962)	0.12
	Meiry (1965)	0.14
Nystagmus	Dohlman (1935)	1.0
	Buys (1937)	0.8
	Buys and Rijlant (1939)	0.8
	Montandon and Russbach (1955)	0.8
Oculogyral Illusion	Christian (1939, 1940)	0.13
	Groen and Jongkees (1948) (using aftersensations)	0.5
	Graybiel, Kerr, Bartley (1948)	0.12

acceleration to the subject. His task is to determine the resultant direction of motion. The time required to detect the motion is termed the latency time. The threshold is determined to be the minimum acceleration for which the subject can judge correctly the direction of rotation for a certain percentage (usually 70 or 75 percent) of the trials. The sequence of the magnitudes and directions of the accelerations, the percentage value of correct judgments of direction, and the maximum latency time allowed all affect the determination of the threshold.

The use to which the threshold data are to be put must also be considered. For the very small threshold of 0.035 deg/sec^2 reported by Mann and Ray (ref. 95), latency times of 20 to 40 sec were recorded. In a closed-loop tracking task such long times for detection of motion are not available to the operator, so that his threshold for effective control must be considerably larger than those represented in Table IX. It should be remembered that the threshold measurements were made on subjects concentrating solely on the task of sensing motion. In a tracking task the operator must evaluate both visual and motion inputs, and he must act to minimize his tracking error. Accordingly, less than full attention is paid to the motion input. To an extent, unknown at present, the human operator's effective threshold is therefore task dependent.

For rotation about the head sagittal (roll) axis, Meiry (ref. 97) obtained a threshold of 0.5 deg/sec^2 using the method of step input accelerations described above. Rotation was about an earth-fixed vertical axis with the subject seated and bent over at the waist with his face down. In this position, normal head/neck posture was retained. In all the literature reviewed, Meiry is the only investigator to measure subjective perception threshold characteristics for rotation about either horizontal axis of the head.

The deviation of the cupula at the threshold can be ascertained from equation 9 and a typical cupulogram. Consider figure 25. The duration of aftereffect following a threshold level stimulation is zero as shown by the intercept of any of the three lines with the abscissa in figure 25. In equation 9 the time, t_u, from onset of stimulation to cessation of the perception of rotation is given as approximately equal to (B/K)/ $\ln(\gamma I/\theta_{min} B)$, so that for threshold level stimulation, $t_u = 0 = \ln \gamma I/ \theta_{min} B$, or

$$\theta_{min} = \frac{I}{B} \gamma_{min} \tag{17}$$

If the ratio I/B can be determined independently, then the deviation of the cupula at threshold can be determined by the cupulogram. Figure 25 shows the lowest threshold for the oculogyral illusion and the highest threshold for nystagmus. For example, if we assume that I/B = 0.1 sec we get θ_{min} = 0.11 deg for perception of the oculogyral illusion, θ_{min} = 0.27 deg for the subjective perception of motion, and θ_{min} = 0.9 deg for nystagmus.

With this independent determination of θ_{min}, we can calculate the acceleration threshold a subject can sense, given sufficient time to perceive the stimulus. For times long enough for the transients to die out, equation 6 reduces to

$$\theta \doteq \frac{\alpha I}{K} \tag{18}$$

Thus the threshold acceleration, α_{min}, is related to the minimum cupula displacement by

$$\alpha_{min} = \frac{\theta_{min}}{I/K} \tag{19}$$

Using the values of θ_{min} determined from figure 25, we get

α_{min} = 0.11 deg/sec^2 for perception of the oculogyral illusion

= 0.27 deg/sec^2 for subjective perception of motion

= 0.9 deg/sec^2 for onset of nystagmus

These values agree fairly well with those shown in Table IX.

A study of the cupulogram thus permits the evaluation of a number of parameters defining the function of the semicircular canals. Using equation 9, the slope of the cupulogram gives the value of the long time constant, B/K. Using equation 17, the intercept of the cupulogram with the abscissa gives the value of the cupula deflection, θ_{min}, at the threshold of perception. Using equation 19, the acceleration threshold, α_{min}, is determined from θ_{min}.

E. LATENCY TIME

The thresholds of perception of angular acceleration have been described above in terms of only one dimension, stimulus intensity. However, in describing thresholds, the time required to detect the stimulus is an important variable. The time from the beginning of the input stimulus until it is perceived is termed the latency time and is a function of the magnitude of the input stimulus and the dynamics of the sensor.

A widely used technique of measuring the threshold of the semicircular canals is to apply a step input angular acceleration and record the time required by the subject to determine the direction of the resultant motion. The determination is made by either the subjective perception of motion or by the perception of the oculogyral illusion (ref. 72). Van Egmond, et al., (ref. 120) suggest that the threshold is associated with a minimum deflection of the cupula which gives rise to perception of motion or a motion-induced effect such as the oculogyral illusion.

The step response of the cupula to an angular acceleration is given by equation 6:

$$\theta \doteq \alpha \frac{I}{K}\left[1 - \frac{K}{B}\left(\frac{B}{K} e^{-Kt/B} - \frac{I}{B} e^{-Bt/I}\right)\right]$$

Since $I/B \ll B/K$ we may drop the second exponential term and simplify the resultant expression to give:

$$\theta \doteq \alpha \frac{I}{K}\left(1 - e^{-Kt/B}\right) \tag{20}$$

If θ_{min} is the deflection of the cupula at the threshold of perception we may write:

$$\theta_{min} \doteq \alpha \frac{I}{K}\left(1 - e^{-K\tau/B}\right) \tag{21}$$

or

$$\tau \doteq \frac{B}{K} \ln \frac{\alpha \frac{I}{K}}{\alpha \frac{I}{K} - \theta_{min}} \tag{22}$$

where τ = latency time

Equation 22 is plotted in figure 27 with data obtained by various researchers. The curve of equation 22 is asymptotic at $\theta_{min} = 0.25$ deg, the cupular deflection at threshold obtained by Van Egmond, et al., (ref. 120). The data shown do not support such a high value of the threshold, Mann and Ray, for instance, having obtained an average threshold of 0.035 deg/sec^2, which corresponds to a cupula deflection of 0.035 deg. For latency times less than 5 sec, equation 22 fits the data of Clark and Stewart (ref. 32) and of Meiry quite well. This equation will be used, because it makes no sense to consider latency times greater than 5 sec in closed-loop tracking tasks.

The latency time data are of interest in that they serve to verify the analytical model of the semicircular canals and give information on the values of θ_{min} and γ_{min}.

F. HABITUATION

1. Effects of Vestibular Training

Individuals whose vestibular systems have undergone continuous or repeated stimulation over a period of time show differences in their vestibular reactions with respect to those of individuals without a history of vestibular "training" and with respect to their own vestibular reactions after their training has been discontinued for a period of time. The class of vestibularly trained individuals would include dancers, acrobats, figure skaters, and fighter pilots in active training.

Vestibular training manifests itself by (1) a decrease in the duration of postrotatory effects: oculogyral illusion, perception of motion, and nystagmus, and (2) an increase in the threshold of perception of these manifestations. The decrease in the duration of postrotatory effects results from two factors: the increase in the threshold of perception and an increase in the rate of decay of the effects themselves. The increase in the decay rate is observed in cupulograms of subjective perception of motion and of nystagmus and is associated with a decrease of the long time constant B/K.

Aschan (ref. 5) studied 100 pilots on active duty in the Royal Swedish Air Force. According to their sensation cupulograms for yawing rotations pilots not in training measured B/K = 10 sec, and pilots undergoing moderate flying activities and pilots with virtually daily flying activities measured B/K = 5 sec. The average for all pilots tested was B/K = 8 sec. Groen (ref. 67) tested a group of ordinary normal subjects and a group of 18 experienced aviators. The value of B/K for yawing motions of the ordinary subjects averaged 8 sec and that of the aviators averaged 6 sec. Vestibular training produces, in some fashion, an habituation to excitation of the semicircular canals and yields a change in the parameters of the semicircular canal system transfer function. Habituation increases the threshold of perception and decreases the bandwidth of the semicircular canal system. No report was found in the literature concerning any change in the value of the short time constant, I/B.

2. Mechanisms of Habituation

The mechanism by which habituation is produced is not known, but several contributory mechanisms have been suggested. Four of these contributory mechanisms are:

- Efferent sensory control
- Arousal
- Directional balance
- Learning

a. Efferent Sensory Control

Gillingham (ref. 48) reviews the work of a number of investigators and concludes that there is abundant evidence of efferent fibers in the vestibular system. (See Chapter II, subsection D.4.) The action of the efferent nerves appears to be localized in the sensory end organs, the cristae. Experiments with cats have associated a marked decline in the effects of habituation with section of the vestibular efferent tracts (ref. 48).

Gillingham states that it "appears very likely that the vestibular system is subject to the same sort of regulatory activity we believe to exist in . . . other sensory systems." The experiments on habituation alluded to above suggest a strong influence by the central nervous system on vestibular information processing. The vestibular efferent system is one physiologic mechanism by which such influence could be asserted.

b. Arousal

Guedry (ref. 70) and Howard and Templeton (ref. 75) report that a subject's state of alertness or arousal has a strong effect on habituation. Activity which keeps the subject alert, such as mental arithmetic, delays or prevents habituation, while lack of attention causes rapid attenuation of nystagmus.

c. Directional Balance

Howard and Templeton (ref. 75) discuss a "directional balance mechanism" the thesis of which is that repeated rotation in both directions produces no habituation and that repeated rotation in one direction produces a decrease in the duration of effects (nystagmus, perception of motion) produced by motion in the practiced direction and an increase in the duration of effects produced by motion in the unpracticed direction. Habituation is thus regarded as a shift in the balance between the effects of opposite directions of rotation rather than as an overall reduction of response following vestibular training.

The weakness in this view of habituation lies in the fact that a unidirectional rotational test requires both a positive and a negative acceleration in the test direction, and it is acceleration which stimulates the vestibular system. Howard and Templeton (ref. 75) report that it has been demonstrated that the relative duration of rotation and rest intervals is a determining factor in vestibular training. If, during training, the rotation interval is short relative to the rest interval, the duration of postrotatory nystagmus in subsequent tests will be greater for rotation in the practiced direction than for rotation in the unpracticed direction. Conversely, if, during training, the rotation interval is long relative to the rest interval, the duration of postrotatory nystagmus in subsequent tests will be less for rotation in the practiced direction than for rotation in the unpracticed direction. From this behavior it is apparent that the amount of habituation which takes place depends on the extent to which the nystagmus occurring during training has been allowed to run its course. Since nystagmus is an indicator of cupula deflection, it is evident that the amount of habituation which takes place depends on the extent to which the cupula, deflected by the starting acceleration, is allowed to restore its neutral position before being deflected by the stopping acceleration of opposite sign. Habituation can occur for both directions provided the nystagmus occurring during training is allowed to run its course in each direction. Such behavior is not accounted for by the directional balance mechanism.

If the directional balance mechanism does operate, we would expect spontaneous nystagmus to occur in a subject at rest who is unidirectionally habituated. Howard and Templeton (ref. 75) report that several investigators have observed such nystagmus.

Other experimenters have observed reduction of caloric nystagmus in either direction following training consisting of repeated unidirectional caloric stimulation. In addition to this observed transfer of habituation to the unpracticed direction, some transfer of habituation to unpracticed planes has also been reported.

In conclusion, it may be said that the directional balance mechanism appears to operate, but it does not account for all the observed phenomena of habituation.

d. Learning

Vestibular habituation is most likely a form of learning. The vestibular apparatus seems best adapted to sense rotations of short duration whereby a starting acceleration is soon countered by a stopping acceleration. In daily life neither animal nor man is exposed to continuous rotation for any length of time. Usually, it is only when man mounts one of his machines that he is apt to be exposed to such continuous rotation for more than a short time. As a result, the motion sensed by his vestibular apparatus may conflict with that sensed visually or proprioceptively. Such a conflict of cues could be resolved by giving a greater weighting to the visual and/or proprioceptive cues, provided the individual "knows" which information is correct. Without such knowledge, severe disorientation can result. With such knowledge, the individual learns to ignore the spurious cues provided by the vestibular apparatus. Learning, then, is probably achieved by giving a greater weight to the visual and/or proprioceptive information.

Of the four mechanisms suggested as possibly contributing to habituation, it is likely that at least three, efferent sensory control, arousal, and learning have a strong effect on the habituation process.

G. MATHEMATICAL MODEL OF THE SEMICIRCULAR CANALS

The dynamics of the semicircular canals can be expressed in the mathematical model represented in figure 28. This representation is adapted from Meiry (ref. 97). The three parallel paths do not represent individual semicircular canals or pairs of canals, but represent the dynamic processing of angular acceleration inputs occurring in each of the three orthogonal axes of the head. As discussed in Chapter II, subsection D.5.b., components of acceleration about either horizontal axis of the head stimulate all four vertical canals.

The orientation matrix, $\left[A\right]$, expresses the orientation of the head axis system with respect to the earth-fixed system. When the input acceleration exceeds the threshold value, associated with some minimum deviation of the cupula, a signal is received by the central nervous system, giving rise to a subjective perception of angular velocity. Throughout the dynamic range of the semicircular canals, the transfer characteristic, F(s), of the central nervous system is presumed to be unity.

Meiry portrays the transfer characteristics for angular motion about a given principal axis of the head in a frequency response plot, as in figure 29, with angular velocity as the input and subjective perception of angular velocity as the output. The deadzone introduced by the threshold is not represented in the frequency response plot. This is not a serious shortcoming of a model intended for use in closed-loop aircraft flight control studies, because the threshold is small compared to the accelerations normally encountered in flight.

The value of the long time constant, B/K, for rotations about each of the principal axes of the head and for various types of subject is given in Table X. Attention is called to figure 26 showing the variability among different subjects of this parameter. The only data found (ref. 120) give the value of the short time constant, I/B, as 0.1 sec. Meiry's determinations of the angular acceleration thresholds of 0.14 deg/sec^2, 0.5 deg/sec^2, and 0.5 deg/sec^2 for yaw, roll, and pitch motions, respectively, are selected.

TABLE X

VALUE OF B/K FOR ROTATIONS ABOUT PRINCIPAL AXES OF HEAD AND FOR VARIOUS TYPES OF NORMAL SUBJECT (DERIVED FROM TABLE VIII)

MOTION	AVERAGE VALUE OF B/K, SEC	TYPE OF SUBJECT
Yaw	10 8 6	Normal sensitive subject Normal average subject Highly-trained subject (fighter pilot in daily training)
Roll	6.5	Normal average subject
Pitch	5.3	Normal average subject

CHAPTER IV

THE UTRICLES

A. INTRODUCTION

It is generally agreed that the utricles are man's primary sensors of linear acceleration. In Chapter II it was shown that stimulation of the utricles evokes various sensations and reflexes including (1) subjective sensations of motion or of changes in orientation with respect to the gravity vector, (2) postural and righting reflexes of the body, and (3) compensatory eye movements, particularly counterrolling, which tend to stabilize the retinal image.

The anatomical structure of the utricle is characterized by a moving mass, the otolith, and a stationary supporting structure, the macula, containing sensory cells. Motion of the otolith relative to the macula and in the plane of the macula stimulates the sensory cells. Components of acceleration in the plane of the macula deflect the otolith and thus constitute the effective stimulus of the utricle.

Since the macula is slightly curved, it is not strictly correct to speak of the plane of the macula. The phrase, plane of the macula, therefore signifies the mean plane of the macula. In each utricle this mean plane is elevated 26 to 30 deg above the horizontal plane in the erect head. Judging by its orientation, the utricle should be sensitive to accelerations along the sagittal, lateral, and vertical axes, although its sensitivity to accelerations in the horizontal plane should be greater than its sensitivity to accelerations along the vertical axis.

Data on the dynamics of the utricles appears to be limited to those of Meiry (ref. 97). His findings are presented in this chapter along with the results of various researchers on the stimulation threshold of the utricles and on the effects of habituation.

B. STATIC CHARACTERISTICS OF THE UTRICLES

There was much argument in the past as to what force constituted the effective stimulus of the utricle. The arguments centered over two rival theories: one asserting that the pressure exerted by the otolith on the macula was the active force, the other that the shear force between the otolith and macula was the active force. If the former were correct, the response of the utricle would vary as the cosine of the angle of head tilt. If the shear force theory were correct, the response of the utricle would vary as the sine of the angle of tilt.

Comparatively recently more experimental evidence has accumulated, and it is now generally agreed that the argument is resolved in favor of the shear force theory.

According to Colenbrander (ref. 35) the following researchers contributed to this resolution:

Ulrich (ref. 118) manipulated the otoliths of the pike and demonstrated reactions to sliding in all directions except toward the medial side.

De Vries (ref. 38) demonstrated that under natural conditions, the otolith is displaced only 0.1 to 0.2 mm.

Löwenstein (ref. 87) and his co-workers recorded action potentials from single fibers of the utricular nerve of the ray and found a frequency modulated signal that was proportional to the shearing force of the otolith along the sensory epithelium of the macula.

More recently the results of Trincker (ref. 117), as cited in Howard and Templeton (ref. 75), provide additional support of the shear force theory. Trincker recorded changes in potential inside the sensory cells of the macula of the guinea pig and found that only shearing forces produced by tangential displacement of the otolith were effective in producing sensory responses. Neither pressure nor tension applied at right angles to the macular epithelium were effective. Trincker also demonstrated with actual recordings from the tilting macula of the guinea pig that the utricular response was a function of the sine of the angle of tilt.

Thus sufficient experimental evidence exists to support the following statements on the function of the utricles:

- The utricle acts as a multidirectional linear accelerometer and, because of its orientation in the head, is capable of sensing components of acceleration along the sagittal, lateral, and vertical axes.
- Components of acceleration in the mean plane of the macula, which produce a shearing force between the otolith and macula, provide the effective stimulus of the utricle.
- The utricle is sensitive to both the direction and magnitude of the acceleration stimulus.

C. DYNAMIC CHARACTERISTICS OF THE UTRICLES

The only data found during the literature search on the dynamic characteristics of the utricles are those of Meiry (ref. 97). He experimented with three subjects experienced in psychophysical studies. In Meiry's experiments, the subject was seated upright in a linear motion simulator with his sagittal axis horizontal and parallel with the direction of motion. The simulator was driven back and forth along its track with a single frequency sinusoidal function. The subject indicated his direction of motion by displacing a light, spring-restrained stick. Recordings were made of the position of the simulator and of the subject's response.

Data were presented in Meiry's report of the phase of the subjective perception of velocity with respect to the velocity of the simulator at each of the test frequencies. Data were given at 0.01 cps intervals from 0.15 cps to 5 cps. Meiry obtained an excellent fit of the phase data with that of a second-order minimum phase system:

$$\frac{\text{subjective perception of velocity}}{\text{input velocity}} = \frac{Ks}{(s + 0.1)(s + 1.5)} \tag{23}$$

This transfer function fits the data for inputs along the sagittal axis with the sagittal axis in the horizontal plane.

D. THRESHOLD OF PERCEPTION

The threshold level of acceleration detectable by the human has been measured by a number of researchers. Two indicators of utricle activity have been employed: subjective perception of motion and the oculogravic illusion (an apparent tilting of a target light in the dark). Table XI (adapted from ref. 124) shows some of the determinations made. Each of the thresholds shown is for subjective perception of motion except that of Graybiel and Patterson which is for perception of the oculogravic illusion.

TABLE XI

THRESHOLD OF PERCEPTION OF LINEAR ACCELERATION
DETERMINED BY VARIOUS RESEARCHERS

RESEARCHER (YEAR)	APPARATUS	PLANE OF MOVEMENT	THRESHOLD g's
Mach (1875)	Balance	Vertical	0.012
Delage (1888)	Parallel swing	Horizontal	0.023
Bourdon (1914)	Trolley pulled by falling weight	Horizontal	0.004 – 0.015
Travis and Dodge (1928)	Oscillating platform	Horizontal	0.003 – 0.016
Kunze quoted by Armstrong (1939)	No details	Horizontal	0.002 – 0.020
Jongkees and Groen (1946)	Parallel swing	Horizontal	0.006 – 0.015
Lansberg (1954)	Parallel swing	Horizontal (subject lying on back)	0.009
Graybiel and Patterson (1954) (oculogravic illusion)	Human centrifuge	Horizontal (subject seated upright)	0.027

A host of factors contributes to the order-of-magnitude difference found in the threshold values by different researchers. These factors include, but are not limited to, the following:

- differences in orientation of the subject with respect to the direction of motion
- variability among subjects
- differences in the degree to which other sense modalities (proprioception, sound, vibration) were excluded
- differences in the test method (The parallel swing, for instance, introduces dynamic effects. See below.)
- differences in interpretation of the data, e.g., did the subject determine merely the presence or absence of motion or did he have to determine the direction of motion as well? What percentage of correct response determined the threshold?

Any test of threshold involving a periodic input, such as in a parallel swing, introduces dynamic effects. If, for instance, the parallel swing has a period of 2.5 sec, then the input acceleration derived from the swing has a frequency of about 2.5 rad/sec. If Meiry's second-order transfer function model of the utricles is accepted, then the subjective perception of acceleration is attenuated approximately 6 dB at 2.5 rad/sec. The threshold measurement would thus be high by a factor of two. Thus, because of dynamic effects, thresholds of acceleration measured with periodic inputs should not be compared directly with those determined using constant values of acceleration.

Walsh (ref. 124) measured the thresholds of normal subjects lying down in various positions on a stretcher suspended in a parallel swing. His results are summarized in Table XII. Motion in the direction of the long axis of the body would produce accelerations nearly parallel to the vertical axis of the head. Motion transverse to the long axis of the body would produce accelerations approximately parallel to the lateral axis of the head in the supine and prone positions and approximately parallel to the sagittal axis when the subject was lying on

TABLE XII

THRESHOLD OF PERCEPTION OF LINEAR ACCELERATION DETERMINED ON A PARALLEL SWING WITH PERIOD = 2.5 SEC (REF. 124)

DIRECTION OF MOTION	POSITION OF SUBJECT	THRESHOLD, g's	NUMBER OF TRIALS
Parallel to long axis of body	Supine	0.0025 ± 0.0022	7
	Prone	0.0019 ± 0.0010	7
	On right	0.0019 ± 0.0016	5
	On left	0.0022 ± 0.0019	4
Transverse to long axis of body	Supine	0.0019 ± 0.0007	7
	Prone	0.0019 ± 0.0010	7
	On right	0.0019 ± 0.0011	5
	On left	0.0016 ± 0.0021	4

either side. The subject was required to indicate the direction of motion he perceived. The mean value of acceleration of from four to seven trials was taken as the threshold. In each trial, the value recorded was of the peak acceleration of the smallest oscillation detected.

The results shown in Table XII do not show the differences in threshold to be expected for stimulation of the utricles along three orthogonal axes. The threshold acceleration along any axis should be inversely proportional to its component of acceleration in the plane of the macula. It is this component of acceleration which displaces the otolith and gives rise to a sensation of motion. The oblique orientation of the utricles in the head (elevated about 30 deg above the sagittal axis) means that accelerations along orthogonal axes will have different components of acceleration in the plane of the macula. Accordingly, the thresholds of perception of acceleration along the sagittal, vertical, and lateral axes should relate to one another in the ratios, $(1/\cos 30^\circ):(1/\sin 30^\circ):1$, respectively.

Meiry (ref. 97) measured the thresholds of three normal subjects on a linear motion simulator. Each subject was exposed to a step input acceleration and required to determine the direction of motion. Meiry obtained thresholds of 0.01g for accelerations along the vertical axis of the head with the subject supine and 0.006g for accelerations along the sagittal axis with the head upright.

The remarks in the previous chapter concerning the applicability of threshold measurements to a pilot model suitable to tracking tasks are pertinent here. The threshold measurements described above were made on subjects concentrating solely on the task of sensing motion. In a tracking task the operator must evaluate both visual and motion inputs, and he must act to minimize his tracking error. Accordingly, less than full attention is paid to motion sensing. To an extent, unknown at present, the human operator's effective acceleration thresholds are therefore task dependent.

E. LATENCY TIME

If, as postulated for the semicircular canals, the threshold of perception is associated with some minimum physical displacement of the sensing element, then the latency time to detect a change in acceleration will correspond to the duration of travel of the otolith from its rest position to the threshold deflection. The minimum acceleration detectable is thus dependent on the time available for detection.

Using Meiry's model of the utricles, given by equation 23, the response to a step input in acceleration, a, is given by

$$\text{subjective perception of velocity} = \frac{aK}{0.15}\left(1 + 0.07e^{-1.5t} - 1.07e^{-0.1t}\right) \tag{24}$$

If the subjective perception is associated with the displacement of the otolith, then the minimum displacement, d_{min}, of the otolith at the threshold may be written as

$$d_{min} = aK_d\left(1 + 0.07e^{-1.5\tau} - 1.07e^{-0.1\tau}\right) \tag{25}$$

where τ = latency time

K_d = constant

The first exponential term is negligible compared to the second exponential and dies out within 1 sec, so that

$$d_{min} \doteq aK_d\left(1 - 1.07e^{-0.1\tau}\right) \qquad \tau \geq 1 \text{ sec} \qquad (26)$$

or

$$\tau \doteq 10 \ln \frac{1.07a}{a - \frac{d_{min}}{K_d}} \qquad \tau \geq 1 \text{ sec} \qquad (27)$$

Meiry measured the latency times of three subjects using step accelerations randomized in direction (sign) and magnitude. Figure 30 shows the mean latency times for three subjects for perception of the input acceleration along the head vertical axis and with the subject in the supine position. The solid curve is that of equation 27 referenced to the experimental data at 0.01g. Such a reference defines the value of d_{min}/K_d for $a = 0.01g$ and $\tau = 5$ sec, giving

$$\frac{d_{min}}{K_d} = 0.01g\left(1 - 1.07e^{-0.5}\right) = 0.00351g \qquad (28)$$

so that for accelerations along the head vertical axis with the subject supine,

$$\tau = 10 \ln \frac{1.07a}{a - 0.00351g} \qquad \tau \geq 1 \text{ sec} \qquad (29)$$

The latency time curve of figure 30 is therefore asymptotic to the line $a = 0.00351g$. Theoretically, the ultimate threshold acceleration is this value, although it would take an infinite time to perceive it.

Figure 31 shows the mean latency time measurements and theoretical curve for perception of acceleration along the sagittal axis with the head upright. The theoretical curve has been referenced to the subjective data to give a good fit. The ultimate threshold for this curve fit is 0.00212g. So for acceleration along the sagittal axis with the head upright,

$$\tau = 10 \ln \frac{1.07a}{a - 0.00212g} \qquad \tau \geq 1 \text{ sec} \qquad (30)$$

Equations 27, 29, and 30 give good agreement with observed latency times greater than one sec, but deteriorate in accuracy as the acceleration increases beyond about 0.1g. The curves of these equations are asymptotic at $\tau = 0.675$ sec (i.e., $\tau = 10 \ln 1.07$). This asymptotic behavior does not reflect the true relationship between latency time and acceleration, but is an artifact of the approximation made when the term $0.07e^{-1.5t}$ was dropped from equation 25.

Meiry noted that because of the orientation of the utricles (assumed to be elevated 30 deg above the sagittal axis), the shear acceleration on the otolith is cos 30 deg times the input acceleration along the sagittal axis and sin 30 deg times the input acceleration along the head vertical axis. Since the theoretical ultimate threshold, d_{min}/K_d, is proportional to the minimum detectable shear acceleration on the otolith, the threshold for perception of acceleration along the sagittal axis should be smaller by a factor of sin 30 deg/cos 30 deg than that for acceleration along the vertical axis. The data bear out this relationship:

$$\frac{\text{ultimate threshold (sagittal axis)}}{\text{ultimate threshold (vertical axis)}} = \frac{0.00212g}{0.00351g} = 0.604 \; ; \; \frac{\sin 30^\circ}{\cos 30^\circ} = 0.577 \qquad (31)$$

In his experiments, based on 75 percent correct vector detection, Meiry obtained thresholds of 0.006g and 0.01g for perception of linear acceleration along the head sagittal and vertical axes, respectively.

F. HABITUATION

Currently available data do not appear to support unequivocally the existence of habituation effects on the function of the utricle. If, however, habituation or vestibular training does affect the function of the utricles, it does not do so as strongly as in the semicircular canals. Since, teleologically speaking, man is designed to function in a 1g environment, and the utricles provide the sensible signals upon which orientation to the vertical is based, logically we would not expect any attenuation in perception nor change in dynamics of the utricles due to repeated stimulation.

If this expectation seems at odds with our knowledge that repeated stimulation of the semicircular canals causes habituation in them, consider the following: In the everyday environment, the semicircular canals are stimulated by short, discrete, angular motions of the head. These motions do not appear to produce habituation. It is the sustained rotations of the head experienced in uncommon activities such as figure skating, gymnastics, and acrobatic flying which appear to be responsible for habituation of the semicircular canals. In the everyday environment, the utricles are stimulated continuously by the gravity vector. The orientation of the head with respect to the gravity vector varies widely throughout the day, being upright a large portion of the time, depressed as much as 45 deg during reading, and nearly horizontal for hours while lying on the back and either side during sleeping. Thus the utricles are stimulated daily by the gravity vector acting over a wide range of directions for periods of hours. Reasonably, such stimulation would not produce changes (habituation) in the function of the utricles which have not already evolved in man.

Meiry distinguishes between long-term and short-term habituation effects. He excludes long-term habituation for the reasons set forth above and cites two studies (refs. 10 and 11) which showed little difference between pilots and nonpilots in their ability to orient themselves. (The degree and recency of vestibular training achieved by the pilots is not known.) Another study (ref. 99) showed that two astronauts had a considerably superior ability to that of two nonpilots in orienting a target to the vertical in the absence of a visual field. Meiry suggests that short-term habituation effects do occur, and that during the first 30 sec or so following stimulation consisting of tilting the subject from the vertical, his perception of the initial tilt angle decreases on the order of 40 percent. As discussed in subsection G.2., the author takes exception to this finding.

1. Tests for Habituation

Studies of the function of the utricles are necessarily restricted to those reflexes and perceptions influenced exclusively, or at least primarily, by the utricles. Additionally, these reflexes and perceptions must be quantitatively measurable. Three manifestations of utricle function meet these requirements: subjective perception of the postural vertical (or horizontal), egocentric visual localization (EVL) of the horizontal (or vertical), and counterrolling of the eyes. All three have been used in assessing the effects of habituation on the function of the utricles.

Subjective perception of the postural vertical is generally tested in a manner similar to the following: The subject is seated in a chair capable of being tilted in the frontal or sagittal plane or in an oblique plane containing the gravitational vertical. His head is immobilized with respect to his body. Visual cues are eliminated by blindfolding the subject or darkening the room. The chair and subject are then tilted away from the vertical (upright) position. The subject is then moved with constant velocity back toward the vertical until he indicates that he is vertical. The error in his judgment is recorded. Variables in this experiment include:

- identity of subject
- magnitude of initial tilt angle
- direction of tilt (left, right, forward, backward)
- rate of motion toward tilt angle
- rate of motion toward vertical
- duration of time at tilt angle
- duration of time away from vertical
- sequence of tilt angles

The data are generally analyzed statistically (analysis of variance predominates) to determine which of the variables affect the accuracy of judgment of the vertical.

Egocentric visual localization of the horizontal is usually tested by either of two methods similar to the following: Method 1 — the subject is seated in a chair capable of being tilted usually in either the frontal or the sagittal plane. His head is immobilized with respect to his body (sometimes the body is immobilized and only the head tilted). A target, usually a line of light or an illuminated rod, is presented. The target can be oriented either directly by the subject or by the experimenter under the subject's direction. Extraneous visual cues are eliminated by darkening the room. The procedure is to tilt the target and subject independently. (The subject's view of the target is obscured during this phase.) The subject then reorients the target to what he perceives to be the horizontal (or vertical). The error in judgment is recorded. Variables in the experiment include:

- identity of subject
- magnitude of subject tilt angle
- direction of subject tilt angle
- magnitude of target tilt angle
- direction of target tilt angle
- duration of time subject is tilted
- sequence of tilt angles

Method 2 — this method is similar to Method 1 except that the subject's chair and the target are mounted on a centrifuge and rotated together. The subject faces either toward or away from the direction of motion. The procedure is similar to that of Method 1 except that, in addition, the centrifuge is spun up to increase the g-level to a given value. In so doing, the gravitoinertial horizontal and vertical are changed. The task of the subject is to orient the target to the gravitoinertial horizontal (or vertical). The error in his judgment is recorded. Variables in this experiment include:

- identity of subject
- magnitude of gravitoinertial force (g-level)
- magnitude of subject tilt angle
- direction of subject tilt angle
- magnitude of target tilt angle
- direction of target tilt angle
- duration of time subject is tilted
- duration of time at given level of gravitoinertial force
- sequence of tilt angles
- sequence of gravitoinertial force levels
- direction of rotation of centrifuge

Counterrolling of the eyes has been measured in the normal 1g environment, in centrifuges providing a greater than 1g environment, and in parabolic flight tests providing both reduced g and zero-g environments. Actual measurements of the counterrolling of the eyes fall into two categories: subjective methods in which the subject indicates the spatial position of an afterimage or of his blind spot. and objective methods in which the experimenter measures the position of some landmark of the eye, which is either artificial (markings, sutures, egg membrane) or natural (iris, conjunctival vessels, the optic disc viewed through an opthalmoscope). The procedure is to tilt the subject in the frontal plane with respect to the gravitoinertial vertical and measure the amount of counterrolling of the eyes. Variables in this experiment include:

- identity of subject
- magnitude of tilt
- direction of tilt
- magnitude of gravitoinertial force
- duration of time subject is tilted

2. Evidence for Habituation from Tests of Perception of the Postural Vertical

An investigation of subjective perception of the postural vertical was conducted by Mann and Ray (ref. 94) by tilting subjects in the frontal plane to an initial angle of 30 deg. They used delay or dwell times of 0 and 60 sec at the initial tilt angle and concluded that the longer dwell time was significant in increasing errors in readjustments to the vertical for slow rates (1.2 deg/sec) of return to the vertical, but was not significant for faster rates of return (2.4 deg/sec). Short-term habituation is suggested in the first test, and denied in the second. These equivocal findings cannot be said to confirm habituation.

Clegg and Dunfield (ref. 33) performed similar experiments in subjective perception of the postural vertical for tilting of the subject backwards or forwards in the sagittal plane. They found no significant effect of delay times up to 105 sec at the initial angle of tilt upon either the magnitude or duration of error in readjustment to the vertical. Again, these results cannot be said to support short-term habituation. Other researchers (refs. 91, 92, 93, and 106) have shown short-term habituation or adaptation effects in similar experiments.

Howard and Templeton (ref. 75) present an excellent review of the literature on judgment of the postural vertical. According to them, Passey and Guedry (ref. 106) report that delay times of 60 sec at an initial tilt angle of 10 deg produced larger errors on return to the postural vertical than did zero delay times. Mann, Passey, and Ambler (ref. 93) and Mann and Passey (ref. 92) extended these findings to periods of delay of 65 sec and initial tilt angles of 55 deg. The results were in substantial agreement: "The apparent vertical was increasingly displaced in the direction of the initial tilt of the body as the duration at the initial tilt was prolonged" (ref. 75). Some degree of short-term habituation is suggested by these findings.

3. Evidence for Habituation from Tests of Egocentric Visual Localization

Numerous studies have been made of man's ability to orient a visual target to the horizontal or vertical. The visual target does not in itself provide an adequate orientation cue. Other visual cues are denied. The only cue available is that provided by the direction of force acting on the subject. In these studies the direction of force acting on the subject is the primary variable. These studies include those in which the subject is merely tilted with respect to the gravity vector (refs. 100, 130, and others) and those in which the acceleration of gravity is augmented by centrifugation, and in which the subject is tilted with respect to the resultant gravitoinertial vector (refs. 25, 56, 60, 99, 102, and others). For reasons of simplicity, the directions of the gravitational and gravitoinertial vectors will both be referred to as the vertical provided no confusion will arise. Similary, lines perpendicular to the gravitational and gravitoinertial verticals, termed the gravitational and gravitoinertial horizontals, respectively, will each be referred to as the horizontal. These two sets of perpendicular lines define two coordinate systems of reference for orientation.

The term egocentric visual localization (EVL) is used here to denote the act of orienting a visual target to the reference axes established by the vertical. The ability to estimate the vertical is a function of the subject's orientation to the vertical. When upright, his estimates are quite precise, but deteriorate as he is tilted away from the vertical. When completely inverted, estimates of the vertical improve considerably over those when tilted ±90 deg. In general, for normal subjects, a vertical reference target will appear inclined in the same direction as the tilt angle for small tilt angles. This illusion is termed the E-phenomenon. The E-phenomenon reaches a maximum at about 45 deg angle of tilt and then decreases as the tilt increases. At a tilt of about 70 deg the E-phenomenon disappears and the target appears to be inclined in a direction opposite to that of the tilt angle. This effect is termed the Aubert- or A-phenomenon, and increases as the tilt angle increases beyond about 70 deg. Figure 32 illustrates the characteristics of these phenomena for a normal subject in a 1g environment. Left/right asymmetries and irregularities in response, especially between successive trials under identical conditions, are the rule rather than the exception.

Comparisons of experiments with normal and labyrinthine-defective subjects (refs. 56 and 102) indicate both otolithic and nonotolithic cues subserving these perceptions. It is reasoned that if these perceptions or illusions are constant in time with no obvious tendency to decrease in magnitude, that habituation of the otolith organs (the utricles) does not take place. Miller and Graybiel, in references 99 and 100, show the time course of EVL of the horizontal for a number of subjects. Their studies were made of subjects in upright, recumbent, and inverted positions. The duration of the tests were 23 min with alternate periods of 2 min with an illuminated background and 5 min with a completely darkened visual background. The perception of the A- and E-phenomena is complicated by the superposition of rotary autokinesis. This illusion consists of random rotation of the target line. Nonetheless, effects of habituation were not seen in these experiments.

A striking difference existed in the errors scored by two astronaut subjects and two other subjects, the experimenters themselves. The errors of the astronaut subjects were only one-third those of the other subjects. Whether the astronauts' superior ability at EVL reflects the effects of habituation, a high level of training, or the highly selective process of choosing astronauts from an already select group of experienced pilots is not known. One test was performed (ref. 99) with the subjects recumbent for 30 min with the visual background completely dark. The error perceived by one subject remained essentially at the same level (rotary autokinesis notwithstanding), but decreased considerably for the other subject.

Clark and Graybiel (ref. 25) experimented with subjects sitting upright in a centrifuge which was rotated to provide gravitoinertial verticals displaced 6 deg and 12 deg from the gravitational vertical. Data of the EVL of the horizontal show no habituation effects during four hours of centrifugation.

To the extent that EVL of the horizontal is subserved by otolithic cues, it appears that the occurrence of habituation is not supported by experiments in EVL.

4. Evidence for Habituation from Tests of Counterrolling of the Eyes

As discussed in Chapter II, subsection E.1.c., counterrolling of the eyes is the only clearly defined utricular reflex in man. Howard and Templeton discuss the findings of Mulder's (1874) investigation of counterrolling during long periods of inclination of the head. Mulder found that after inclining his own head at an angle of 86 deg to the vertical for 45 min, his counterroll decreased from 6 deg to a value of 5 deg. The counterroll of a second subject decreased 2 deg in the same time. Another investigator (M. H. Fischer in 1930) is reported to have observed no decrease in counterroll after 5 min of sustained head tilt.

The evidence of habituation from studies of counterrolling of the eyes is somewhat equivocal. Mulder's findings suggest some degree of habituation. Fatigue of the ocular muscles could have played a role in his findings, however.

5. Summary of Evidence on Habituation of the Utricles

Evidence gathered in three phenomenological areas manifesting utricular activity, perception of the postural vertical, egocentric visual localization (EVL) of the horizontal, and counterrolling of the eyes, fails to show unequivocally the effects of habituation on the utricles. Clearly, in tests of the perception of the vertical, the lack of evidence affirming habituation in the utricles does not force the conclusion that habituation does not occur. Perception of the vertical is dependent upon both otolithic and nonotolithic cues and the genesis of the phenomena involved in EVL is quite complicated.

The most compelling evidence for habituation of the utricles is that presented by Mulder on counterrolling of the eyes. Aside from the results of Fischer, cited in Howard and Templeton, no other studies supporting or refuting Mulder's findings were uncovered in the literature search.

No studies of any kind on the effects of habituation on the dynamics of the utricles were found. This is in contrast to the moderate abundance of reports on the effects of habituation on the dynamics of the semicircular canals.

G. MATHEMATICAL MODEL OF THE UTRICLES

1. The Model Based on Meiry's Work

The only data on the dynamic function of the utricles which were found in the literature are those obtained by Meiry. These data, which provide the basis of the mathematical model of the utricles portrayed in figure 33, were obtained for linear acceleration inputs along the sagittal axis with the head upright.

There is nothing about the anatomical structure of the utricles or about their responses to stimulation along the other principal axes of the head to suggest that this model would not be an appropriate representation of the utricular response to accelerations along the lateral or vertical axes. The sensitivity of the utricles depends, of course, on their orientation with respect to the applied acceleration, as discussed in section D.

In the model shown in figure 33, the input to the utricles is a gravitational force or a combination of gravitational and inertial forces, the gravitoinertial force vector, resolved into components parallel and normal to the plane of the macula by virtue of the orientatic of the utricles with respect to the applied gravitoinertial vector. The component in the plane of the macula displaces the otolith in accordance with the second-order model.

The transfer characteristics of the utricles are portrayed in a frequency response plot shown in figure 34 with velocity as the input and subjective perception of velocity as the output. The deadzone introduced by the threshold is neglected in the frequency response plot. Meiry's determinations of acceleration thresholds are considered the most appropriate for closed-loop control tasks. He obtained thresholds of 0.01g for accelerations along the vertical axis of the head with the subject supine and 0.006g for accelerations along the sagittal axis with the head upright. When the input acceleration exceeds the threshold value, associated with some minimum displacement of the otolith, a signal is received by the central nervous system giving rise to a subjective perception of velocity and of tilt with respect to the apparent vertical.

Concerning the gain of the utricular transfer function, Meiry concludes from a study of Schöne's work (ref. 109) on subjective estimates of the angle of elevation of the horizontal by a subject tilted in the sagittal plane that habituation effects reduce the subjective estimate to 60 percent of the initial subjective response. However, for short exposures to tilt from the vertical, Meiry suggests that habituation does not take place, so that the subjective estimate of tilt angle is nearly equal to the actual tilt angle. Thus he concludes that for short time exposures to stimulation the gain of the utricles is unity, and for long exposures the gain is approximately 0.6.

2. An Alternative Model of the Utricles

The model and its frequency response, represented in figures 33 and 34, respectively, are adapted from Meiry's work, described in section C. The output of Meiry's model is subjective perception of velocity. The transfer function of the model is expressed by equation 23. This model suggests that for a step input acceleration or a constant tilt angle, the subject has a perception of velocity in accordance with equation 24. His perception of acceleration, according to this model, declines exponentially:

$$\text{subjective perception of acceleration} = 0.715aK\left(e^{-0.1t} - e^{-1.5t}\right) \quad (32)$$

Experience and numerous experiments (refs. 25, 60, 99, 100, 102, and others) tell us that we can perceive a change in acceleration and that the perception does not die out with time. The questions are whether the perception is interpreted as one of velocity or acceleration and whether the perception dies out with time.

In tests of egocentric localization of the horizontal, discussed in section F and in reference 109, a change in acceleration is interpreted as a change in tilt angle. As discussed in section B, the effective stimulation of the utricle is provided by the component of linear acceleration in the plane of the macula. A change in tilt of the head in a gravitational field produces a change in the component of gravitational acceleration in the plane of the macula. Logically a perception of tilt when the head is accelerated must be interpreted as equivalent to a perception of acceleration rather than velocity.

Schöne (ref. 109) investigated the egocentric visual localization of the horizontal for various angles of tilt of the head in the sagittal plane and for gravitoinertial force fields of from 1 to 2.1g. He found the subjective perception of the horizontal to vary linearly with the shear force on the utricular otolith. The subjective inclination thus corresponds to the shear force on the otolith and varies not as the angle but as the sine of the angle of objective tilt of the utricular macula. (It is assumed that the head and body are tilted together, otherwise the action of the neck reflexes upsets this relationship.) The sine function is nearly linear for small angles, so that in a 1g environment, the subjective perception of tilt is fairly accurate (±10 deg) for acceleration vectors acting within ±55 deg of the normal to the plane of the macula.

For a macular plane elevated 30 deg above the sagittal axis, this would correspond to head tilt angles between 25 deg back and 85 deg forward. Thus within its range of linear operation the "gain" of the utricular transfer function is unity.

This author concludes from the considerations above that the subjectiv perception of acceleration does not diminish with time, but has a steady-state component, and furthermore, that within limits the steady-state component is equal to the applied acceleration.

Accordingly, the author proposes a model in which the subjective perception of acceleration is related to the input acceleration as follows:

$$\frac{\text{subjective perception of acceleration}}{\text{input acceleration}} = \frac{0.15}{(s + 0.1)(s + 1.5)} \tag{33}$$

The subjective response to an input step acceleration is

$$\text{subjective perception of acceleration} = a\left(1 + 0.07e^{-1.5t} - 1.07e^{-0.1t}\right) \tag{34}$$

The expressions for the threshold displacement of the otolith and for latency time, given in equations 25 and 27, remain the same, but are associated with a perception of acceleration rather than velocity.

The proposed model of the utricles is portrayed in figure 35 and its frequency response in figure 36. The frequency response is derived from Meiry's data by assuming the subjects in his experiments perceived acceleration rather than velocity.

CHAPTER V

DISORIENTATION AND ILLUSION

A. INTRODUCTION

The incorrect perception of attitude and/or motion in space is termed spatial disorientation. Spatial disorientation may result from the normal reactions of the vestibular system to the stimulation of motion in three-dimensional flight or may result from visual illusions arising from erroneous interpretation of information from the visual field. For example, the threshold and dynamic characteristics of the semicircular canals are such that angular accelerations of sufficiently small magnitude are completely unperceived, the perception of rotations of prolonged duration gradually subside with time, and at the termination of a prolonged rotation in one direction, an aftersensation of rotation in the opposite direction is perceived. The gravity sensing apparatus, the utricles, cannot distinguish between linear acceleration and the acceleration of gravity, and thus their combined vector, the gravitoinertial vector, is interpreted as denoting the vertical.

An individual experiencing such a false or illusory perception of attitude or motion is said to be spatially disoriented, the particular type of disorientation being characteristic of the stimulation involved. A pilot is disoriented when his sensations of motion and attitude do not correspond to the physical facts, despite his awareness or lack of awareness of the difficulty. When he senses a condition of attitude and motion which differs from the physical facts of the condition, he is (1) disoriented and (2) suffering an illusion. He may feel inverted when flying right side up or feel banked to one side when flying straight and level. He is disoriented and he suffers the illusions of inversion and the leans, respectively.

Spatial disorientation is often referred to as vertigo. In this context vertigo has a different meaning than the dictionary definition of a feeling of dizziness associated with sensations of rotary motion of the body or surroundings. Pilots use the term vertigo in referring to many types of confusions with respect to attitude and motion during flight. Vertigo has come to denote almost any type of experience in flight which does not correspond to objectively verifiable physical events (ref. 23). The term disorientation will be used in this report because it encompasses the meanings of vertigo, as used by pilots, and avoids the ambiguity in meaning which might arise.

There is a natural tendency to trust one's senses, and without an outside visual reference to correct his illusory sense of orientation, a pilot insufficiently trained or inexperienced in instrument flight may disregard his instruments in favor of his senses. A stressful situation is created by the conflict in information provided by the pilot's instruments and his vestibular senses. The additional stress itself may compound his difficulties. When stressed, there is a tendency for an individual to revert to a more primitive level of behavior, which in this situation would be for the pilot to rely on his vestibular senses rather than flight instruments.

A curious characteristic of spatial disorientation is that a given set of linear or angular accelerations may produce illusory phenomena under one set of conditions and not under another highly similar set of conditions. An adequate external reference suppresses or eliminates most illusions. Some illusions, however, are compelling and may overpower the inhibiting influence of the most adequate external visual field. Even if deprived of an outside visual reference, a pilot may not always perceive illusory phenomena when experiencing the same erroneous vestibular cues on different occasions. Fatigue, anxiety, mental stress, and inexperience in instrument flight are predisposing factors in the perception of the illusions of spatial disorientation.

The importance of disorientation as a hazard to flight safety is emphasized in the following reports:

> "I was flying Number 2 in a two-ship (F86F) formation in night weather. During a left penetration turn I thought I was turning right, and when we rolled out I felt as though we were inverted. I kept on flying the wing and took a glance cross check of my instruments and finally everything straightened out." (ref. 104)

> "I was leading an element in a night formation flight. I had only a few hours in jets. I got into a diving turn to my left after looking at my wingman. I recovered by having my right wing pilot monitor me and talk me into believing my instruments. I recovered at approximately 1,400 ft." (ref. 104)

> "In a TBM while attempting a rendezvous on section leader on a dark night, the section leader seemed to be at the same altitude so I glided down. He seemed to remain at my altitude. By the time I realized that I was looking at a star I was down to 400 ft..." (ref. 123)

Isolated incidents, these episodes of disorientation? Judge by the following statistics.

1. Statistics of Disorientation

Of a group of 137 naval and marine corps aviators, who individually possessed experience in jet aircraft of from 100 to 2200 hours, 96 percent had had one or more experiences with disorientation in flight (ref. 24).

A study by Nuttal and Sanford (ref. 105) of 685 pilots in the USAFE Command showed that experiences of severe disorientation were five times more frequent in jet aircraft than in piston engine aircraft. This higher incidence of disorientation in jet aircraft is probably related to the higher acceleration capability of jet aircraft compared to piston engine aircraft and their generally cleaner design (smaller drag/weight ratio), which insures a faster build up in speed during nose-down attitudes. If a pilot suffering disorientation gets into trouble in a jet, it develops more quickly and recovery is more difficult than in a piston engine aircraft.

Information from the Aero Medical Safety Division of the Office of the Inspector General showed that during 1955 and 1956 there were 24 cases in which the pilot's last statement before diving into the ground was to the effect that he was changing radio channels. (During procedural turns, moving the head to view or adjust improperly located instruments is a common cause of the Coriolis illusion, discussed in section C.) During the same period there were 107 unexplained accidents involving 155 fatalities wherein disorientation was suspected of being the cause (ref. 121).

Nuttal and Sanford (ref. 105) report that in the USAFE Command during 1955 and 1956, spatial disorientation was determined to be the cause of 4 percent of all flying accidents in that command and 14 percent of all fatal accidents in the command. They also found that almost all the pilots in the command had experienced disorientation at least once, and some had experienced as many as 20 episodes of spatial disorientation.

With the exception of maneuvers involving rapid rotations, such as spins and rapid rolls, the presence of a good outside visual reference obviates most problems of disorientation. Following loss of the visual reference and before a successful transition to IFR flight can be made, disorientation may occur. A large fraction of disorientation incidents have occurred shortly after deteriorating weather conditions restricting the outside visual field have forced pilots to make the transition from VFR to IFR flight. Similar incidents have occurred following transition to IFR flight during formation flight in weather when formation elements have become separated.

2. Time Required to Change from VFR to IFR Flight

Kraus (ref. 82) reports a study in which measurements were made of the time to change from VFR formation flight to an instrument reference and perform a breakaway maneuver. Tests were made in two F-100F aircraft in which the subject occupied the rear seat of the wing aircraft. The formation would commence one of several test maneuvers, an instrument hood would be lowered without warning over the subject, and he would have to perform a single needle-width turn (3 deg/sec) of 30 deg away from the lead ship's last heading. The formation maneuvers consisted of straight and level flight, right and left plunging turns, and a right climbing turn. The subject's aircraft occupied right or left wing positions during the tests. The times required for three test subjects to change from VFR to IFR and perform the breakaway ranged from 19 to 36 sec and the averages of the three subjects ranged from 24 to 26 sec. There were no abnormal deviations in flight path during transition in any of the tests. The pilot's experience in jet aircraft ranged from 157 to 1118 hrs, and their experience in F-100's ranged from 22 to 239 hrs. The differences in experience were uncorrelated with the results.

A second series of tests was performed to determine the time required during flight without visual reference for the aircraft to assume an attitude from which recovery would have been impossible if the aircraft had been flying 10,000 ft above the terrain. The trials were initiated with the aircraft in the following positions: straight and level, level turn to right 30 deg bank, and level turn to left 30 deg bank. On a signal from the safety pilot, the subject closed his eyes and attempted to maintain straight and level flight. The time required to assume an unrecoverable attitude ranged from 20 to 135 sec and the averages of the three subjects ranged from 44 to 67 sec.

It may be concluded that a jet aircraft flying at 10,000 ft can assume an attitude from which recovery is impossible in as little time as 20 sec if the pilot is deprived of a visual reference. These studies emphasize the absolute necessity of a continuous visual reference, provided either by a view of the outside world or instruments, in maintaining a safe flight attitude.

3. Contents of the Chapter

This chapter considers the illusions of attitude and motion evoked by motion stimulation of the vestibular system. In section B some of the results of research on illusions conducted in centrifuges, simulators, and flight tests are discussed. In section C the illusions experienced by pilots in flight and the vestibular mechanisms and motion stimulation which are responsible for their genesis are discussed. Illusions experienced in flight and based on visual phenomena are also discussed in section C.

The motor theory of egocentric visual localization provides an explanation for the visual illusions elicited by stimulation of the vestibular system. Most of these illusions cannot be explained on the basis of eye movements. This theory, discussed in section D, is based on a psychophysiological integration which provides for the visual perception of apparent motion without either motion of the eyes or of the retinal image.

Sections E, F, and G consider, respectively, typical episodes of disorientation in flight, factors contributing to disorientation, and suggested preventive measures.

B. ILLUSIONS EXPERIENCED IN CENTRIFUGE, SIMULATOR, AND FLIGHT TESTS

A number of visual illusions and illusions involving false sensations of motion and body position, all elicited by stimulation of the vestibular system, have been studied extensively in the laboratory and under carefully controlled conditions during flight tests. The illusions to be discussed fall into two categories: illusions based on stimulation of the utricles and illusions based on stimulation of the semicircular canals.

1. Illusions Based on Stimulation of the Utricles

a. Oculogravic Illusion

1) Background. The oculogravic illusion is a visual illusion elicited by a change in the angle of the gravitoinertial force vector (G vector) relative to the subject. Associated with the visual illusion is a postural illusion of tilt. According to strict definition, only the visual aspect of the sensations evoked is considered the oculogravic illusion, but some authors include the postural aspect as well. In this report we shall speak of both the visual and postural illusions while adhering to the strict definition that only the visual aspect is the oculogravic illusion.

Most research (refs. 21, 26, 27, 28, 53, 56, 57, 58, 61, and others) on the oculogravic illusion has been conducted in centrifuge tests of various features of the illusion, while a few studies have been made (refs. 18, 19, 20, 29, 62, and 63) of the illusion and the associated postural illusion in actual flight tests. The discussion which follows is based largely on the work of Graybiel in references 53 and 56 and on the work of Clark and Graybiel in references 28 and 61.

2) Description of the Illusion. The oculogravic illusion is most readily observed in a darkened room. The subject is seated on a centrifuge at some distance from the center of rotation and accelerated rapidly to a constant rate of rotation. The subject observes an illuminated target, usually a line of light,

a cross, or a star, which rotates with him and thus maintains a fixed position relative to the subject. The angular acceleration undergone at the start of the test stimulates the semicircular canals producing undesired effects, but these soon decline to zero.

As the centrifuge speed increases, the subject has a sensation of tilt, the direction of which depends on the subject's orientation with respect to the center of rotation of the centrifuge.

3) Observation of the Illusion in the Frontal Plane. When the subject faces the direction of motion with the center of rotation on his left, as illustrated in figure 37, his sensation of tilt is to the right in accord with the gravito-inertial vector, which is the resultant of the gravitational and centrifugal force vectors. In addition to the sensation of tilt, the subject feels that the structures supporting him have tilted similarly. The chair, floor, and bite board between his teeth all seem tilted. The apparent change in position occurs rapidly at first, then slows gradually to a stop at an angle more or less commensurate with the degree of change of the angle φ of the G vector. The sensation of changing tilt, however, extends over a much longer period than that of the angular acceleration of the centrifuge.

The illuminated target, originally horizontal, will appear to rotate clockwise rapidly at first, then more slowly, until it too appears to be inclined to the right at an angle roughly equal in magnitude to the inclination of the G vector from the gravitational vertical. The time required for the target to complete its rotation is several times that of the angular acceleration of the centrifuge. If the subject is free to rotate the target line physically and instructed to orient the target so as to keep it aligned with what he perceives to be the horizontal, he will rotate the target in a counterclockwise direction as indicated in figure 37. After the lag in his perception of the apparent motion of the target, he will have aligned the target fairly close to the gravitoinertial horizon as indicated in figure 37.

The time course of the subject's rotation of the target line can be recorded and compared with the actual change in the angle φ to give a quantitative measure of the lag effect. Figure 38 shows such a comparison for values of φ equal to approximately 20 deg and 30 deg. Although not shown in figure 38, there is often an overshoot in the subject's rotation of the target after the angle φ of the G vector is reduced to zero by stopping the centrifuge. If φ is of the order of 30 deg, an overshoot of about 5 deg is typical.

4) Observation of the Illusion in the Sagittal Plane. When the subject faces the center of rotation, the sensations of tilt will be experienced in the sagittal plane as illustrated in figure 39. Facing toward the center of rotation, the subject will feel a sensation of being tilted backwards as the centrifuge gathers speed. In a fashion similar to that described above, the supporting structures will also seem to tilt backwards. The illuminated target will appear to rise smoothly upwards. The lag effect will be observed in the displacement of the target, and the rate of motion of the target will be compatible with its displacement. The apparent angular displacement of the target (vertex at the subject's eye) will be nearly equal in magnitude to the change in φ. The illusion is compelling, in that despite the subject's knowledge that the target has not moved physically, he cannot abolish the illusion. On stopping the centrifuge, the sensation of tilt declines and the target descends to its original position, often with a small amount of overshoot.

When the subject faces away from the center of rotation of the centrifuge, the reverse of the phenomena described above takes place. On acceleration of the centrifuge, he feels tilted forward and the target descends. When the centrifuge is stopped, the target rises to its original position.

5) Visual Afterimages. The experiments described above have also been conducted using a visual afterimage superimposed on the real target image. In every trial the afterimage and the real image moved together as described for the real image alone. These results are strong evidence that the oculogravic illusion is not caused by eye movements. If eye movements were responsible, the afterimage and real image would move in opposite directions. The afterimage, being fixed on the retina, would appear to move in the same direction as the eye; the real image of a stationary object would track across the retina and appear to move in the opposite direction. The illusion is explained by the motor theory of egocentric visual localization described in section D.

6) Experiments with an Illuminated Visual Field. Graybiel (ref. 53) describes an experiment in a lighted room which illustrates that the inhibiting effect on the illusion of an illuminated visual field can be overcome if the stimulation evoking the illusion is strong enough.

In this test the subject faced the center of rotation and, instead of fixating the target, "...the subject regarded the horizontal centrifuge platform and the vertical walls of the circular room. On being exposed to gradually increasing centripetal acceleration, the subject perceived the platform as horizontal and the walls as vertical until the change in direction of the resultant force was 10 deg to 15 deg." (Apparently the walls of the room appeared to tilt at this level of acceleration.) "When the change in direction of resultant force reached a level of about 56 deg, ...the platform suddenly appeared to tilt upward and become stationary like a coin on edge. The subject then regarded himself as motionless and lying on his back. The walls of the room then appeared like an endless band rotating around the centrifuge platform. This phenomenon is not unlike that which an aviator experiences when he goes into a spin."

At low levels of stimulation of the vestibular system the rivalry between visual and vestibular orientation cues is resolved strongly in favor of visual cues. At increasing levels of vestibular stimulation the resolution in rivalry begins to shift toward vestibular cues until at very high levels of stimulation the vestibular cues overwhelm the visual cues.

7) Flight Tests of the Oculogravic Illusion. A number of flight tests have been conducted by Graybiel, Clark, and their co-workers to investigate the oculogravic and oculogyral illusions. In each test the subject was seated in the back seat of an SNJ-6 aircraft facing the direction of flight or to one side. He fixated a collimated star target and described its apparent motion and displacement as the aircraft negotiated various maneuvers providing different magnitudes and directions of linear and angular acceleration. The subjects perceived various aspects of the oculogravic and oculogyral illusions in general accordance with the findings of centrifuge experiments.

The tests showed that a maneuvering aircraft can evoke visual effects of considerable magnitude on objects in a restricted visual field. Similar illusory effects could contribute to a hazardous condition of disorientation during night flying.

b. The Aubert and Müller Phenomena

The Aubert or A-phenomenon and the Müller or E-phenomenon refer to bias errors in the judgment of horizontality of a target line observed in the dark as a subject is tilted in the frontal plane. As the subject is tilted from the upright, the line appears tilted toward the subject so he rotates it in the opposite direction, thereby overestimating his angle of tilt. This is the E-phenomenon. As the subject's objective tilt angle increases, the effect begins to reverse and he perceives the line to be tilted away from his own direction of tilt. He compensates by rotating the line toward himself, thereby underestimating his angle of tilt. This is the A-phenomenon. These illusions are also discussed and illustrated in Chapter IV, section F. These illusions serve to illustrate the behavior of the otolith organs, and probably are not of particular importance to orientation perception during flight.

c. Elevator and Oculoagravic Illusions

The elevator illusion is similar to the oculogravic illusion, but involves a displacement of objects in the visual field as the magnitude rather than the direction of the gravitoinertial vector is changed. The literature reviewed on the subject (refs. 4, 9, 17, 49, 75, and 103) considers only orientation of the G vector along the vertical axis of the head.

If the G vector is aligned with the head vertical axis and its magnitude is changed, then, due to the inclination of the utricle, the shear force on the utricular otolith is changed in the sagittal plane. A similar change in shear force is produced by a forward or backward tilting of the G vector as occurs during tests of the oculogravic illusion. Since the utricle cannot discern the difference between the two types of stimulation, we would expect the visual illusions produced to be the same or strongly similar. While there appear to be subtle differences in the two illusions (ref. 108), there are also strong similarities. Niven, Whiteside, and Graybiel (ref. 103) suggest that the elevator illusion is a special condition of the oculogravic illusion in which the G vector changes only in magnitude and not in direction.

Observations of the elevator illusion have been made in high speed elevators (ref. 103) and in flight tests (refs. 107, 108, 125, and others). The phenomenon is described as follows: As the G vector increases in magnitude, a target image fixated in the dark and stationary relative to the subject appears to rise. If the G vector decreases in magnitude, the target image appears to descend. A visual afterimage, when observed in the absence of a real target, appears to be displaced in a direction opposite to that observed for a real target (ref. 108). If a visual afterimage is present and a real target is fixated, both the real target and visual afterimage move together in the manner described for a real target only. The apparent position of a visual afterimage can be changed by voluntary eye movements, but the apparent position of a real target is unaffected by voluntary eye movements.

Thus eye movements themselves are not responsible for the illusion of motion of a real image. Niven, et al., (ref. 103) reported that during an abrupt change from 1g to zero-g, subjects experienced an involuntary upward eye movement of about 1 to 1.5 deg which lasted at least 150 ms. The results of this test were complicated by various artifacts, such as the acceleration reaching a peak of −1g between the 1g and zero-g conditions. The fact that minimal involuntary eye movements are elicited by sudden changes in the G vector supports other research on compensatory eye movements (see Chapter II) and lends credence to the motor theory of egocentric visual localization which provides a tenable explanation for the elevator illusion (see section D).

The apparent displacement of a real target and a visual afterimage viewed separately during parabolic maneuvers in an aircraft are illustrated in figure 40. The term "oculoagravic illusion" is sometimes used to denote the illusion experienced during the zero-g phase of flight, but this may cause confusion with the term oculogravic illusion. In this report the term elevator illusion will denote the illusion experienced during increased, decreased, and zero-g conditions.

During flight tests designed to investigate the phenomenon, a parabolic maneuver is flown to provide a period of zero-g flight. Preceding the parabolic portion of the flight path the aircraft pitches up sharply, pulling several g's, and then pushes over in a downward pitching motion during the parabola. To preclude the possibility that the pitching motion of the aircraft was contributing to the creation of the illusion, a test was made (ref. 125) in which the pitching motion during the parabola was reversed. This was achieved by executing a 180 deg roll just prior to and following the parabola. The elevator illusion was experienced as described for other tests, indicating that pitching motion was not a factor.

The time course of the elevator illusion apparently has not been measured. Travel limits in elevators and time limits during parabolic maneuvers in aircraft preclude prolonged tests of the elevator illusion.

As in the oculogravic and other visual illusions, the presence of a well structured visual field inhibits the elevator illusion.

d. Inversion Illusion

A sensation of a sudden reversal of up/down has been experienced by subjects participating in studies of weightlessness during parabolic flight maneuvers. Some of the Russian cosmonauts have reported a feeling of being upside down during the weightless phase of flight. This illusion has been termed the inversion illusion and is attributed to stimulation of the otolith organs. Experiments with labyrinthine defective (L-D) subjects have had negative results. The L-D subjects did not experience the inversion illusion (refs. 55 and 56).

Graybiel (refs. 55 and 56) describes the results of an experiment with two normal and three L-D subjects, each of whom was exposed to twenty parabolic flight maneuvers in two days. The subjects were physically restrained in what would otherwise be an upright position, but were displaced in four positions: upright, 30 deg, 60 deg, and 90 deg tilt (presumably in the frontal plane). Both normal subjects reported a sensation of sudden reversal of body position from head-up to head-down on entering weightlessness and a return to the head-up position on the pullout. The sensation occurred for all positions of tilt. None of the L-D subjects experienced the illusion on any occasion.

In another series of experiments, five normal and four L-D subjects walked on the overhead of the aircraft while exposed to a negative acceleration of about 0.05g for 6 to 10 sec. Three of the normals experienced the feeling that they were walking upright in an inverted aircraft. The other two normals, sophisticated subjects experienced in parabolic flight tests, did not experience the illusion. None of the L-D subjects experienced the illusion, all feeling upside down relative to the cabin.

Three of the Russian cosmonauts experienced a feeling of inversion immediately on entering the period of weightlessness during their orbital flights. In two other cosmonauts the inversion illusion developed gradually and persisted throughout the entire period of weightlessness whether or not their eyes were open. The cosmonauts could suppress or even eliminate the illusion by gaining a foothold on the chair by straining their muscles. This phenomenon suggests the participation of proprioception in the perception of orientation relative to the vehicle. None of the American astronauts is reported to have experienced the inversion illusion during the Mercury and Gemini series of orbital flights.

Provocative questions arise as to why an individual should feel upside down rather than simply unaware of the vertical, what precipitates the illusion in one situation and not another, and what accounts for individual differences in perception of the illusion. The answers to these questions await additional research.

2. Illusions Based on Stimulation of the Semicircular Canals

a. Oculogyral Illusion

1) Background. The oculogyral illusion involves motion and displacement of objects in the visual field following stimulation of the semicircular canals by angular acceleration. Most tests of the illusion are conducted on a centrifuge or other rotating device in a darkened environment with the subject regarding an illuminated three-dimensional target fixed relative to himself. Darkening the environment precludes the optokinetic stimulation which would otherwise be produced by the rotating visual field. The use of a three-dimensional target, such as a cube with illuminated edges, largely abolishes autokinesis (see subsection C.3.a.) which otherwise would complicate the illusory motions.

The threshold of stimulation of the oculogyral illusion is the lowest of the three manifestations of semicircular canal stimulation, being approximately 0.2 deg/sec^2 for yawing accelerations. Graybiel and Hupp (ref. 66), in the most extensive study of the illusion found during the literature search, describe the illusion as follows:

2) Description of the Illusion. If a subject is rotated rapidly in a dark environment and observes an illuminated target which rotates with him so that there is no relative motion between subject and target, a whole series of illusory motions of the target will be perceived. If the subject is given a rotational acceleration to the left in the horizontal plane (for a period of about 7 sec) and then rotated at constant velocity (25 rpm), the following is observed: As the subject is accelerated, the target appears to move rapidly to the left and is displaced to the left, but not more than about 30 deg. At first the motion is smooth but changes to a series of jerks and then gradually slows to a stop. This is the first positive effect of the oculogyral illusion. The target may then move slowly to the right, but without apparent displacement. This is the second positive effect and is observed by some, but not all subjects. As the constant rotation continues, apparent motion of the target ceases. When the subject is suddenly stopped the target appears to move rapidly to the right, often as much as 60 deg, a motion which persists for 30 or 40 sec, but which gradually subsides to zero with the target directly in front of the subject. Initially the target appears to move in a series of surges which smooth out and then sometimes reappear. This apparent motion is termed the first effect after rotation or the first negative effect. A second negative effect follows in which the target appears to move slowly to the left without displacement of more than a few degrees and may endure for longer than the first effect. A third short-lived, negative effect may follow in which the target appears to move slowly to the right.

The first effects are associated with displacement of the cupula following angular acceleration. The second and third effects are more difficult to explain. With decreasing strength of stimulus the second positive and third negative effects become inconstant and disappear. The second negative effect was still observed by three of four subjects following rotation at 2 rpm.

The first effects are dramatic at 10 rpm but less so at 5 rpm, whereas their durations are nearly the same in both instances.

3) Visual Afterimage. Graybiel and Hupp also report the appearance of the illusion using a visual afterimage as a target. The direction of motion of a visual afterimage was exactly the opposite of that described for a real target. When both a visual afterimage and a real target were superimposed, they moved in opposite directions with the onset of rotation of the centrifuge, while following cessation of rotation, each reversed course and moved in directions opposite each other again.

The experiment described was repeated by Whiteside, Graybiel, and Niven (ref. 129). They report than on sudden stopping of the centrifuge, the afterimage and real target separated momentarily due to the difficulty of fixation, but that as soon as the subject was able to fixate the real target, the afterimage became superimposed on the real target and the two then appeared to move as described for the real target alone.

4) Participation of Nystagmus. The behavior in which a visual afterimage and a real target appear to move in opposite directions supports the participation of eye movements (nystagmus) during at least a portion of the oculogyral illusion. An assumption in this argument is that vision is inhibited during the quick phase of nystagmus but not during the slow phase. Consequently, objects in the visual field sweep across the retina during the slow phase, thus appearing to move in the direction opposite the slow phase. An afterimage, being fixed with respect to the retina, would appear to move in the same direction as the eyes during the slow phase. The participation of nystagmus in the perception of the oculogyral illusion is thus tenable. However, there is considerable evidence (refs. 15, 51, 75, and others) that the oculogyral illusion is not caused by nystagmus.

Gray (ref. 51) reports that the oculogyral illusion and nystagmus may occur independently of each other, but admits that nystagmus of an amplitude below the detection threshold of his instruments may have taken place at all times during observation of the oculogyral illusion. Byford (ref. 15) presents more compelling evidence in the form of a subject whose right external rectus muscle was absent, but who experienced the illusion equally well with either eye or both. Under conditions in which the slow phase of nystagmus should have been to the right, no nystagmus could be recorded, but the visual illusion was perceived by this subject.

Other features of the illusion argue against nystagmus being even one of the contributory causes (ref. 75). These features are the following:

- The threshold for the oculogyral illusion is lower than that for nystagmus.
- The slope of the oculogyral cupulogram is less than that of the nystagmus cupulogram.
- The oculogyral illusion is perceived before nystagmus is evident and persists longer than nystagmus.
- The illusion is observed when nystagmus is inhibited by fixation or is otherwise absent, as in patients suffering paralysis of the eye muscles.
- The apparent speed of the oculogyral illusion is influenced by the direction in which the visual target (an arrow or aircraft) appears to point.

These features of the illusion seem to eliminate nystagmus as the cause of the oculogyral illusion, but it is obvious that nystagmus and the illusion frequently occur concurrently. Nystagmus may therefore contribute to some features of the oculogyral illusion, such as the oppositely directed movements of an afterimage and a real target and the incompatibility of rate of movement and displacement. The motor theory of egocentric visual localization, discussed in section D, offers an explanation of the illusion which does not depend on eye movements but upon the eye reflexes elicited by stimulation of the canals and counteracted by voluntary innervation of the eye muscles during fixation on a real target.

5) Moving Target in the Dark. The oculogyral illusion has been reported to occur while a subject observes a moving target in the dark (ref. 64). The illusion tends to mask the real motion of the target resulting in a conflict of information (ref. 17). In one example, a subject observing a target moving physically to the right was subjected to a strong angular motion giving rise to an apparent motion to the left. The target then appeared to be moving to the left, but the subject had to move his head to the right to observe the target passing out of his field of vision to the right.

6) Flight Tests of the Oculogyral Illusion. These tests were discussed briefly in subsection B.1.a. Subjects observing a collimated star target in the back seat of an SNJ-6 aircraft reported (refs. 29, 62, and 63) apparent displacement of the target as the aircraft turned. The apparent motion observed was in accord with the findings of centrifuge experiments. The fact that the illusion can be evoked in flight underlines its potential hazard. The illusion can best be avoided during night flying by avoiding sudden recoveries from maneuvers involving prolonged rotations of the aircraft about one of its axes (ref. 23).

b. Erroneous Perception of Rotation

In the normal terrestrial environment, angular accelerations of the head in one direction are regularly followed by stopping accelerations in the opposite direction as the head is moved through relatively small angles. In this situation the semicircular canals evoke sensations of motion and compensatory eye movements which are appropriate to the motions undergone by the head. In a centrifuge, rotating simulator, or a maneuvering aircraft, the individual may be exposed to angular accelerations of longer duration than experienced in the usual terrestrial environment and which may not be followed immediately by a stopping acceleration in the opposite direction. In such situations the sensations of motion and compensatory eye movements evoked by stimulation of the semicircular canals are inappropriate to the motion undergone. The reasons for this behavior are discussed in Chapters II and III. The following paragraph describes, in general, the subjective experience of an individual exposed to prolonged rotation in one direction.

Following an initial acceleration to a constant rotational speed, the subjective feeling of rotation gradually subsides over a period of about 20 sec. This is the first effect. After a momentary lag most subjects will perceive a slow rotation in the opposite direction which soon dies out. This is the second effect. A sudden cessation of rotation will then give rise to a sensation of rotation in the opposite direction which will persist for about 30 sec. This is the first negative effect, and it is followed by a second negative effect consisting of a sensation of slow rotation in the original direction of motion which eventually dies out. Illusory sensations of rotation equivalent to the first effects described above are commonly experienced by pilots flying under reduced visibility. Illusions of turning when instruments indicated straight and level flight were experienced by 62 percent of a group of naval aviation students (ref. 31).

Clark and Graybiel (ref. 22) studied illusory perception of rotation following constant speed turns in a Link Trainer. They found that the duration of the aftersensation following rotation at 10 rpm increased sharply as the period of constant speed rotation was increased from zero to 30 sec and increased less sharply as the period of constant speed rotation increased from 30 to 60 sec.

These observations are in accord with the dynamic model of the semicircular canals discussed in Chapter III. A period of constant rotation allows the effects of the first acceleration to subside (produced by the cupula returning to its neutral position). The deceleration then is sensed as an acceleration in the opposite direction (produced by the inertial action of the endolymph deflecting the cupula in the direction opposite its initial deflection).

The erroneous perception of rotation following prolonged rotation of the aircraft during conditions of restricted visibility gives rise to various illusions characteristic of the stimulation involved in the particular situation. A number of these illusions, commonly experienced in flight, are examined in section C.

c. Coriolis Illusion

1) Description of the Illusion. The Coriolis illusion involves the angular motion and displacement of objects in the visual field as well as a sensation of angular motion in response to an inclination of the head while the head is undergoing a passive rotation, ω, about an axis not aligned with the tilt axis. The perceptions of angular motion and of angular motion of the visual field are generally about an axis orthogonal to both the head tilt axis and the passive rotation axis. Although exceptions have been reported (ref. 114), the sensation of apparent rotation is usually in the same direction as that of the precession of a wheel spinning about the ω axis in response to a torque about the head tilt axis. Objects in the visual field move in the same direction as described for the sensation of rotation.

Table XIII lists the direction of apparent motion of a fixated target and the rotation sensation perceived during the Coriolis illusion for various directions of passive rotation and head tilt.

Repeated Coriolis stimulation produces a considerable habituation in the responses evoked (refs. 55 and 65).

TABLE XIII

ROTATION PERCEIVED IN THE CORIOLIS ILLUSION AS A FUNCTION OF DIRECTION OF CONSTANT ROTATION AND HEAD TILT

CONSTANT ROTATION	HEAD TILT	APPARENT MOTION OF FIXATED TARGET AND ROTATION SENSATION PERCEIVED
Yaw right, r	Pitch up, θ	Roll left, −p
Pitch up, q	Roll right, φ	Yaw left, −r
Roll right, p	Yaw right, ψ	Pitch down, −q
Yaw right, r	Roll right, φ	Pitch up, q
Roll right, p	Pitch up, θ	Yaw right, r
Pitch up, q	Yaw right, ψ	Roll right, p

The illusion has been explained by a number of researchers (refs. 54, 71, 114, and others) solely on the basis of Coriolis accelerations acting on the semicircular canals. Others (refs. 17, 70, and 75) recognize the exception taken by Groen (ref. 68) to the appropriateness of the term Coriolis. Groen asserts that Coriolis effects are small compared to what he terms momentum excess and that the latter is responsible for the illusions perceived.

Actually the term Coriolis is entirely appropriate as the stimulation of the semicircular canals giving rise to the illusion can be expressed completely in terms of Coriolis forces. There is, however, some merit in Groen's approach in that the stimulation of the canals responsible for the illusion can also be expressed in terms of the component of the passive rotation vector, ω, which stimulates those canals as the head is tilted. This view of a component of ω stimulating the semicircular canals results in a more straightforward derivation of the expression of the stimulation of the canals than is achieved by considering Coriolis forces. Whether we consider Coriolis forces or components the results are the same, for we are merely describing the same phenomenon in two different ways.

The angular accelerations giving rise to the Coriolis illusion are examined in Appendix A using both techniques.

2) Results of Analysis. The usual circumstance in which the Coriolis illusion is experienced by pilots is following head movements while the aircraft is in a turn. The results of the analysis presented in Appendix A will therefore be particularized for a constant yaw rate of the aircraft.

If a pilot rolls his head through an angle φ while the aircraft is undergoing a constant yaw rate, r, his head will experience a pitching acceleration given by equation A-19, rewritten below as equation 35:

$$\dot{q} = r \cos \varphi \frac{d\varphi}{dt} \tag{35}$$

where r = yaw rate of the aircraft

φ = tilt angle of the head in roll

The change in pitching velocity of the head following its tilt is given by equation A-20, rewritten below as equation 36:

$$q = r \sin \varphi \tag{36}$$

During a coordinated turn, of course, there is a constant pitch rate of the aircraft given by $q = r \sin \varphi$ where, here, φ is the bank angle of the aircraft. The vertical semicircular canals will gradually equilibrate to this steady state pitching velocity. Any subsequent rolling motion of the head will stimulate the vertical semicircular canals according to equations 35 and 36.

Pitching motions of the head while the aircraft is turning introduce rolling motions of the head according to equations 37 and 38.

$$\dot{p} = -r \cos \theta \frac{d\theta}{dt} \tag{37}$$

$$p = -r \sin \theta \tag{38}$$

where r = yaw rate of the aircraft

θ = tilt angle of the head in pitch

The vertical semicircular canals will be stimulated accordingly.

3) Asymmetry of the Coriolis Illusion. If, in the examples above, the head is kept tilted long enough for the semicircular canals to equilibrate to the imposed angular velocities, then moving the head back to the upright position causes the sensations and illusions experienced on tilting the head to reverse in sign. However, the magnitude of the illusions do not appear to be symmetrical with respect to tilt and return movements of the head. For example, Guedry (ref. 70) reports that during clockwise rotation on a turntable, subjects who tilted the head toward the left shoulder reported a diving sensation with high velocity but very little displacement. After equilibration of the canals in the tilted position, head return to the upright produced a climbing sensation with great apparent displacement but no unusual velocity.

The analyses of semicircular canal stimulation during the Coriolis illusion indicate that the perceptions should be equal and opposite for tilt and return head movements. The asymmetry of the sensations may be attributable to the difference in orientation of the gravity vector in the two head positions. Benson and Bodin (ref. 8) have shown that the threshold and rate of decay of post-rotational responses are dependent upon the orientation of the gravity vector relative to the planes of the canals. They state that "...the rate of decay of inappropriate post-rotational responses is greater when the linear acceleration is coplanar with the stimulated canals and least when normal to the plane of the canals..." Their findings also show that the threshold of stimulation is also greater when the gravity vector is coplanar with the stimulated canals and least when normal to the plane of the canals.

According to this behavior, aftersensations elicited by stimulation of the vertical canals would be expected to require a higher stimulus threshold and subside more quickly when the head is upright than when the head is tilted. Thus when the head is tilted to the left during clockwise rotation, the magnitude and duration of the perceived pitching velocity would be greater than the reverse sensation when the head is returned to the upright. The action of the neck reflexes may play a part in the asymmetry of the sensations as well.

Guedry (ref. 70) and Guedry and Montague (ref. 71) also report asymmetries, with respect to tilt and return movements of the head, in the visual illusions perceived. Subjects rotated on a turntable reported that the velocity of a target light viewed during the Coriolis illusion was not always appropriate to the apparent displacement, e.g., the target may have appeared to move fast without getting very far. The asymmetric response and the apparent discrepancy between rate and displacement suggest the participation of nystagmic eye movements.

Part of the explanation of this behavior may lie, as before, in the difference in orientation of the gravity vector relative to the stimulated canals. The orientation of the gravity vector has been shown (ref. 84) to affect nystagmic responses of the eye, nystagmus being more intense and of longer duration the greater the angle between the gravity vector and the plane of the stimulated canals.

In summary, the asymmetry of the subjective sensations and visual illusions experienced during equal and opposite tilt and return movements of the head are not explained by differences in the Coriolis force stimulation of the semicircular canals. The orientation of the gravity vector relative to the planes of the stimulated canals has been shown to affect the stimulation threshold and the rate of decay of responses, including nystagmus, of the stimulated canals. The difference in orientation of the gravity vector between tilted and upright positions of the head may, therefore, play a part in the asymmetry of the Coriolis illusion.

C. ILLUSIONS EXPERIENCED IN FLIGHT

The illusions experienced in flight arise primarily from stimulation of the vestibular system and from visual phenomena. Illusions arising from visual phenomena refer to illusory perceptions of orientation or motion resulting from erroneous processing of visual information and are distinguished from visual phenomena caused by compensatory eye movements and eye reflexes elicited by stimulation of the vestibular system. While kinesthetic and auditory perceptions are involved in some illusions, they play a secondary role. The discussion which follows is organized in terms of the sensory mechanism primarily responsible for the associated illusion.

1. Illusions Based on Stimulation of the Gravity Sensors

The accelerations associated with motion in three-dimensional space produce inertial reaction forces which combine vectorially with the gravitational force to yield the so-called gravitoinertial force or, simply, the G force. Variations in the magnitude and/or the direction of the G force are responsible for a number of postural and visual illusions.

In ordinary life man's orientation to the earth is based on visual and gravitational cues. Either cue is sufficient in the absence of the modality sensing the other. In flight, however, the situation changes dramatically. Visual reference to the natural horizon still subserves orientation to the earth, but gravitational cues are no longer adequate and are, in fact, misleading. With the loss of a visual reference, there is a tendency for the pilot to base orientation to the earth on gravitational cues (ref. 23). The disorientation that results is caused by the G vector being displaced and/or in motion with respect to the true vertical. The illusions associated with this form of disorientation are divided into two categories: postural and visual illusions.

a. Postural Illusions

1) Unperceived Bank. In a coordinated turn the G vector lies in the vertical plane of the aircraft, creating a sensation of sitting erect. The degree of disorientation is determined by the angle of bank. This illusion is common to passengers who are unaware of the maneuvering of the aircraft, but is rare among pilots unless they enter a coordinated turn without realizing it (ref. 23).

2) Sensation of Climbing in a Turn. In a coordinated turn when the horizontal turn and bank are not perceived, the increased G force in the turn yields a sensation of climbing or a nose-high attitude. The resultant tendency is for the pilot to push the stick forward. This illusion is caused by the fact that the plane of the utricles is elevated with respect to the sagittal axis of the head. The increased G force acting along the vertical axis of the head has a component acting backward in the plane of the utricles and thus yields a sensation of backward tilt. An extensive study of this and related phenomena is reported by Schöne (ref. 109).

Although not mentioned in the literature reviewed, a second modality probably contributes to this illusion. As the turn is entered, the aircraft pitch rate increases, reaching a constant value dependent on the degree of bank. ($q = r \sin \varphi$, where q = pitch rate, r = aircraft yaw rate, and φ = bank angle.) The semicircular canals are stimulated by this motion and sense accordingly a pitch-up motion as in a climb. As the turn continues, the sensation of pitching motion declines to zero as the canals equilibrate.

3) Sensation of Diving When Recovering from a Turn. When recovering from a turn, the decreasing G force gives a sensation of a dive or a nose-down attitude. The explanation for this is as follows: The backward pull on the otolith decreases as the G force decreases during the turn recovery. The otolith thus

shifts forward in a similar manner as in a subject who is raised from a backward to an upright position under normal gravity (ref. 109). The resultant tendency in this illusion is for the pilot to pull the stick back (ref. 9).

Although not mentioned in the literature reviewed, another effect, due to stimulation of the semicircular canals, would appear to contribute to the perception of diving when recovering from a turn. The effect is this: As mentioned in 2), above, an aircraft in a coordinated turn has a positive pitch rate to which the semicircular canals equilibrate in a prolonged turn. As recovery from the turn is made, the positive pitch rate decreases to zero, giving rise to a sensation of pitching in the opposite direction, down. The downward pitching motion would be associated by the pilot with a diving motion.

4) Sensation of Opposite Tilt in a Skid.* If the aircraft skids during a turn, the centripetal acceleration producing the skid also acts on the pilot. The resultant G vector is no longer perpendicular to the transverse or lateral axis of the aircraft. The sensation is created that the aircraft is banked in the direction opposite its true position (ref. 9).

5) Sensation of Nose-High Attitude During Takeoff. During the rapid acceleration of a high performance aircraft at takeoff, the resultant G force is at such an angle that the pilot may have a sensation of being tilted backward or that he is in a nose-high attitude (fig. 41). He may correct for this sensation by pushing the stick forward, which would increase the acceleration and the sensation and result in the aircraft impacting the ground.

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*An aircraft in a turn with an insufficient bank angle will skid away from the center of the turn due to the centrifugal force exceeding the centripetal component of lift.

6) Sensation of Nose-Down Attitude During Deceleration. In level flight during a deceleration of the aircraft, as when the speed brakes are extended or the power reduced, the resultant G force is at such an angle that the pilot may have a sensation of being tilted forward or being in a nose-down attitude. He may correct for this by pulling back on the stick, which would result in a stall. However, the accelerations produced in the pitch-up maneuver would tend to inhibit the illusion. While this illusion has been reported to occur during flight tests specifically designed to investigate the illusion (ref. 19), Gillingham (ref. 49) states that the illusion has not yet been reported as causing an operational hazard.

7) Sensation of Nose-High Attitude or Inversion During Push-Over from a Climb to Level Flight. As a high-performance aircraft pushes over into level flight from a climb, it will accelerate along its flight path. The combination of the rotating gravity vector, the increasing tangential acceleration, and the centripetal acceleration resulting from the curved flight path yield a resultant G vector which rotates backward and upward relative to the pilot (fig. 42). The pilot has the sensation that he is tilting over backward until nearly inverted at the apex of the climb (ref. 96). He has a tendency to compensate for this illusion by pushing forward on the stick, which results in intensifying the illusion. Safe recovery may not be possible from the resultant nose-down, negative angle-of-attack attitude. Martin and Jones (ref. 96) give an excellent analysis of this illusion and its possible consequences.

b. Visual Illusions

1) Oculogravic Illusion. The oculogravic illusion involves the motion and displacement of objects in the visual field in accordance with a change in the direction of the gravitoinertial vector. A detailed description of this illusion is given in section B. The oculogravic illusion has been demonstrated in

flight (refs. 18, 19, 20, 29, 30, 56, 62, 63, and others). Striking displacements and rotations of visual targets were reported by subjects seated in various positions in maneuvering aircraft. The durations of the effects were in accord with recorded accelerations of the aircraft. Large changes in the visual field are associated with strong G forces during climbing and diving turns (refs. 62 and 63) and spins (refs. 23 and 79).

When a subject or pilot fixates an illuminated target in an otherwise dark environment and is subjected to rotational variations of the G vector in the frontal plane, the oculogravic illusion manifests itself as a lateral tilting of the target. Subjects facing to the left in an aircraft observed the radiating lines of a collimated "star" target to appear to rotate clockwise during linear deceleration of the aircraft and to appear to rotate counterclockwise during acceleration (refs. 18, 19, and 20). When the subject or pilot is subjected to rotational variations of the G vector in the sagittal plane, the oculogravic illusion manifests itself as a vertical displacement of the target. Subjects facing forward in an aircraft observed a target light to appear to displace downward on deceleration of the aircraft (refs. 18 and 19). For a 0.28g deceleration the subjects perceived a mean downward displacement of 24 deg. The illusion can, therefore, be quite intense for the accelerations encountered in flight.

The oculogravic illusion is suppressed by a good outside visual reference, but even a good visual reference can be overcome if the stimulation is large enough (section B and ref. 53). With only a dimly lit instrument panel as a visual reference, it is possible for the oculogravic illusion to reinforce the postural illusions associated with changes in direction of the G vector. In situations such as described in subsections C.1.a.5) and 7) the occurrence of the oculogravic illusion would cause the instrument panel, and hence the nose of the aircraft, to appear to rise as the G vector rotates backward. This would reinforce the sensation of a nose-high attitude. No reports of this specific form of the visual illusion occurring in flight were found in the literature. Gillingham (ref. 49) does mention the possibility, however, but in connection with the elevator illusion.

2) Elevator Illusion. The elevator illusion involves the motion and displacement of objects in the visual field in accordance with changes in the magnitude of the gravitoinertial vector. The elevator illusion is thus distinguished from the oculogravic illusion, which is caused by changes in the direction of the gravitoinertial vector. A detailed description of the elevator illusion is given in section B. The illusion has been demonstrated in flight tests made specifically to investigate the phenomenon (refs. 107, 108, 125, and others) and is described elsewhere as well (refs. 4, 9, 17, 49, 75, and 103). The elevator illusion is characterized by an apparent upward displacement of a real target image during an increase in G force and a downward displacement of the real target image during a decrease in G force and during weightlessness in parabolic maneuvers. A visual afterimage, when observed in the absence of a real target, appears to be displaced in a direction opposite to that observed for a real target (ref. 108). Appearance of the elevator illusion during a parabolic maneuver is portrayed in figure 40.

The term "oculoagravic illusion" is sometimes used to denote the phenomenon experienced during weightlessness, but this may cause confusion with the term oculogravic illusion.

The presence of a well-structured visual background or a good outside visual reference tends to inhibit the elevator illusion. The relationship between the degree of inhibition and the strength of the visual field apparently has not been investigated. It is not unlikely that the strong vestibular stimuli produced by large acceleration forces might prevail over the inhibiting influence of a well-structured visual field and produce the illusion as is possible in the oculogravic illusion (ref. 53).

With only a dimly lit instrument panel as a visual reference, it may be possible for the elevator illusion to be elicited by a sufficiently strong acceleration stimulus. If this occurs, the illusion would serve to reinforce the concurrent postural sensations. For instance, in a pull-up the increase in G force would be felt as a backward tilt, and the elevator illusion would cause the instrument panel, and hence the nose of the aircraft, to appear to move up. The directions of both the postural sensation and visual illusion would be in accord with that of the actual motion of the aircraft, a pitching up, and would not be expected to cause difficulty. However, the magnitudes of the sensations may not be compatible with the aircraft attitude. A corrective action by the pilot of pushing the stick forward would tend to abolish the pitch-up of the aircraft, the sensation of backward tilt, and the illusion of a nose-high attitude.

No reports of formidable sensory or perceptual complications inimical to safe aircraft control and arising from the elevator illusion were found in the literature.

2. Illusions Based on Stimulation of the Semicircular Canals

Angular accelerations stimulate the semicircular canals. Rotations of moderate intensity and short duration, as commonly experienced in daily life, give rise, through stimulation of the semicircular canals, to faithful perceptions of rotation and appropriate compensatory motion of the eyes. Rotations of very small intensity or long duration give rise to erroneous perceptions of rotation and inappropriate eye movements.

The illusions evoked by stimulation of the semicircular canals derive from four factors:

- Threshold of perception of angular acceleration
- Dynamic characteristics of the semicircular canals

- Compensatory eye motions
- Compensatory eye reflexes

Postural illusions involving erroneous perceptions of bank angle derive from rotations in which the angular acceleration is less than the threshold of perception. Erroneous perceptions of rotation derive from the dynamic characteristics of the semicircular canals, as described in Chapter II, section C; in Chapter III, section B; and in section B of this chapter. In the context of this discussion of illusions, compensatory eye motions are distinguished from compensatory eye reflexes as follows: Inappropriate compensatory eye motions cause a streaming of the visual field across the retina, giving rise to a perception of rotation in the opposite direction. Compensatory eye reflexes which are counteracted by voluntary control of the oculomotor muscles, as when an object in the visual field is fixated, do not result in motion of the eyes, but do give rise to an apparent motion or displacement of the visual field. A theory explaining this and other phenomena is presented in section D. The illusions elicited by stimulation of the semicircular canals are discussed on the basis of the following classification:

- Postural illusions deriving from threshold phenomena
- Erroneous perceptions of rotation deriving from semicircular canal dynamics
- Visual illusions deriving from compensatory eye motions and reflexes

The classification is somewhat arbitrary because a given illusion may be produced by the action of phenomena in two or all three of the above classifications and may also be subserved by stimulation of the utricle. However, each illusion is classified according to its predominant cause.

a. Postural Illusions

1) The Leans. The leans is probably the most commonly experienced form of spatial disorientation (ref. 49) and is caused by the aircraft rolling in one direction at an acceleration level below the threshold of perception and rolling

in the opposite direction with an acceleration level above threshold. The pilot perceives only the suprathreshold roll displacement and, thinking he has been displaced from the upright, leans his body in the opposite direction to compensate. The sensation may persist even though cockpit instruments inform the pilot that he's flying straight and level. The leans also occurs in a similar manner for rotations about the pitch axis, but this, apparently, is less common. The leans is commonly experienced in turbulence. The aircraft may roll rapidly to the right and then recover slowly to the left. The pilot perceives the rolling displacement to the right but not the recovery. He feels that he is tilted to the right and leans to the left to compensate. He feels properly oriented, but has the sensation that the aircraft is flying right wing down, even though his instruments tell him otherwise. The illusion may be generated in reverse of that described above. The aircraft may roll slowly to one side, then recover quickly. The pilot senses only the recovery and leans in the opposite direction to compensate. The leans may die out gradually or persist until a good outside visual reference is available.

2) Estimating the Degree of Bank. The rolling acceleration on entering a turn may be below the threshold of perception, in which case the bank angle attained is underestimated. This causes the pilot to bank too much going into a turn and to overcorrect when recovering from the turn, thus causing a bank in the opposite direction.

b. Erroneous Perceptions of Motion

1) Unperceived Motion. This illusion is a threshold phenomenon and is related to those discussed above, each of which depends partially on unperceived motion. Angular accelerations below the threshold of perception are, by definition, not perceived. The threshold level of acceleration

is determined by a number of factors, some of which are discussed in Chapter III, sections D and E. Threshold data will not be given here, because such data invariably have been taken under idealized laboratory conditions and depend greatly on the experimental methods used to obtain and evaluate them. Threshold levels of acceleration also depend on the time required (latency time) for their perception.

In flight the acceleration thresholds are much higher than measured in the laboratory. The pilot in a plane is in a more stressful environment than in the laboratory. He is preoccupied with the control and navigation of his aircraft; he may be involved in a mission, communication with his base, or setting up a rendezvous with other aircraft. Each of these activities distracts him from the task of orientation and motion detection and serves to increase his thresholds of motion perception. Accordingly, disorientation in the form of unperceived motion occurs when an angular acceleration below the stimulation threshold takes place.

2) Illusion of Turning. This illusion can occur when an aircraft enters a gradual unperceived turn. When the pilot becomes aware of the turn he may correct for it by applying sharp rudder. After recovering from the turn he then has a strong sensation of turning in the opposite direction. The illusion is caused by a combination of threshold and dynamics phenomena. Initially the turn is unperceived because the angular accelerations are below threshold. The rapid recovery is brought about by an angular acceleration in one direction only, which deflects the cupulae in the horizontal semicircular canals. The cupulae return to their neutral positions slowly, giving rise to the aftersensation of turning.

The illusion can be initiated in another manner as well. If an aircraft recovers rapidly from a prolonged turn, the pilot may have a sensation of turning in the opposite direction. Dynamics phenomena of the semicircular canals are responsible for this illusion. Initially, the sensation of turning dies out as the turn is maintained. This in itself is an illusion and is caused by the cupulae of the horizontal semicircular canals gradually returning to their neutral positions by virtue of their own elasticity. Recovery from the turn deflects the cupulae in the opposite direction from which they return slowly to their neutral positions, thus giving rise to an aftersensation of turning in the opposite direction.

3) Graveyard Spin. When an aircraft enters a spin the initial angular accelerations in roll and yaw are perceived by the pilot, giving him an appropriate sensation of the angular motion of the spin. As the spin continues, the sensation of angular motion gradually subsides as the cupulae of the affected semicircular canals return to their neutral positions. As the pilot effects a recovery from the spin, he experiences angular accelerations in roll and yaw in the direction opposite the spin which deflect the cupulae in the direction opposite their initial deflection, giving rise to a sensation of spin in the direction opposite the initial spin. The pilot may then correct for this sensation by reentering the original spin. This eventuality is known as the graveyard spin (ref. 49).

The problem of spin recovery is complicated by the inappropriate compensatory eye movements which accompany prolonged spins (ref. 79). Spins exceeding about 20 sec duration are especially dangerous, particularly for pilots inexperienced in spin recovery. Jones (ref. 79) presents a thorough discussion of vestibulo-ocular problems during spins. He also discusses the more drastic disorientation which occurs in the inverted spin, disorientation which is severe enough to produce crashes even in clear, daylight conditions (ref. 104).

Similar problems of vestibulo-ocular disorganization occur during rapid rolls (ref. 78). The ability of the eye to track in roll is limited by the restricted ocular motility about the visual axis. Rotatory nystagmus about the visual axis with a magnitude of 18 deg peak-to-peak has been recorded during rapid rolls (ref. 78), but this compensatory eye movement may not be sufficient to stabilize the retinal image during rapid maneuvers. A pilot making a 330 deg/sec roll reported that the horizon appeared as a blurred impression of dark and light. Difficulty can be experienced after only a few seconds, leading to loss of control of the aircraft. A maneuver of three or more revolutions or any rapid roll can cause difficulty in recovery.

The termination of a prolonged series of rolling maneuvers causes rotatory nystagmic eye movements to reverse direction and gives rise to visual and subjective sensations of rolling in the opposite direction. This condition may persist for several seconds.

4) Graveyard Spiral. This illusion is similar to that experienced in the graveyard spin; the semicircular canals equilibrate to the constant angular velocity in the spiral and the motion sensation subsides to zero. The aircraft motion in the spiral is that of a descending, coordinated turn. The novice pilot, noting the decrease in altitude, may attempt to correct for it by pulling back on the stick and adding power. This worsens the situation by tightening the spiral. If the pilot takes the appropriate action of correcting his bank angle first, then his turn rate and descent, he may experience an illusion of turning in the opposite direction, correct for this illusion, and reenter the original spiral.

5) Coriolis Illusion. If the aircraft is negotiating a constant rate turn, ω, to which the pilot's semicircular canals have equilibrated, and the pilot then moves his head about a second axis not aligned with the ω axis, he may experience a sensation of rotation and tilt about a third axis, which is approximately orthogonal to the ω axis and the head tilt axis (ref. 70). The experience, termed variously as the Coriolis

illusion, Coriolis phenomenon, Coriolis reaction, or Coriolis effect, can be extremely strong, producing postural disorientation, strong visual effects, and nausea. A more thorough description of the illusion is given in section B and an analysis is presented in Appendix A. Although exceptions have been reported (ref. 114), the sensation of apparent rotation is usually in the same direction as that of the precession of a wheel spinning about the ω axis in response to a torque about the head tilt axis. The pilot will also perceive the head tilt which initiated the reaction. Objects in the visual field will move in the same direction as described for the sensation of rotation. Table XIII in section B lists the direction of apparent motion of a fixated target and the rotation sensation perceived during the Coriolis illusion for various directions of constant rotation and head tilt. A pilot in a turn to the right who pitches his head up will have a sensation of rolling to the left, and objects in the visual field will rotate to the left. Similarly, if he pitches his head down he will have a sensation of rolling to the right, and objects in the visual field will rotate to the right. The directions of perceived motion can best be remembered either by recalling the analogy with the precession of the spinning wheel or by noting the cyclic permutation pattern in Table XIII.

As discussed in section B and in Appendix A, the term Coriolis is entirely appropriate because the expressions for the stimulation of the semicircular canals responsible for the illusion can be derived using Coriolis forces. During the Coriolis illusion, the visual and subjective sensations of motion perceived are truly representative of the angular motion undergone by the head and not spurious sensations. As the head is tilted about one axis while undergoing continuous rotation ω about a second axis not aligned with the first, a component of the rotation vector ω is projected onto a third axis orthogonal to the first two axes. It is this component of the rotation vector ω which stimulates the semicircular canals to give rise to an "illusion" of rotation about the third axis, a rotation which is taking place physically. The subjective sensations of motion are illusory only in the sense that they are unexpected. The head is tilted in one direction while rotating in a second direction and, presto, rotation is perceived in a third direction. The movements of the visual field during the Coriolis illusion are indeed illusory since objects fixed with respect to the pilot do appear to move.

The Coriolis illusion is frequently evoked while the pilot is in a turn and lowers his head to look at a map or turns his head around to change frequencies on his radio. The feelings of disorientation can greatly exceed in duration the physical stimulation causing them (ref. 23).

c. Visual Illusions

1) Coriolis Illusion. The visual illusions attending the Coriolis illusion have been discussed in section B and in subsection C.2.b., above.

2) Oculogyral Illusion. The oculogyral illusion involves the motion and displacement of objects in the visual field in response to angular accelerations imposed on the head. A detailed description of the illusion is given in section B. While the oculogyral illusion is usually accompanied by nystagmic eye movements, a body of evidence has accumulated (refs. 15, 51, 75, and others) which indicates that nystagmic eye movements are not responsible for the illusion. The oculogyral illusion may be observed during flight in the daylight, but is more prominent at night (ref. 62). With an illuminated visual field, stronger vestibular stimulation is required before the visual effects are observed. The illusion has been demonstrated during flight tests (refs. 29, 30, 62, and 63). However, the concomitant occurrence of angular acceleration and strong linear acceleration during the maneuvers in

these tests makes it difficult to associate the resultant visual effects with their respective causes.

Everyone has experienced after a period of spinning about the body's longitudinal axis that objects in the visual field appear to be revolving about the observer. If a full visual field is present, greater stimulation is required to produce the illusion than is required if the visual field is restricted to only a point of light. If the subject is rotated while viewing a full visual field, the visual aftereffect is compounded by stimulation of the semicircular canals and by the optokinetic stimulation induced by the rotating visual field. Therefore, the oculogyral illusion is usually studied in a darkened environment with the subject fixating a simple illuminated target which is fixed relative to the subject during the period of rotation (ref. 75). The oculogyral illusion may be described as follows:

If a subject is rotated rapidly in the dark while observing an illuminated target which rotates with him, thereby remaining fixed relative to the subject, a series of illusory motions of the target will be perceived. As rotation starts, the object will appear to move rapidly in the direction of rotation. As a constant speed of rotation is reached, the target will appear to slow down, stop, and then may appear to move in the opposite direction. As the real rotation is slowed to a stop, the target appears to move rapidly in the direction opposite that of the rotation, and may appear to be displaced as much as 60 deg. The target then appears to slow down and stop in front of the subject after 30 or 40 sec. The target then moves slowly in the direction of the original motion for 40 or 50 sec, following which it may reverse direction again for a shorter period.

If the target moves physically relative to the subject and in the same direction as apparent movement of stationary objects, the target appears to move too fast for its apparent displacement. If the real and apparent movements are in the opposite direction, subjects make the paradoxical observation that the target is moving in one direction but is being displaced in the opposite direction.

It is obvious that the strong illusory sensations involved in the oculogyral illusion could cause confusion and disorientation in flight, particularly at night when the visual field is restricted. These illusions are most likely to constitute a hazard to flight safety during rapid changes in angular motion of the aircraft as in rolls, spins, and aerobatic flight. However, strong stimulation is not required to evoke the illusion. The threshold of perception of the oculogyral illusion is a fraction of a deg/sec^2. Clark, et al. (ref. 29), report that subjects observed illusory motion during 78 percent of the trials in which an aircraft made only a 10 deg bank.

3. Illusions Based on Visual Phenomena

A visual reference is the sine qua non of orientation in flight. Not even the birds have evolved a system capable of maintaining orientation in flight without a visual reference. A study was made in which pigeons were blindfolded and released from a height. They flew hopelessly erratic courses, indicating a high degree of disorientation, then cocked their wings at a high dihedral angle (a spirally stable configuration) and glided safely to the ground (ref. 82). Flight instruments provide an adequate visual reference, but not even the most skillful instrument pilot accords the same confidence in his instruments that he does to direct visual perception of the outside world. A good outside visual reference is the most reliable and readily interpreted visual reference.

Unfortunately, the visual framework of the outside visual reference is often reduced by smoke, haze, fog, inclement weather, or darkness. In such situations the pilot's interpretation of visual cues becomes more difficult, illusory perceptions of orientation or motion resulting from erroneous processing of visual information may occur, and visual phenomena themselves may contribute to disorientation. These eventualities are discussed in the following paragraphs.

a. Autokinesis

This illusion consists of an apparent motion of isolated lights viewed in a meager visual framework. If an isolated light is viewed continually in the dark, it will appear to wander about at random over a small area. The apparent motion may extend as much as 15 deg (ref. 59) and is indistinguishable from real motion. The illusion is readily reduced by increased structuring of the visual field, but is difficult to abolish. In tests of the illusion in a Link trainer (ref. 59), the illusion persisted in spite of the presence of the illuminated panel of the trainer. A faint horizon reduced but did not eliminate the illusion. The presence of two lights reduced the illusion, as did a horizontal bar of light.

Autokinesis has been observed under controlled conditions during flight at night when there was a substantial visual framework, including stars, ground lights, and windscreen supports (ref. 23).

Pilots have reported attempts to join up with a formation of stars, buoys, lights on bridges, and street lights which appeared to be moving and were interpreted as other aircraft. Other illusions, such as the oculogyral and oculogravic illusions, may also have been involved in these experiences, but autokinesis was a likely contributor. Pilot's reports of disorientation incidents, discussed in section E, indicate that autokinesis occurs in flight, and that under the right conditions it is a potential flying hazard (ref. 23).

b. Fascination

Clark and Graybiel (ref. 23) define fascination "...as a condition in which the pilot fails to respond adequately to a clearly defined stimulus-situation in spite of the fact that all of the necessary cues are present for a proper response, and the correct procedure is well known to him." Clark and

Graybiel go on to classify fascination experiences into two categories. Type A fascination is perceptual in nature. The pilot concentrates so hard on one aspect of the stimulus-situation that he fails to perceive other aspects that he may later recall to have been present at the time. Type B fascination occurs when the pilot perceives all the significant aspects of the situation and still fails to respond properly. Pilot reports of fascination are given in section E.

The factors contributing to fascination are not well understood. Fatigue, anxiety, hypoxia, drugs, and basic personality structure might be contributing factors in fascination (ref. 49).

c. Target Hypnosis

Target hypnosis is really a form of fascination and exhibits features of both Type A and Type B fascination. Target hypnosis is characterized by a pilot becoming so intent on hitting a target during an attack that he fails to pull up in time to avoid hitting the target. Whether the pilot fails to perceive that he is too close to the target (Type A fascination) or merely fails to respond properly to the situation (Type B fascination) is a moot question.

d. Illusory Effects Due to Inadequate Stimuli

Restriction of the visual field by smoke, dust, haze, fog, rain, or darkness can produce gross discrepancies between physical entities and their appearance as perceived by the pilot. The pilot's attempt to restructure the physical entity from his meager perception of it may result in a false identification and consequent disorientation. Inadequate stimuli may contribute indirectly to other illusory effects. The pilot's concentrated attempt to restructure the physical entity from the inadequate stimulus it presents may lead to fascination. Inadequate stimuli have an adverse effect on the perception of depth and the judgment of distance. As the visual framework is reduced, cues to depth are also reduced.

e. Improper Grouping of Lights at Night

The tendency to group items in the perceptual field can contribute to illusory effects. A small cluster of isolated lights on the ground on a dark night with a high overcast may be interpreted as the lights of a formation flight. Attempts to join up with such a group could lead to disaster. A cluster of bright stars may also be interpreted as the lights of a formation flight. Needless to say, an attempt to join up would be futile, but such efforts have been made and are reported in section E. A field of scattered lights on the ground on a dark night with a high overcast may be mistaken for stars with the resultant illusion that the aircraft is flying upside down.

f. Illusions of Relative Motion

Experiences of illusions of relative motion are numerous. To an observer in a fast aircraft crossing the path of a much slower aircraft at a different altitude, the slower aircraft appears to be flying sideways and backwards. Illusions of relative motion can be especially provocative and potentially hazardous during formation flights at high altitude or at night when cues to forward speed are absent. If the leader of the formation should suddenly increase his speed, the wingman may develop the illusion that the lead plane is stationary and that his own plane is flying backwards. This is an extreme example, but pilots flying in formation during bad weather or nighttime when visual motion cues are absent, except for cues of relative motion between elements of the formation, are especially prone to disorientation. Changes in motion or attitude of another aircraft may be interpreted by a pilot as changes in motion or attitude of his own aircraft and vice versa. In formation maneuvers the pilot's difficulties are likely to be augmented by erroneous vestibular cues. Since he must maintain his position within the formation, he must rely on an external visual reference and is unable to resolve his sensory conflict by referring to his instruments (ref. 7).

An illusion of relative motion can result from another phenomenon termed reversible perspective. This occurs when the direction of the silhouette of an aircraft against the sky or earth background is ambiguous. The direction of flight of the aircraft thus seen is indiscernible and may appear to change as the aircraft is observed. This can be a startling experience if a collision is anticipated and may result in extreme but unnecessary evasive maneuvers.

g. Illusory Horizons

The preeminent cue to the vertical is the visible horizon; using this cue the pilot can orient his aircraft properly and with great precision. Under conditions of restricted visibility the horizon may become obscure or occulted. Under these conditions the pilot may rely on some other indicator which he believes to represent the horizontal. Under certain other conditions and in perfectly clear weather the pilot may orient his aircraft improperly despite using the visible horizon as a reference. Various types of disorientation produced by reliance on a fictitious horizon are discussed below.

1) Tilted Cloud Banks. The use of cloud banks as an indicator of the horizontal is fraught with danger, because, while most cloud banks are horizontal, some are inclined at a considerable angle. The pilot may feel a compelling desire to align the wings with a tilted cloud bank, especially if the clouds command the visual field or if he's flying on top of a sloping cloud deck.

A recent fatal midair collision between two commercial airliners is attributed to either or both pilots' use of a tilted cloud bank as a horizontal reference. The aircraft were flying intersecting courses, but at different altitudes. Apparently, because of a tilted cloud bank in the field of view, the pilots of one or both aircraft thought that they were on a collision course, and in the evasive maneuvers which followed, the aircraft changed altitude and collided.

2) Confusion Between City Lights and Stars. If a pilot at low altitude cannot distinguish between city lights and stars, he may mistake one for the other and align the wings or nose of his aircraft to the resultant fictitious horizon. This in turn can result in a misjudgment of altitude as illustrated in figure 43. The pilot may think he's flying straight and level when actually he's in a bank and losing altitude. When he finally notices from his instruments the change in altitude and bank angle, he may not have time to make the transition from a visual to an instrument reference and effectuate a safe recovery. (The problem of transition is discussed in section A.)

3) Depressed Horizon Due to High Altitude Flight. At high altitude the true horizon is depressed below the so-called sensible horizon due to the curvature of the earth. (The sensible horizon is defined as the plane normal to the vertical at the observers location.) For altitudes at which aircraft are capable of flying, the horizon is depressed an amount approximately equal to $\alpha \doteq 0.56\sqrt{h_k}$ deg, where h_k is the altitude in thousands of feet. At 50,000 ft the horizon is depressed about 4 deg, so that if the pilot aligns his right wing with the horizon and looks to the left, he'll make the confusing observation that his left wing is elevated 8 deg above the horizon (see fig. 44). Similarly, at night a pilot at high altitude may observe the moon and stars apparently below the horizon, and may subsequently feel that he's flying in a bank or even inverted.

4) The Robert MacDougall Phenomenon. This illusion is characterized by the appearance of the horizon during level flight to be above eye level. Robert MacDougall found at Harvard in 1903 (ref. 14) that the fixated upper edge of a stimulus figure at the objective eye level of the observer appeared to be above eye level. An explanation of the illusion is offered in section D. The horizon formed by the ocean viewed from adjacent mountains may appear elevated several degrees so that the sky seems full of ocean.

Sir Francis Chichester remarked (ref. 16) that during his recent solo voyage around the world he sometimes saw strange things. "Just before crossing the equator the boat looked to be sailing up a gently sloping sea surface, uphill. I was worried at the time, but when I was 240 miles north of the line I noticed the same thing again. This time it seemed uphill in every direction, as if I were sailing in a saucer."

Although not reported as a flying hazard in the literature reviewed, this illusion conceivably could cause confusion in the pilot.

5) False Perception of Altitude Due to a Fictitious Horizon. Many incidences of a false perception of altitude have occurred because the pilot judged his height above the terrain with respect to a fictitious horizon. This generally occurs at night or in weather when the aircraft is flying in an unperceived abnormal attitude, either in a bank or nose-high, and judges his height above the terrain from objects or lights viewed on the ground. Figures 43 and 45 illustrate how such an erroneous determination can be made.

A representative sample of pilots' experiences of various illusions and episodes of disorientation is presented in section E. Unfortunately, those pilots who suffered most from these experiences, those not lucky enough to recover, are unavailable for comment, so that little can be determined from accident statistics about the role of falsely interpreted visual cues in aircraft accidents. However, Gillingham (ref. 49) expresses well the truism that "...when sensorily deprived and adequately stressed, one will perceive what he needs to perceive in order to perform, even though it may mean supplying an illusory perception."

D. THE MOTOR THEORY OF EGOCENTRIC VISUAL LOCALIZATION

A number of phenomena involving movement and displacement of objects in the visual field have been discussed in the sections above. Most of these phenomena are elicited by stimulation of the vestibular system, but the mechanism causing apparent motion and displacement of objects in the visual field remains largely unexplained. Compensatory eye movements, such as nystagmus, may participate in the genesis of some of the illusions, but cannot account for that of others. Indeed there are a number of visual illusions of movement which arise unaccompanied by demonstrable eye movements.

Throughout the literature (refs. 46, 74, 129, and others) there are suggestions that the pattern of stimulation in the oculomotor muscles participates with retinal stimulation in determining the visual sense of direction and movement of objects in the visual field. [A visual sensation of movement of objects in the visual field may occur even when tracking of their retinal images is lacking due to immobility of the eyes (ref. 74).]

Gibson (ref. 46) formulated a theory which embodied the idea of the visual sense of direction changing with the pattern of stimulation or innervation of the oculomotor muscles. Whiteside, Graybiel, and Niven (ref. 129) present evidence supporting this idea in the cases of autokinesis, the oculogravic illusion, and the oculogyral illusion.

The concept was further embellished by Bruell and Albee (ref. 14). Their theory, modified herein, formalizes the concept of efferent activity giving rise to the visual perception of movement and provides a tenable explanation for numerous visual phenomena involving space and movement perception.

The theory formalized by Bruell and Albee is termed the motor theory of egocentric visual localization. Judgments concerning the position of objects relative to the observer are referred to as egocentric localization

1. Egocentric Localization

Stimulation of the fovea of the eye produces the sensation that the object causing the stimulation is located in the direction toward which the fovea is pointing. If the fovea is stimulated with the eye in the primary position, i.e., looking straight ahead, the stimulus object will be perceived as being straight ahead of the individual. Similarly, if the fovea is stimulated with the eye turned to the right, the object will appear to be to the right of straight ahead. The same applies if the eye is turned to the left, up, down, or obliquely. In a similar fashion, objects stimulating peripheral areas of the retina are localized in space relative to the foveal direction in accordance with the anatomic positions relative to the fovea of the retinal areas stimulated.

The position in space where one localizes an object is thus determined by the position relative to the fovea of the retinal area stimulated by the object and by information concerning the position of the eye itself. When we say information concerning the position of the eye we refer to some nervous signal or combination of signals which denote eye position to the brain. The genesis of this signal denoting eye position to the brain forms the crux of the motor theory of egocentric visual localization.

2. Absence of Conscious Position Sense in the Human Eye

Merton (ref. 98) cites considerable evidence to the effect that there is no conscious position sense in the human eyes. The classical experiments of Helmholtz (ref. 74) showed that no information about the position of the eyes is derived from sense endings in the eye muscles. Consider an individual observing objects in his surroundings. As he directs his gaze from one object to another they appear stationary even though their retinal images move. Clearly the brain changes some spatial reference to make an allowance for eye movements, otherwise the movements of the retinal images would be interpreted as movements of the objects themselves. The means by which the allowance for eye movements is made is revealed by considering passive instead of active movements. If the eye is moved passively by physically pushing on the eyeball, objects in the visual field appear to move about. In this situation movement of the retinal images is interpreted as movement of the objects themselves. Apparently the brain has not adjusted the spatial reference to account for the passive eye movement. If the brain based its spatial reference adjustment on signals from position sensing receptors in the eye muscles, then an allowance for eye movement should have been made both during the passive and active eye movements, because both types of movement excite these receptors. Allowance for eye movements must therefore be based on some function other than position sensing in the eye muscles.

This conclusion is supported by the behavior of a visual afterimage observed during active and passive motions of the eye. The apparent motion of an afterimage during active and passive eye motions is the inverse of that of the image of a real object. An afterimage at the fovea appears to move with the direction of the fovea during active voluntary eye movements. However, during passive eye movements, an afterimage fixated in the dark or against a featureless background does not appear to move at all. This behavior of the afterimage is the keystone in the argument against a spatial reference being based on position sensing in the eye. The fixity of the afterimage during passive eye movements neatly disposes of the objection that traction on orbital structures does not produce the same stimulation of the receptors of the extrinsic eye muscles that is produced by natural movements. This inappropriate stimulation would in turn produce an incorrect allowance for eye movement resulting in the apparent movement of objects which is observed. The immobility of the afterimage shows that there is no question of an inappropriate allowance being made; there is no allowance made at all, and hence the visual field is viewed during passive eye movements as though the eyes had not moved.

Now, an account must be made for the means by which the space reference is changed as the eyes are moved actively, that is, by the oculomotor muscles themselves. Two types of eye movement must be considered: voluntary and involuntary. With respect to voluntary commands, it is evident from the discussion above that the space reference changes as a function of the voluntary command itself, and does so regardless of whether or not the command is executed by the oculomotor system. An example of the space reference changing with the voluntary command but not the execution is observed in a patient with paralyzed eye muscles who, in a vain attempt to move the eyes in a given direction, perceives instead the visual field to move in that direction. The patient's sensations are based not on his actual eye movements but on his commanded eye movements.

Several visual phenomena support the notion that the visual space reference also changes as a function of involuntary commands to the oculomotor system. The observation of a visual afterimage during counterrolling of the eyes is an example. If an afterimage is fixed on the retina while the head is upright and the head is then tilted to one side, the afterimage will appear to be tilted in the direction of counterroll of the eye. In fact, this is one of the methods of measuring counterroll. Since the afterimage is fixed with respect to the retina, any change in apparent position of an afterimage must be associated with a change in the space reference. This particular phenomena will be discussed in more detail later.

To formalize and elucidate the concept of the visual space reference changing in response to innervation of the oculomotor muscles, the notion of retinal space values is introduced.

3. Retinal Space Values

We might think of the brain as assigning a space value to each point on the retina, as depicted in figure 46. With the eye in the primary position, retinal points to the right of the median plane are assigned negative space values, those to the left are assigned positive space values, and the fovea is assigned zero. Objects A and B stimulate retinal points with negative space values and are perceived as being to the left; objects D and E stimulate retinal points with positive space values and are perceived as being to the right. Object C stimulates the fovea and is perceived to be straight ahead. Figure 46b portrays the eye turned voluntarily to the right. Object C on the observer's median plane stimulates a portion of the retina peripheral to the fovea, but is still perceived as being straight ahead, and object E stimulates the fovea, but is still perceived as being to the right. Obviously the space values of the retinal points changed when the eye was turned voluntarily to the right.

These observations lead us to postulate that whenever the dextrorotators (levorotators) of the eyes receive voluntary innervation, the fovea assume positive (negative) space values, and concomitant changes occur in the space values of all retinal points. Similarly, the postulate holds for voluntary innervation of the elevator, depressor, and torsion muscles.

This postulate is the first of two proposed by Bruell and Albee (ref. 14) in their paper on a motor theory of egocentric visual localization. Their second postulate asserts that the retinal space values do not change when the oculomotor muscles receive involuntary innervation. However, if this second postulate is accepted, it does not appear possible to account for the apparent motion of visual afterimages.

Consider, for example, the apparent rotation of an afterimage during counterrolling of the eyes. Counterrolling is an entirely involuntary reflex elicited by a change in the direction of the gravity vector acting on the utricle as the head is tilted in the frontal plane. Figure 47 portrays the essentials of an experiment conducted by the author. The afterimage was generated using a flashbulb and a suitable mask. In part (c) of the figure the head is tilted to the right 90 deg and an afterimage fixed on the retina as shown. In this head position the eye has counterrolled to the left through an angle γ relative to the median plane. The amount of counterroll is indicated by the black triangular indices on the periphery of the retina. The cross pattern of the afterimage extends vertically and horizontally in this head position. Retinal points from the center upward (relative to the head) to the periphery of the retina in the median plane are assigned a space value of zero. Clockwise from this line retinal points become increasingly positive; counterclockwise from this line retinal points become increasingly negative. As the head is rolled to the left to the upright position, shown in figure 47b, the counterroll decreases to zero as indicated by the alignment of the triangular indices with the median plane. The afterimage is now physically displaced to the right of the median plane through the angle γ. The afterimage is of course fixed to the retina and hence will appear to be displaced only if the space values of the retinal points have changed. The afterimage is indeed perceived to be tilted to the right, thus forcing the conclusion that the space values of the retinal points have changed. As the head is tilted 90 deg to the left, as in figure 47a, the eye counterrolls to the right through an angle δ displacing the retina and afterimage further clockwise relative to the median plane. The afterimage is now physically displaced clockwise from the median plane through an angle equal to the sum, $\gamma + \delta$, of the counterroll angles. The space values of the retinal points change accordingly, and the afterimage is perceived to be rotated clockwise relative to the median plane through the angle $\gamma + \delta$.

It must be admitted that the amount of physical counterroll was not measured during this experiment, but the apparent displacement of the afterimage in the various head positions was consonant with the estimated amount of counterroll. For instance, with the author as subject and with the head tilted 90 deg to the left, the afterimage was judged to be tilted 20 deg to the right of the median plane. This would correspond to a counterroll of 10 deg for head tilt to either side, which is close to the estimate of 11 deg made for this subject.

Our postulate may now be modified to account for changes of the retinal space values during both voluntary and involuntary innervation of the oculomotor muscles.

> **Postulate 1:** Whenever the oculomotor muscles are innervated, either voluntarily or involuntarily, points on the retina assume space values which would tend to preserve the apparent fixity of stationary objects in the visual field if the eyes were to move in response to the command.

A corollary to Postulate 1 may be enunciated which specifies what happens when the eyes do not respond to the voluntary command to move.

> **Corollary 1:** Failure of the eyes to move in response to voluntary or involuntary innervation of the oculomotor muscles, due to paralysis or other causes, results in an apparent motion and/or displacement of objects in the visual field in the direction of voluntary or involuntary innervation.

Thus, for example, when the dextrorotators are innervated the space values of all retinal points change to account for a movement of the eye to the right, regardless of whether or not the movement takes place. If the movement of the eye to the right does take place, objects in the visual field appear to be stationary. If the eye is prevented from moving by paralysis or other means, objects in the visual field appear to move to the right in accord with the changes in space values of all points on the retina.

Now we must consider what happens when both voluntary and involuntary innervation of the oculomotor muscles are present at the same time in antagonistic eye muscles. What governs the change in retinal space values in such a situation? Imagine, for example, that the eye is exposed to a stimulus evoking a reflex (involuntary) eye movement to the right, but that the individual is voluntarily fixating an object in the visual field which prevents the eye from responding to the reflex. Numerous phenomena (a few of which will be discussed later) indicate that in such a situation the voluntary innervation is dominant over the involuntary innervation and controls the direction of change of the space values of retinal points. In the example cited, the fixated object would appear to be displaced in the direction of voluntary innervation or to the left. The amount of apparent displacement would depend on the strength of the reflex tending to move the eye to the right. We now add a second postulate.

> **Postulate 2:** Whenever both voluntary and involuntary innervation occur simultaneously in antagonistic eye muscles, voluntary innervation takes precedence over involuntary innervation in determining retinal space values so that the apparent fixity of stationary objects in the visual field would be preserved if the eyes moved in response to the voluntary command.

A corollary to Postulate 2 may be enunciated which specifies what happens when the eyes do not respond to the command to move.

> **Corollary 2:** Failure of the eyes to move, due to a balance of voluntary and involuntary innervation of antagonists or for any other reason, results in an apparent motion and/or displacement of objects in the visual field in the direction of voluntary innervation.

The apparent position and/or motion of objects in the visual field can now be predicted using these postulates provided we know the pattern of innervation of the oculomotor muscles. We will now consider some of the factors determining this pattern of innervation.

4. Factors Determining Innervation of the Oculomotor Muscles

Innervation of the oculomotor muscles may be either voluntary, involuntary (reflex), or both. The involuntary reflexes of interest in this study are those elicited by visual (retinal) stimulation and by vestibular stimulation.

In man the most important source of involuntary innervation of the oculomotor muscles derives from visual inputs themselves. Motion of objects in the visual field evokes the following reflex, examples of which are familiar to everyone. For instance, the eyes exhibit a special type of following reflex when passing scenery is viewed from a moving vehicle. The eyes exhibit a slow phase movement in the direction of apparent motion of the scenery and a fast phase in the opposite direction. This behavior is called optokinetic nystagmus, is entirely reflexive, and persists as long as the individual pays attention to the scenery.

Another example of the following reflex is the tendency of the eyes to move in the direction of a visual stimulus so that it may be fixated by the fovea, the area of greatest visual acuity on the retina.

The fixation reflex is, in essence, the same as the following reflex, but is considered to act after the image of the object of regard is placed on the fovea by movement of the eyes brought about by the following reflex (ref. 2). The fixation reflex serves to keep the image of the object of regard on the fovea. The attention value of the object of regard determines the strength of the fixation reflex. Other objects in the visual field may possess greater attention value or may merely be distracting. This situation tends to inhibit the fixation reflex and allow the following reflex to take over and divert the eyes toward the other objects. This type of behavior can lead to an illusion with regard to the apparent position of the fixated object.

Consider the situation portrayed in figure 48 in which a subject fixates an object C located in his median plane. The presence of a second object F of equal attention value tends to evoke the following reflex in the direction from C to F. Fixation of C can be maintained only through voluntary innervation of the levorotator muscles equal in strength to the reflex innervation of the dextrorotator muscles elicited by the following reflex. According to Postulate 2, Corollary 2, the fixated object, C, will appear to be displaced in the direction of voluntary innervation, or to the left of the median plane.

We may generalize from the above arguments that if the position of the eyes in a given stimulus situation is known, it is possible to infer whether eye position is being maintained by involuntary reflex innervation alone or in concert with voluntary innervation (ref. 14). Knowing the pattern of innervation, the postulates on retinal space values may be applied to determine the apparent position and/or motion of objects in the visual field.

Various visual phenomena can now be explained on the basis of our two postulates and the pattern of innervation of the oculomotor muscles, which we can infer from a knowledge of the position of the eyes and the visual and vestibular stimuli acting in a given situation.

5. Illusions Evoked by Visual Stimulation

a. Dietzel-Roelofs Phenomenon

Bruell and Albee (ref. 14) describe experiments conducted independently by Dietzel and Roelofs in which a luminous figure was fixated in an otherwise dark room. One edge of the figure was placed in the objective median plane of the subject, the remainder of the figure extending to the right. The subject was instructed to fixate the left edge of the figure and to judge its position relative to the median plane or the straight ahead. The experiment was thus quite similar to that illustrated in figure 48. We may predict the outcome of such an experiment.

In order to fixate the left edge (corresponding to point C) of the stimulus figure, the subject had to innervate voluntarily the levorotators of his eyes to counteract the innervation of the dextrorotators elicited by the following reflex. The following reflex tended to turn his eyes to the right toward the center of the visual stimulus field. According to Postulate 2, Corollary 2, the voluntary innervation to the left would result in the fixated edge of the figure appearing to be displaced to the left of the median plane. Similarly, if the right edge of a stimulus figure extending to the left were aligned with the median plane, the fixated edge, according to the theory, would appear to be displaced to the right of the median plane.

Dietzel and Roelofs did, indeed, obtain these results, and they have been confirmed by more recent experiments conducted by Bruell and others. These experiments show that the apparent straight ahead tends to shift in the direction of the center of the stimulus field. If this center differs from the objective straight ahead, then the subjective and objective straight ahead do not coincide.

Usually, the visual field is filled with stimuli and retinal stimulation is sufficiently symmetrical that the subjective and objective straight ahead are coincident. Under some conditions, as illustrated by the experiments described, this symmetry does not prevail and an illusion results. This leads us to consider the next illusion.

b. The Robert MacDougall Phenomenon

This phenomenon was described in subsection C.3.g., and is the up/down analog of the Dietzel-Roelofs phenomenon. In the Robert MacDougall phenomenon the fixated upper edge of a stimulus figure placed at the objective eye level appears to be above eye level. The phenomenon is explained in a manner similar to that of the Dietzel-Roelofs phenomenon. Fixation of the upper edge of a stimulus figure, in an otherwise featureless visual field, can be maintained only by voluntary innervation of the elevator muscles of the eyes in order to counteract the tendency of the eyes to move downward toward the center of the stimulus field in response to the following reflex. The space values of the retinal points change in the direction of voluntary innervation and, as expressed by Postulate 2, Corollary 2, the upper edge of the figure appears to be displaced upward in the direction of voluntary innervation.

MacDougall's experiments were inspired by the fact that to an observer on the deck of a ship the horizon appears to be above eye level.

c. Autokinesis

This phenomenon of apparent motion of a fixated target light in the dark has been described briefly in subsection C.3.a. Autokinesis has been studied extensively by psychologists in an effort to determine its cause. Controversy still exists as to whether eye movements are responsible for the illusion. Hard data appear to be lacking which would serve to quantify the direction and extent of autokinesis, concomitant eye movements, and the pattern of innervation of the oculomotor muscles, so that contributory causes of autokinesis cannot be identified unequivocally.

However, Howard and Templeton (ref. 75) cite a number of studies indicating that the direction and extent of autokinesis is associated with the direction and extent of tonus (i.e., the state of innervation) of the oculomotor muscles. The association has been made by many others as well (ref. 129). Autokinesis may therefore belong in the class of phenomena in which the absence of eye movements in the presence of innervation of the oculomotor muscle is an explicit condition for apparent movement.

6. Illusions Evoked by Vestibular Stimulation

a. Oculogravic Illusion

This illusion has been discussed in subsections B.1.a. and C.1.b., and consists of an apparent movement and displacement of objects in the visual field in accordance with a change in direction of the G vector relative to the observer. The oculogravic illusion has been observed by a subject fixating an illuminated target in the dark while both subject and target are rotated together on a centrifuge to produce a change in the orientation of the G vector.

If the subject faces the center of rotation the target appears to rise as the centripetal acceleration increases. A sufficiently strong stimulus will make the target appear to rise higher than could be accounted for by movement of the eyes. In addition, subjects report that the target remains distinct, indicating foveal vision. Eye movements are thus ruled out as a cause of the apparent movement of a real target during the oculogravic illusion.

The illusion can be explained by the motor theory of egocentric visual localization. As the centripetal acceleration increases, the shear force, acting backward in the sagittal plane, on the utricles increases. This has been shown (Chapter II, section E) to produce a reflex in the eyes, innervating the depressors (inferior recti) and tending to move the eyes downward. The subject is able to maintain fixation by innervating the elevators (superior recti). According to theory (Postulate 2, Corollary 2), the fixated target should appear to move up in the direction of voluntary innervation of the oculomotor muscles. The experimental results bear out the predicted movement.

We may speculate that the lag effects (described elsewhere) observed in the perception of the oculogravic illusion may be accounted for as a characteristic of the dynamics of the change in retinal space values. In turn, these dynamics may be studied through their effects on this and other illusions.

The oculogravic illusion is also observed under the same experimental conditions as described above, but using a visual afterimage rather that a real target. In this case the afterimage appears to move in a direction opposite that of the real target. Also, motion of the afterimage is associated with movements of the eyes (ref. 129). The apparent movement is explained by the theory. Without a real target to fixate, the eyes follow the reflex to move downward in response to the increase in centripetal acceleration. According to Postulate 1, the space values of retinal points change in accordance with the involuntary innervation of the oculomotor muscles, and the apparent position of the afterimage changes accordingly. Thus the eyes move in response to the reflex, and the afterimage is perceived to move accordingly.

When both an afterimage and a real target are fixated simultaneously during the oculogravic illusion, they appear to move as described for a real target alone. In this case, retinal space values are determined by the direction of voluntary innervation established by fixating the real target, so both targets move as described for the real target alone.

The apparent tilting of an illuminated target when the G vector is tilted relative to the subject in the frontal plane is explained by the motor theory of egocentric visual localization in the same terms as above. In this form of the oculogravic illusion we are concerned with innervation of the oblique muscles of the eyes rather than the elevators and depressors. Tilting of the G vector in the frontal plane evokes the counterrolling reflex in the eyes. Our theory requires that fixation of a real target innervates the oculomotor muscles antagonistic to those producing the counterroll, even though there is no voluntary control over torsional movements of the eyes. Presuming such innervation takes place and that we can qualify it as voluntary, the apparent rotation of a horizontal target line is in the direction of "voluntary innervation" as prescribed by our theory.

Descriptions of the behavior of an afterimage while experiencing the oculogravic illusion in the frontal plane were not found in the literature. An apparent rotation of a visual afterimage in the direction of counterroll of the eyes would be expected from the theory (Postulate 1 and Corollary 1). The amount of apparent rotation of the afterimage would be expected to be nearly equal to the amount of rotation of the G vector and hence would exceed the amount of counterroll.

b. Elevator Illusion

This illusion has been suggested to be a special case of the oculogravic illusion in which the G vector changes in magnitude but not direction. The illusion was described in subsections B.1.c. and C.1.b. The illusion may be explained in the same terms as the oculogravic illusion in the sagittal plane.

During increased gravitoinertial force, there is a reflex innervation of the depressors of the eyes. In fixating a real target this reflex innervation is counteracted by innervating the elevator muscles of the eyes, making the target appear to rise. An afterimage, fixated alone, appears to descend in response to the downward reflex innervation.

During decreased gravitoinertial force, there is a reflex innervation of the elevators of the eyes. In fixating a real target this reflex is counteracted by innervating the depressors, making the target appear to descend. An afterimage, fixated alone, appears to rise in response to the reflex innervation.

An afterimage and real target, fixated simultaneously, appear to move as described for a real target only. Fixating the real target produces a voluntary innervation which opposes the reflex innervation, and both targets appear to move in the direction of voluntary innervation.

Reflex eye motions of short duration elicited by abrupt changes in magnitude of the G vector were actually observed during tests of the elevator illusion (ref. 103). The movements evidently took place before the fixation reflex had time to counteract them.

c. Oculogyral Illusion

This illusion was described in subsections B.2.a. and C.2.c. and consists of an apparent displacement of objects in the visual field in response to angular acceleration stimulation of the semicircular canals. While eye movements may account for some phases of the illusion (see subsection B.2.a.), other phases occur without observable movement of the eyes. These phases are readily accounted for by the motor theory of egocentric visual localization.

The oculogyral illusion can be observed by a subject regarding an illuminated target light which rotates with him on a centrifuge in a dark enclosure. If the subject is seated upright and given an angular acceleration to the left up to a constant velocity, the following takes place: The stimulation of the semicircular canals elicits a reflex innervation of the dextrorotators of the eyes. To fixate the target the subject must voluntarily innervate the levorotators. As a result, the target appears to move to the left in the direction of voluntary innervation. As the semicircular canals equilibrate to the constant rotation rate, the reflex innervation of the dextrorotators decreases. The strength of voluntary innervation in the antagonists required to counteract the reflex decreases accordingly, and the target appears to decrease its speed to the left and slowly come to a stop. Following this first effect, there may be a second effect. The second effect of the oculogyral illusion, described in subsection B.2.a., is an apparent slow motion of the target in the direction of rotation. We may speculate that this second effect is associated with the dynamics of the change in space value of the retinal points, similar to that which occurs during the overshoot in perception of the oculogravic illusion. On stopping the centrifuge, the above phenomena are reversed.

The apparent motion of a visual afterimage during the oculogyral illusion is the opposite of that described for a real target.

Although experiments correlating eye movements and the apparent motion of an afterimage during the oculogyral illusion were not found in the literature, it is presumed (by the author) that there is such a correlation, just as there is in the oculogravic illusion. In such a case, the theory predicts that as the eyes follow the reflex to move to the right during rotation to the left, the space values of retinal points change in the direction of involuntary innervation. The afterimage is thus seen initially to move to the right. As the canals equilibrate to the constant rotation to the left, the reflex innervation of the dextrorotators decreases and the afterimage slows to a stop. A second effect consisting of an apparent motion of the afterimage to the left may follow. Again, this possibly could be accounted for by the dynamics of the change in retinal space values, but this is the purest conjecture.

d. Coriolis Illusion

This illusion was described in subsections B.2.c. and C.2.c. The Coriolis illusion is evoked by stimulation of the semicircular canals, and the visual illusions which result are entirely appropriate to the stimulation. The explanation of the illusion therefore follows identically that of the oculogyral illusion, with due regard for the fact that the Coriolis illusion is usually experienced in roll and pitch while the oculogyral illusion is usually experienced in yaw. Each may be experienced in any direction, however.

7. Summary

- Various visual illusions involving apparent displacement and/or motion of objects in the visual field occur in the absence of demonstrable eye movements.

- These illusions can be explained on the basis of the pattern of innervation of the oculomotor muscles prevailing in a given situation.

- Knowledge of eye position, the nature of the visual stimulus, and the characteristics of the vestibular stimulus permits a determination of the pattern of oculomotor innervation prevailing in a given stimulus situation.

- During fixation of a real target, or a real target and visual afterimage together, by a subject undergoing vestibular stimulation, a visual sensation of apparent displacement and/or motion of the target or targets is observed to occur in the direction of innervation of the oculomotor muscles antagonistic to those innervated by the vestibular stimulation.

- During fixation of a visual afterimage alone by a subject undergoing vestibular stimulation, a visual sensation of apparent displacement and/or motion of the afterimage is observed to occur in the direction of innervation of the oculomotor muscles innervated by the vestibular stimulation.

- The apparent displacement and/or motion of a visual afterimage observed by a subject undergoing vestibular stimulation is associated with the reflex eye movements induced by the vestibular stimulation.

- Data found in the literature are insufficient to correlate for all illusions the relative magnitudes of eye movements and associated apparent motions of a visual afterimage.

- It is speculated that the lag and overshoot effects in perception of the oculogravic illusion and the so-called second and third effects in the oculogyral illusion may be associated with the dynamics of the change in retinal space values responsible for these illusions.

E. EPISODES OF DISORIENTATION

The purpose of presenting this section on episodes of disorientation is to illustrate graphically the nature and extent of disorientation experienced by pilots, to implicate through example the conditions contributing to disorientation, and to relate the pilots' subjective interpretations of the intensity of the sensations experienced. The episodes are classified on the basis of their most likely cause, although it should be recognized that more than one contributory factor is frequently involved, and that one type of disorientation experience may elicit another.

1. Illusions Based on Stimulation of the Gravity Sensors

> "While circling the field at night in an SNJ aircraft and knowing the plane was in good trim, I got the sensation the plane was in excessive bank. My instruments said under a 15 deg bank, but I was leaning into the turn and actually thought I was losing altitude. To correct this feeling I leveled wings and stopped looking at lights below on field. The incident seemed to start again as soon as I would concentrate on one portion of the field like RDO position and try to keep left wing on him." (ref. 23)

> "While flying tail chase on a daylight formation hop in an F8F, I encountered vertigo. I had the sensation of being on my back, and although I had enough reference to realize I was in a mild bank, I could not get rid of the sensation. As soon as the tail chase was concluded and we assumed a normal wing position the feeling disappeared." (ref. 23)

> Night flight in F8F-1: "Then the leader took the formation out over the water at an altitude of about 3,000 ft. We went out straight and level for some time, then started a gentle 180 deg turn back. I was in Number 4 position and the flight turned into me. After about 90 deg of turn I became disorientated. I felt as though the bank continued to steepen until we were inverted." (ref. 23)

> In a daylight flight in an SNJ aircraft attempting a slow roll: "After getting on my back and believing I was making a normal recovery, I discovered I was in reality finishing the roll with the nose headed toward the deck, while believing I was in a normal recovery attitude." (ref. 23)

"I was in a climb out of Edwards AFB through a solid overcast. Tops were reported at 20,000 ft, and I was perturbed when I didn't break clear. I thought I was in a straight climb, but on looking at the gyro, I found I was in a 60 deg bank. I concentrated on the instruments and in a few seconds the feeling disappeared." (ref. 24)

On a night formation flight (Africa, very dark) two F84F aircraft: "I was chase pilot on a night checkout. Lead aircraft had no light on wing tip in the dim position so I requested that he go to bright. Then I moved out in order that the excessively bright white light on the fuselage wouldn't blind me. Somehow I got into a slight climb and had to drop my left wing to keep the leader in sight. I checked my altimeter and saw 12,000 ft. (Flight level was 20,000 ft.) The lead aircraft appeared well below me and I was having to pull power off to stay with him. I advised him on the radio that I was at 12,000 ft and that he appeared dangerously low. He replied that he was flying on instruments and advised me to do the same. I was then in a steep dive following a barrel roll around him and was nearly inverted. I recovered at 3,000 ft, 17,000 ft below the leader." (ref. 104)

2. Illusions Based on Stimulation of the Semicircular Canals

a. Postural Illusions

"Flying at 37,000 ft in the 'soup' I experienced a good case of vertigo. I was flying in the Number 2 position in a flight of three when the leader, who was on my left, started a slight turn to the right passing in front of me. I found myself in a column position with the sensation that I was flying in over 90 deg of bank and almost going over on my back. After rechecking my instruments and moving out to a wing position this feeling went away." (ref. 24)

"Flying formation at night with a hazy horizon, the leader rolled into a 30 deg bank and rolled back out. I felt that the leader was in 90 deg of bank. This resulted in my tensing and more or less fighting the controls. Referring to the gyro horizon, I knew we were straight and level. This sensation persisted for about 30 sec." (ref. 24)

"I was flying an F9F-6 aircraft in a climb-out. I was flying Number 4 in a four-plane division. We were under CIC control and they gave us heading changes. After about the second turn, the instruments showed the wings level and climbing, and I thought I was in a 90 deg bank. Then we hit another turn in the same direction, and I thought we were upside down. We continued to climb and turned in the opposite direction and the feeling disappeared." (ref. 24)

b. Erroneous Perceptions of Motion

"I had a sensation of rolling with result that I rolled in opposite direction. I was leader of section of two aircraft in GCA in clouds at 5,000 ft and had just rolled out of 180 deg procedure turn. Started to roll in opposite direction, but instruments indicated no roll so I ignored sensation and stayed on instruments." (ref. 104)

In three-ship formation flight in day weather; cloud base 700 ft topped at 35,000 ft. "I was flying in F86 and this was my first formation flight in weather. I had never had a serious case of vertigo before. The formation was just rolling out of a 450 deg left climbing turn and went into clouds. The visibility in the clouds was about 500 yd and I saw the rest of the section but was disoriented. I didn't go on the dials right away because I was afraid of collision. I had a sensation of turning to the right and therefore corrected to left by reflex; as I did this I became confused and felt that the formation was above me and that I was looking up at them. Flight leader called and told me to go on gauges and that I was climbing in an inverted position. I was thoroughly confused but finally did go on instruments. By this time my airspeed was building up and apparently I was in a dive from a split S. I immediately put out speed brakes and reduced power as I broke through clouds and saw the ground coming up fast. I had already pulled back on the stick. I blacked out but recovered on the deck. I had a 9-1/2g pullout." (ref. 104)

"The pilot took a waveoff as he attempted to land the helicopter on a spot lighted probably by four flashlights. Because of the extreme denseness of the fog he was unable to find the spot. As he circled to attempt a second landing apparently he became completely disoriented. While he was in vertiginous state, he circled to the right but thought he was turning to the left. Although he was on instruments he does not remember altitude or airspeed. As he crashed he stated he became just a passenger and rode it in." .(ref. 23)

"The pilot involved was one of a flight of eight AD-4 aircraft on an authorized operational low-altitude daytime flight from CV-32. He was the wingman of a section of two attempting to fly through a narrow squall. The section leader's statement read, 'I was on instruments for approximately thirty seconds, and just prior to breaking clear, heard my wingman call over the radio, "507, are you turning?" As soon as I was in the clear, I looked back and saw a large fire on the water directly astern of me.'" (ref. 23)

c. Coriolis Illusion

"While in the procedure turn (2,500 ft), the rubber band holding my let-down chart to the knee board broke, and down went the chart to the cockpit deck. I reached down to pick it up and my next look at the instruments brought a chill of horror. The needle was against the left peg, the gyro horizon was showing an eight ball, and the altimeter was plummeting downward. I felt as though I was in a right bank and pulling g." (ref. 23)

"The flight was normal until I ran into the vertigo problem. I had been airborne about 3/4 of an hour. I attempted to dial in a frequency on my radio while I was in a turn. As I did my bank steepened and my gyro horizon tumbled. When I looked up from the radio, I was disoriented. I was at 35,000 ft at the time. I tried to orient myself by visual means and by instruments. There were several thin layers of clouds in the area at the time and I was zooming in and out of them. One moment I'd be descending rapidly and the next I'd be climbing. I was losing altitude as a result, and I made up my mind that I'd eject if I went below 20,000 ft. As I passed through this altitude and still was not oriented, I ejected. I had a normal ejection and a safe landing." (ref. 24)

Clark and Graybiel (ref. 23) noted the intensity and duration as unusual features of the following episode:

"...a senior flight instructor in the torpedo squadron took his flight on a night tactics hop in TBF/M type planes. Weather was contact. Takeoff and rendezvous were normal. Captain M. made frequent rapid turning movements of his head from side to side to see that his flight was intact. Vertigo suddenly developed. He had a feeling that his plane was peeling off in a steep left hand dive, and had a strong desire to use right rudder and right aileron, but saw by his instruments that he was flying straight and level. 'It took all the guts I had to believe those instruments,' he said, 'but I knew they were right and that my sensations were wrong.'

"Captain M. led his students on the one-hour flight, which included banks, turns, and dives, entirely on instruments. Throughout the flight he had the sensation that his plane was falling off in a left-hand dive. He approached the landing field and came into the groove still on instruments. Just before landing he shifted to contact flight in spite of the fact that the runway seemed to him to be at a 45 deg angle incline upward to the starboard, and appeared to oscillate. He landed port wing and port wheel down, started to ground loop, but corrected it. Vertigo continued for about fifteen minutes after he was on the ground.

"Captain M. stated that no combat experience had frightened him as had this attack of vertigo. He felt helpless and had a cold fear of impending doom. He had a strong tendency to tighten up and freeze at the controls.

"After reassurance, he took off the next night and made an uneventful flight over the same area." (ref. 23)

"I was in the back seat of a T33 on a single-ship weather flight. We were in considerable turbulence at altitude and I was bending over to tune in the radio compass; when I sat up straight I became extremely dizzy and disoriented. I looked at the instruments to see what was going on and could not believe them. I am convinced that I couldn't have hacked it if the other pilot hadn't been there." (ref. 104)

"On a GCI after completing a turn to proper heading I tried to visually make contact with another aircraft and upon looking back at the instruments I thought I was upside down in a slight dive, at first glance at attitude gyro. I started to roll the aircraft but stopped to recheck gauges. Aircraft was actually in normal attitude in a slight climb. I felt that I needed more instrument practice." (ref. 104)

3. Illusions Based on Visual Phenomena

a. Autokinesis

"While in a night bounce pattern at Kingsville, I followed a group of lights up wind thinking it was another plane. Not until I was almost over it did I realize that it was a lighted oil well. It seemed as though it was moving, but in no particular direction." (ref. 31)

"While night flying, I was flying in the upper pattern orbiting the field. On one pass around the field, I momentarily lost sight of the plane ahead. I picked his running lights up a moment later (I thought) and kept him in sight. However, he seemed to be moving away rapidly so I added power to keep up with him. I suddenly snapped out of it and realized that I was actually flying towards a radio tower, although it did seem to be moving away from me. I felt perfectly at ease and flew the plane in a normal manner." (ref. 23)

b. Fascination

"While on final approach to a landing and a half mile from touchdown under controlled VFR (visibility was about 1 mile, smog and haze), the tower informed me they couldn't see me and asked if I had the field in sight. My instructor, sitting next to me, also asked if I had the field in sight. I replied that I did. As I passed over the tower a hundred yards left of the runway, the instructor took over and initiated a go-around. What I thought was the runway was the roof of a hangar a quarter mile past the end of the runway. I was concentrating so hard to line up on the "runway" in the gloom that I failed to see the real runway, which was plainly visible a few degrees to the right of my concentrated field of vision." (Author's own experience in a light plane.)

"...my instructor was teaching me how to make emergency landings on a small field. I had made one or two tries and hadn't been very successful. The next time I was determined to make a good approach. Both the instructor and I were so completely engrossed in this task that we failed to hear the landing gear warning horn; consequently, we landed with the wheels in the up position." (ref. 23)

"...I went into a skidded turn stall during a small field shot. I knew I was in unbalanced flight during the last turn. But as I recall, I was so determined to get a straight away before hitting the field that I didn't seem to care what happened. The plane stalled and the instructor took over." (ref. 23)

c. Target Hypnosis

"On a gunnery hop I became fascinated with the tow on one of my overhead runs. I concentrated hard on trying to hit the target and soon lost all sense of anything else. I noticed the sleeve getting bigger and bigger but it didn't soak in for a long time. It was sort of like a semi-coma. My flying of the plane was completely automatic, so much so that I don't remember much of what I did on the run. Finally, it dawned on me I was getting close to the tow and I ceased firing." (ref. 23)

d. Illusory Effects Due to Inadequate Stimuli

"As a cadet he had a vivid experience at about 500 ft. He was behind two planes which were going away from him, and separating. He thought they were lights of houses approaching (separating of lights). It was a moonlight night. He apparently went into a steep glide and almost crashed into some houses, which he finally distinguished in the moonlight. Since then, he said he has watched for it, without a repetition. 'You have no sense of distance at night.'" (ref. 23)

"At one time during a rendezvous with little difference between sky and water I could not judge how far away the plane was that I was joining on. I continued but was ready to break off in case I could not lose the sensation. Later I managed to regain my depth perception." (ref. 31)

e. Improper Grouping of Lights at Night

"While orbiting over Rodd Field one night, waiting to make bounce landings at Waldron Field, I thought I saw an airplane coming towards me. It had a red light and two white lights — I made a turn to the right to prevent a collision course. After observing the lights, it seemed as if the plane was doing a slow roll and right through the orbiting pattern. After a closer look at the 'plane' it became stationary. In reality it was three lights around some object in the water off Padre Island." (ref. 31)

"A pilot saw a green and a red light on a bridge at night while flying at about 1500 ft. He mistook them for lights of another plane and pushed over in order to avoid them. He did not realize that they were a bridge until too late and attempted a recovery from dive. He hit the ground in a level attitude and slid to a stop. Plane was a strike, but pilot was unhurt." (ref. 31)

"After takeoff on a night formation hop, I followed a distant light on the ground for some time thinking it was the plane ahead of me. My feelings were normal and I flew plane normal. I finally realized it was not another plane and looked about for the actual plane which I found ahead of me." (ref. 31)

f. Illusions of Relative Motion

"On a join up with another plane from a lower altitude I could not see the details of his plane since the sun was partly blinding me and all I could see was his silhouette in a three-quarter view. He seemed to be going away from me and his plane seemed to be getting smaller. All of a sudden I saw that he was coming toward me very fast in another attitude altogether different and I slid under him at the last moment, missing him by inches." (ref. 31)

"In making a join up on a single plane, I often find myself unable to tell whether the plane I'm joining on is in a turn or not. If I am joining on more than one plane I have no trouble of this kind." (ref. 31)

"While night flying, orbiting the field at 1500 ft, it seemed as if all the stars were moving and the planes were standing still. The combination of plane lights, ground lights, and stars gave the effect of mass movement of lights." (ref. 23)

"Night. I was Number 3, joining up on the other two, following their lights. I thought they were going away, but actually they were approaching at a fairly sharp angle. I had to do almost a split-S to get away. They were coming in too fast — I could see their exhaust flames get brighter too fast." (ref. 122)

"'Looking up at lead plane on a turn, across path of moon: Had a vivid sensation that the stars were moving in a circle, and they (the planes) were standing still.' (Fell off, recovering after a loss of several hundred feet.)" (ref. 122)

g. Illusory Horizons

"After leaving the British coast and flying in good visibility toward the lighthouse of Cape Gris-Nez, the pilot reduced the engine power setting to keep below clouds. The aircraft gradually lost altitude until the trailing antenna struck the water. The crew did not realize that the angle of incidence was greater than before throttling back and, therefore, viewed the lighthouse below its fictitious horizon. The light gave the pilots a wrong sensation of their height, whereas the shock felt when the antenna struck the water warned them of their true position." (ref. 23)

"Night: Lights along the shore aren't horizontal— they form an apparently tilted line. Once I got the plane into an attitude corresponding to this horizon, I saw by the instruments that I wasn't level— saw the difference between the apparent horizon and that shown by the instruments." (ref. 122)

4. Disorientation During Transition Between VFR and IFR

"Flying wing in formation flight day weather, IFR letdown: During penetration we made a teardrop turn and I felt we were in a 90 deg bank. I didn't break formation, but it was very difficult to control my sensations. My formation flying ability was seriously affected and I felt it would be safer to break off and go on the gauges. The feeling became more and more severe, and when we leveled off I did not feel that we were level. I didn't recover from the sensation until we broke into the clear." (ref. 104)

"Two of the most severe vertigo reactions I have had occurred while flying formation in weather. In the first incident several years ago I felt that the plane was upside down and lost control of the aircraft, broke formation, and went into a spin. I did an instrument recovery in the overcast. Recently while flying wing I felt I was in a turn to the right during a left turn. It was very difficult to control, but I maintained formation. You have to relax and cross-check your own instruments. I never have any trouble on the gauges alone." (ref. 104)

"I became disoriented while descending through clouds in formation. I was on the wing and had to break formation. I lost control of the aircraft during transition to instruments and went into a split S. I pulled 8-1/2 g's and the altimeter read 200 ft just before I blacked out in the pull-up." (ref. 104)

"I have frequent vertigo. The worst experience occurred in a day formation flight when we unexpectedly ran into marginal weather with poor visibility. We were at low altitude and very erratic flight occurred and I nearly spun in. A four-ship formation behind our flight crashed into a mountain. My difficulty probably resulted from trying to fly both VFR and IFR in IFR conditions." (ref. 104)

"In transitioning from wing to the gauges I am frequently completely confused and have great difficulty in focusing on the instruments. One time I lost 10,000 ft while transitioning from formation to instruments." (ref. 104)

> "Most recent case of vertigo was last month in formation flight in weather. It resulted from day fighting over an overcast and I went into overcast in a stalled condition. I had great difficulty transitioning to my instruments. I was able to get partially on the instruments to the extent of turning on the slave gyro and radio compass, but I realized the unusual attitude too late and didn't recover on instruments. I broke out in a vertical dive and fortunately had enough altitude to recover contact." (ref. 104)

The following incidents in helicopters illustrate the dangers inherent in losing the visual reference to both instruments and the external world. In the first episode, transition from VFR to IFR was not made because of very low altitude. In the second example, transition to IFR was ineffective apparently because of the pilots' refusal to believe their instruments.

> "I was in an H-19 making a landing on fresh snow. Our altitude was approximately 30 ft. We were approaching this landing area into the wind. We were preparing the helicopter to hover and the snow started kicking up all around the aircraft and cut off vision completely and suddenly we could not see in front of us at all. Since we were so close to the ground we did not want to go on instruments too much. Snow was whirling around in front of us. We could not see the ground at all. I was not flying at the time but the pilot experienced the same sensation that I did. I was sitting in the left seat and I felt as if we were slowly sliding off to the side. Our forward motion had been stopped and I felt that we were going off from right to left. As it turned out we were moving left to right, when we touched down in the snow. Perhaps we were even moving slightly backwards. I was shook but we went on and landed. The snow was soft and we eased down onto it. Because it was soft no harm was done to the aircraft." (ref. 41)

A platoon of seven H-21 helicopters encountered conditions of lowering ceiling and rising terrain during a daylight cross-country flight. At least three pilots lost visual reference to the ground, and a 180 deg turn was ordered to return to the base. Three aircraft lost control and crashed, two fatally. Damage reports of the two fatal crashes indicated ground impact at unusual attitudes, but no midair collision. The comment of the pilot of the helicopter which crashed without fatalities is as follows:

> "I was fighting the controls. I felt like we were in a nose-high position. The artificial horizon was inoperable" (or so the pilot thought). "I nosed the helicopter forward. We came out of the clouds in a nose-low position with the aircraft tilted sharply to the left and zero airspeed. I leveled the helicopter and made contact with the ground. The helicopter then rolled on its left side." (ref. 47)

The statement of the copilot is perhaps more dramatic:

> "I assisted the pilot in an instrument check. Everything appeared normal, except the artificial horizon indicated an unusual position during descent. It appeared to me we were in level position but I could not tell if we were going to the right or left." (ref. 47)

F. FACTORS CONTRIBUTING TO DISORIENTATION IN FLIGHT

First among factors leading to disorientation in flight and, indeed, the factor common to virtually all forms of disorientation is the impoverishment of the exterior visual field brought about by darkness or bad weather. Disorientation may occur even in good visibility, however. Clark and Graybiel (ref. 24) studied a group of 137 naval and marine corps jet pilots and report that 13 percent of the disorientation incidents experienced by this group occurred when visibility was judged to be good or excellent.

Accident reports, questionnaires, and pilot reports of disorientation incidents have revealed a number of factors which predispose the pilot to experience disorientation. These factors may relate to one or more of the following:

- a given flight condition
- a given procedure by the pilot
- inability to establish an orientation reference
- a particular maneuver or sequence of maneuvers
- level and recency of training of the pilot
- misinterpretation of visual phenomena
- physical and mental condition of the pilot

The factors most commonly reported by pilots as responsible for evoking disorientation have been determined from pilot reports of disorientation episodes, accident reports, and questionnaires. The following list is derived from references 4, 7, 9, 23, 24, 31, 37, 49, 104, and 105. The factors are grouped according to the listing above.

Factors related to a given flight condition:

(1) Flight during conditions of reduced visibility

(2) Formation flying in weather

(3) Formation flying at night

(4) In-flight refueling in weather

(5) Flying alone

(6) Transitioning from an outside visual reference to an instrument reference

(7) Night takeoffs

Factors related to a given procedure by the pilot:

(8) Head movements, during a turning maneuver, such as are occasioned by trying to maintain position in a formation, or by trying to view or adjust an improperly located instrument

(9) Shifting control of stick from one hand to the other to change a radio channel during a maneuver under instrument conditions

Factors related to the inability to establish an orientation reference:

(10) Failure of pilot to monitor attitude and motion

(11) Attempting semicontact flight, attempting to mix the outside visual reference and the instrument reference

(12) Trying to fly visually in marginal weather

(13) Waiting until the last moment to make the transition from a visual to an instrument reference

(14) Conflict between instrument reference and sensations of motion and orientation

Factors related to a particular maneuver or sequence of maneuvers:

(15) Prolonged constant speed turns with rapid recovery

(16) Unusual maneuvers at night

(17) Slow unperceived turn entries

(18) Sudden acceleration or deceleration

(19) Flight during and immediately following aerobatics, prolonged spinning, or rolling maneuvers

(20) Flight following large pressure changes produced by ascent or descent

Factors related to the level or recency of training of the pilot:

(21) Inexperience with instrument flight

(22) Lack of recent instrument experience

(23) Flight following a period of flying inactivity

Factors related to misinterpretation of visual phenomena:

(24) Prolonged fixation of isolated lights at night

(25) Flight over sparsely lighted terrain

(26) Flight at high altitude (causing fictitious horizon due to curvature of the earth)

Factors related to the physical and mental condition of the pilot:

(27) Deteriorated physical and mental state of pilot caused by hypoxia, hyperventilation, toxic agents, fatigue, illness, alcohol, drugs, anxiety, etc.

Accident statistics (see section A) show that spatial disorientation is a significant safety hazard in flying. Nuttal and Sanford's study (ref. 105) of the disorientation experiences of 685 pilots of the USAFE Command during the two-year period from 1954-1956 indicated that almost 100 percent of disorientation incidents were of the attitude and motion type, and that illusions due to visual phenomena were rare. Their study also showed no significant correlation between vestibular stimulation susceptibility, as indicated by the duration of postrotatory nystagmus, and susceptibility to spatial disorientation.

Nuttal and Sanford also reviewed ten aircraft accidents in which disorientation was the probable cause. While no common sequential pattern of events was revealed, several factors appeared to be common to two or more accidents. Other authors, as well, appear to agree that the following factors are most frequently implicated in cases of severe disorientation:

(1) Inadequate total or recent experience in the flight conditions under which the accident occurred

(2) Head movements and/or shift of the control stick from one hand to another to change radio channels during a turning maneuver under IFR conditions

(3) Changing from one orientation reference to another, particularly from wing reference during formation flight to instrument reference

(4) Mixing the outside visual reference and the instrument reference by dividing attention between the two

(5) Mental stress

G. PREVENTIVE MEASURES SUGGESTED FOR PILOTS

It is not likely that illusions contributing to disorientation can be prevented entirely, but certain measures are available which, if followed, should help the pilot to minimize the occurrence of inappropriate sensations and to develop the mental discipline required to disregard such sensations if they do occur. These preventive measures were derived from recommendations to pilots given in references 4, 6, 17, 23, 41, 49, 79, and 105, and relate to the four categories of pilot training, cockpit procedure, VFR/IFR transition procedure, and restrictions of maneuvers. These measures are now enumerated on the basis of this classification.

Measures related to pilot training:

(1) Develop proficiency in instrument flight.

(2) Develop confidence in and a willingness to accept the fact that during restricted visibility the flight instruments display more accurate information of the aircraft's attitude and motion than is otherwise perceived by the pilot.

(3) Recognize that spatial disorientation can be a serious problem and can occur to anyone regardless of his skill and training.

(4) Be aware of the conditions conducive to the development of disorientation.

(5) Develop knowledge of the sensations and illusions produced by vestibular stimulation which contribute to disorientation, and thereby be made manifestly aware of the unreliability of their sensations in providing proper orientation.

Measures related to cockpit procedure:

(6) Monitor all attitude and motion instruments; don't concentrate attention on only one.

(7) Scan the visual field; don't concentrate on only one object. The likelihood of fascination is thereby reduced.

(8) While the aircraft is turning, avoid head movements out of the plane of rotation. This should diminish or preclude the occurrence of the Coriolis illusion.

(9) Avoid fixating isolated lights or stars at night. This should mitigate autokinesis.

(10) Should disorientation be experienced, turn over control of the aircraft to the copilot if possible; if not, try to relax.

Measures related to VFR/IFR transition procedure:

(11) Maintain either an outside visual reference or an instrument reference, but don't try to mix the two.

(12) Transfer to an instrument reference before entering a cloud.

(13) If possible, continue straight and level flight for at least 30 to 45 sec after transitioning from visual to instrument reference.

Measures related to restrictions of maneuvers:

(14) Avoid aerobatics at night.

(15) Avoid multiple turn spins and rolls exceeding 5 to 10 sec in duration.

(16) If spin training is undergone, approach multiple turn spins in stages, even if an experienced pilot.

(17) During spins, whether erect or inverted, direct head and eyes toward the horizon to inhibit the effects of roll stimulation of the vestibular system.

Disorientation can be a particularly serious problem in jet aircraft, but there are means available to cope with it. Proper instrument training; recognition of the problem, its features, and their origins; and the application of a few simple preventive measures should help minimize the occurrence of disorientation and its consequences.

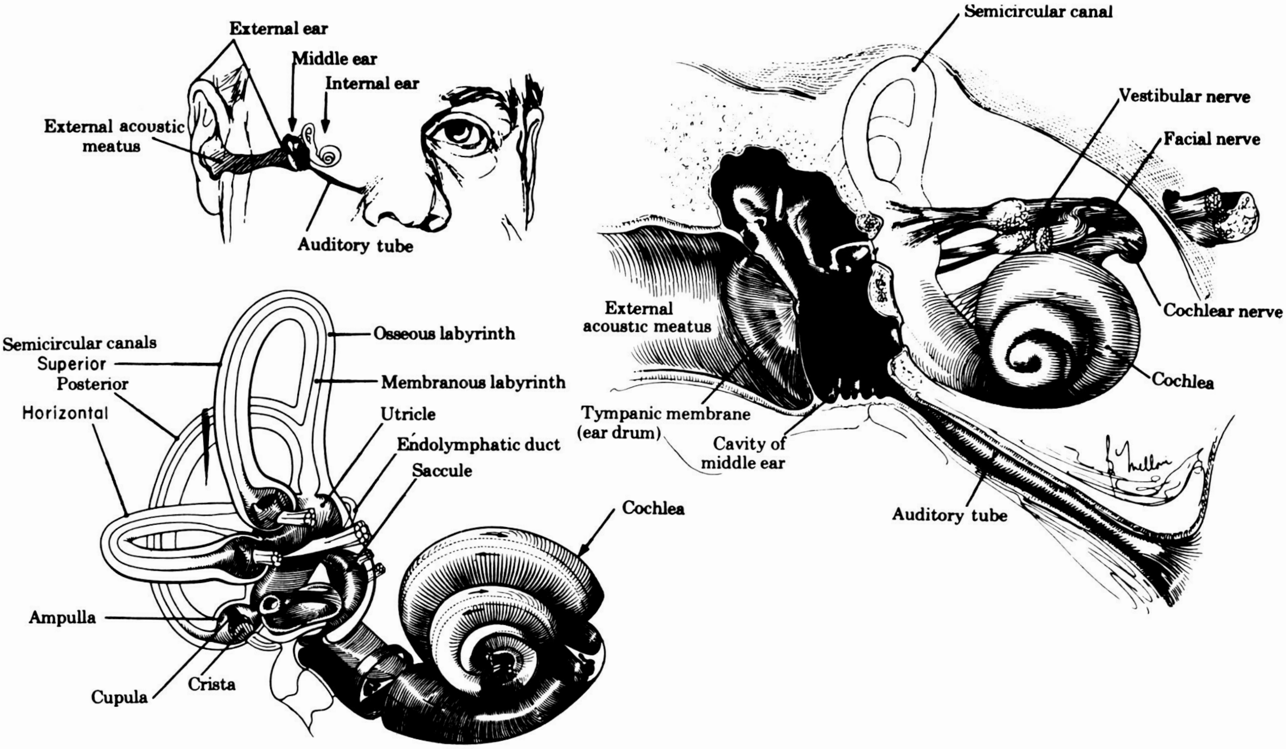


Figure 1a. External and internal structures of the ear From Dorland's Illustrated Medical Dictionary, 24th ed., W. B. Saunders Co. (Philadelphia), 1965

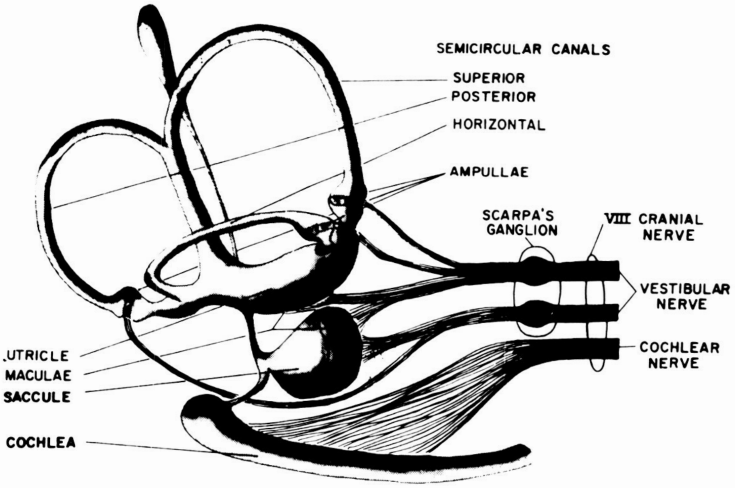


Figure 1b. Diagrammatic representation of the lateral view of the membraneous labyrinth of the right ear. The cochlea has been included and the separation of the utricle and saccule increased [From Benson, A. J.: Spatial Disorientation in Flight. A Textbook of Aviation Physiology. J. A. Gillies, ed., Pergamon Press (New York), 1965, pp. 1086-1129; by permission of the Controller of Her Britannic Majesty's Stationery Office]

Figure 1. Structure of the Semicircular Canals

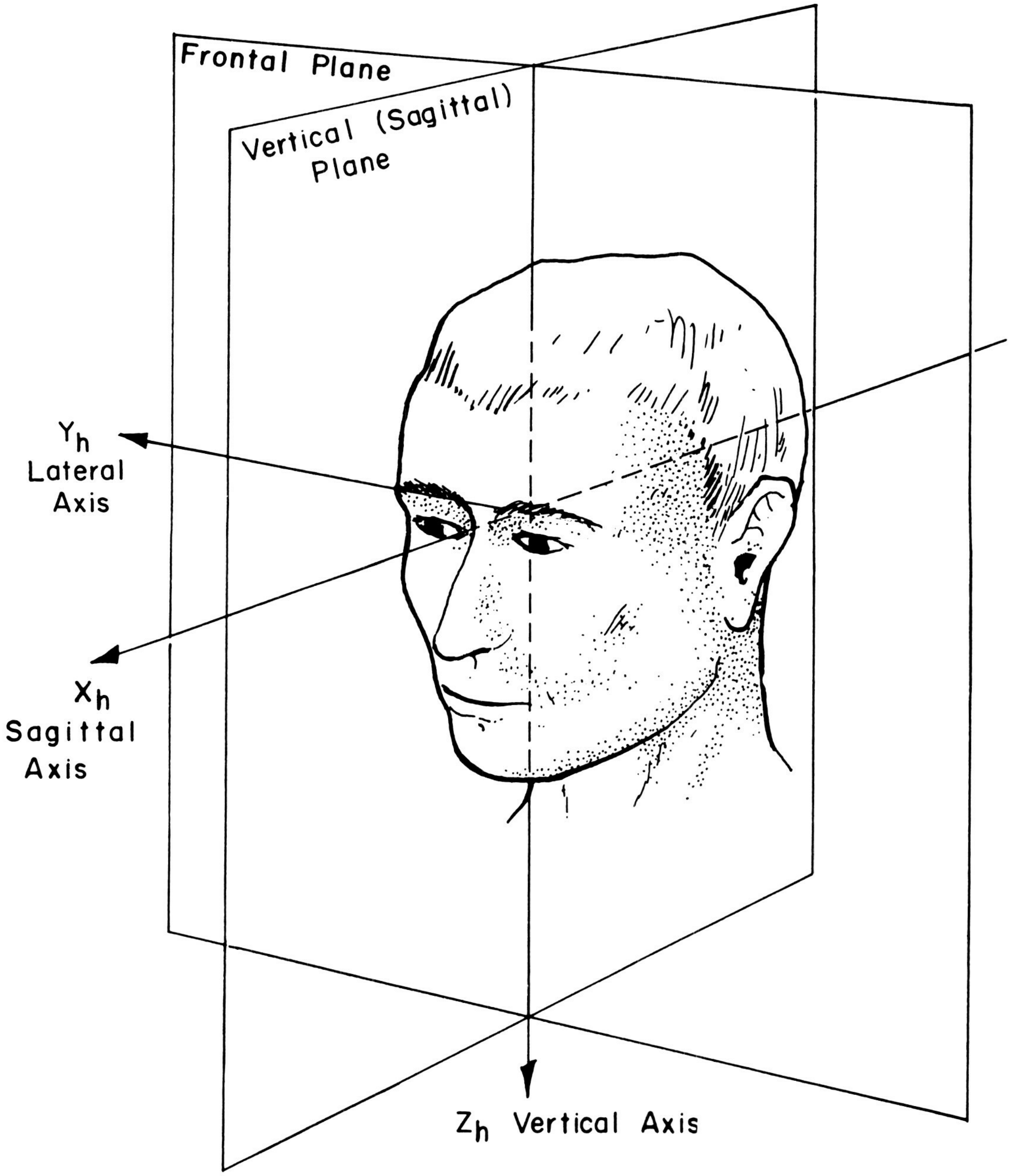


Figure 2. The head planes and the head axis system (From Meiry, J. L.: The Vestibular System and Human Dynamic Space Orientation. Doctor's Thesis, MIT, June 1965)

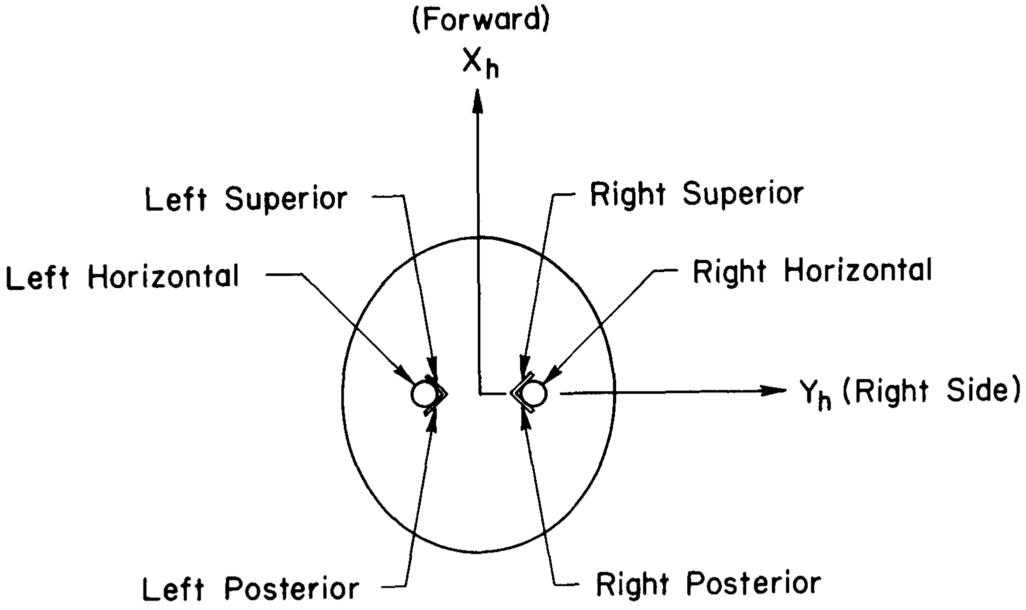


Figure 3. Top view of head showing approximate orientation of semicircular canals

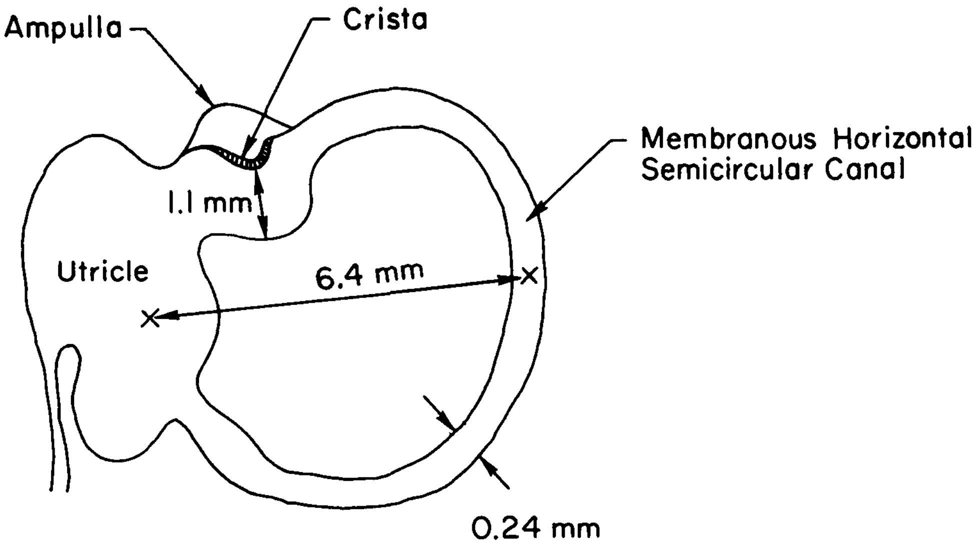


Figure 4. Average dimensions (ten subjects) of membranous horizontal semicircular canal (From Igarashi, M.: Dimensional Study of the Vestibular End Organ Apparatus. Second Symposium on the Role of the Vestibular Organs in Space Exploration, NASA SP-115, Jan. 1966, pp. 47-54)

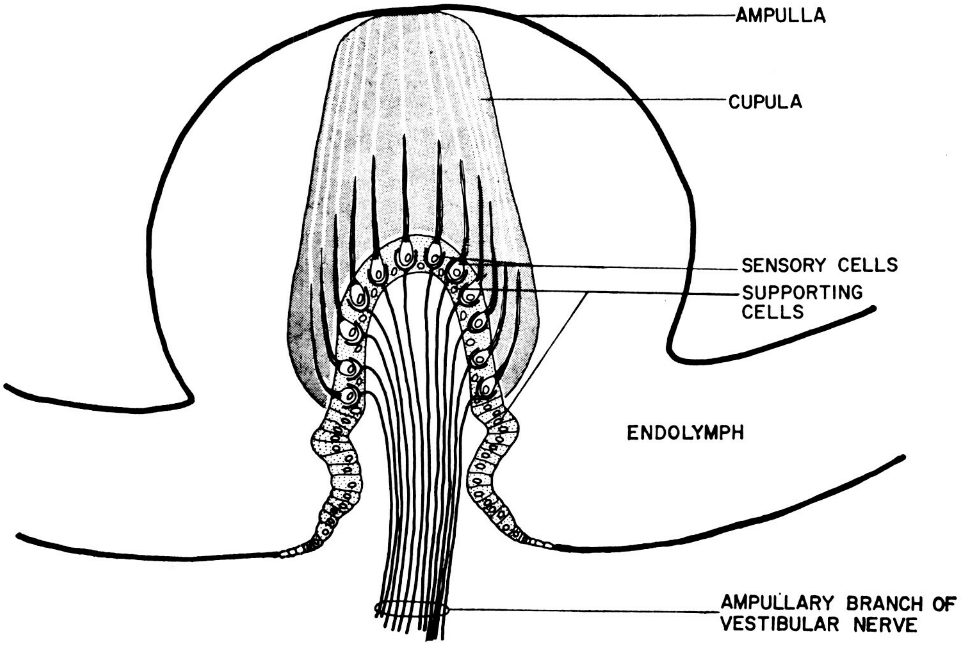


Figure 5a. Simplified diagram of the ampulla of a semicircular canal sectioned in the plane of the canal. The hairs of the sensory cells pass into fine canals in the gelatinous cupula which surmounts the crista. (Benson, A. J., op. cit., by permission of the Controller of Her Britannic Majesty's Stationery Office.)

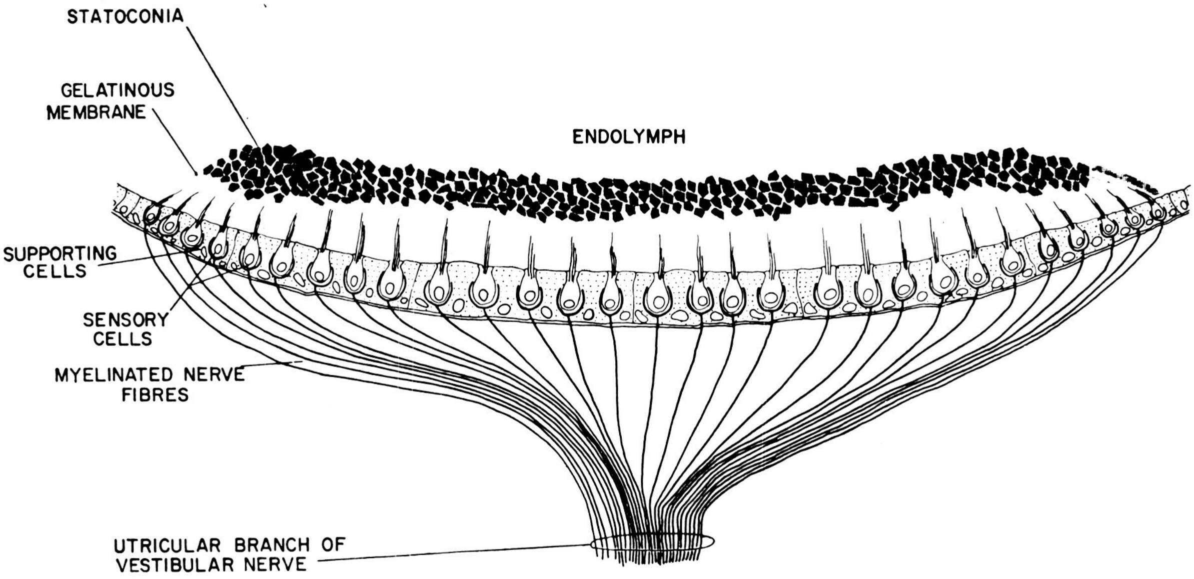


Figure 5b. Simplified diagram of a vertical section through the utricular macula. The hairs of the sensory cells pass into the fine canals of the gelatinous otolithic membrane, in the upper part of which there are many crustals of calcium carbonate — the statoconia. (Benson, A. J., op. cit., by permission of the Controller of Her Britannic Majesty's Stationery Office.)

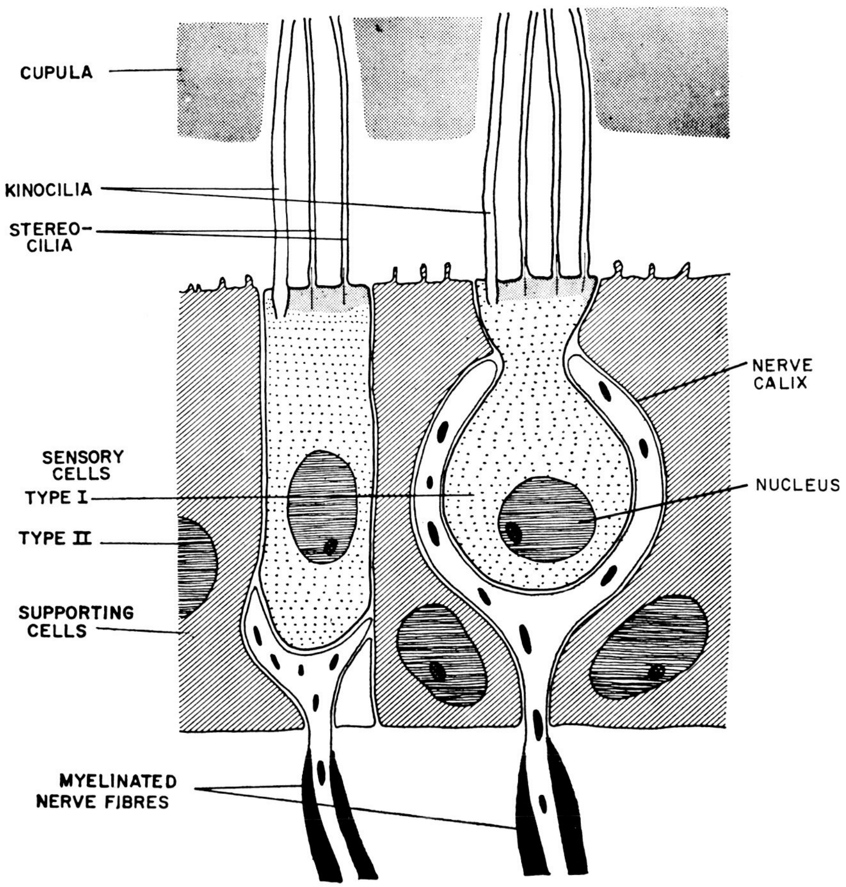


Figure 6. Highly simplified diagram of the two types of sensory cells found in the crista ampullaris. The Type II cells are more frequent in the peripheral regions of the crista. (Benson, A. J., op. cit., by permission of the Controller of Her Brittanic Majesty's Stationery Office)

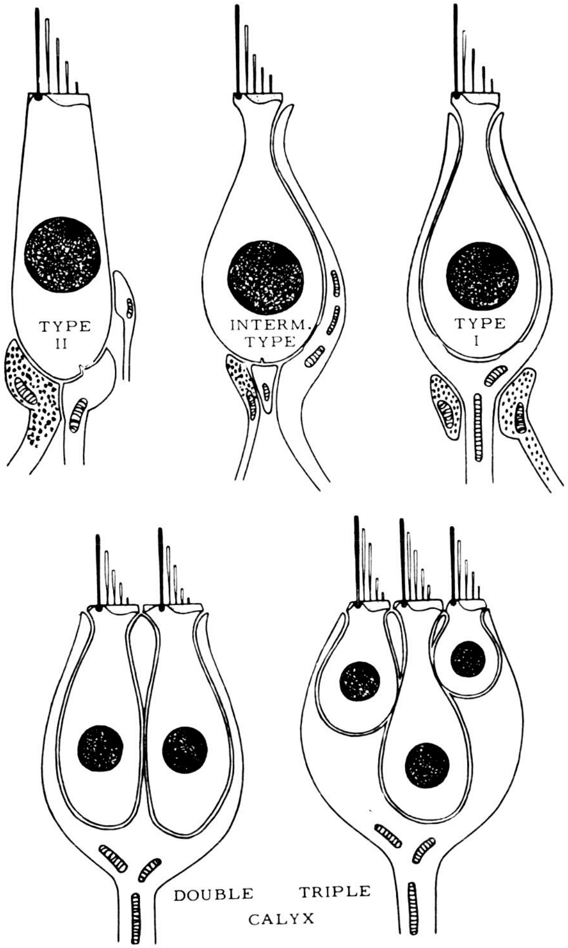


Figure 7. Schematic drawing showing further complexities of sensory cell arrangement and nerve endings which may be found in same region of vestibular sensory epithelium. (From Ades, H. W.; and Engstrom, H.: Form and Innervation of the Vestibular Epithelia. NASA Symp. on the Role of the Vestibular Organs in the Exploration of Space, NASA SP-77, Jan. 1965, pp. 23-41)

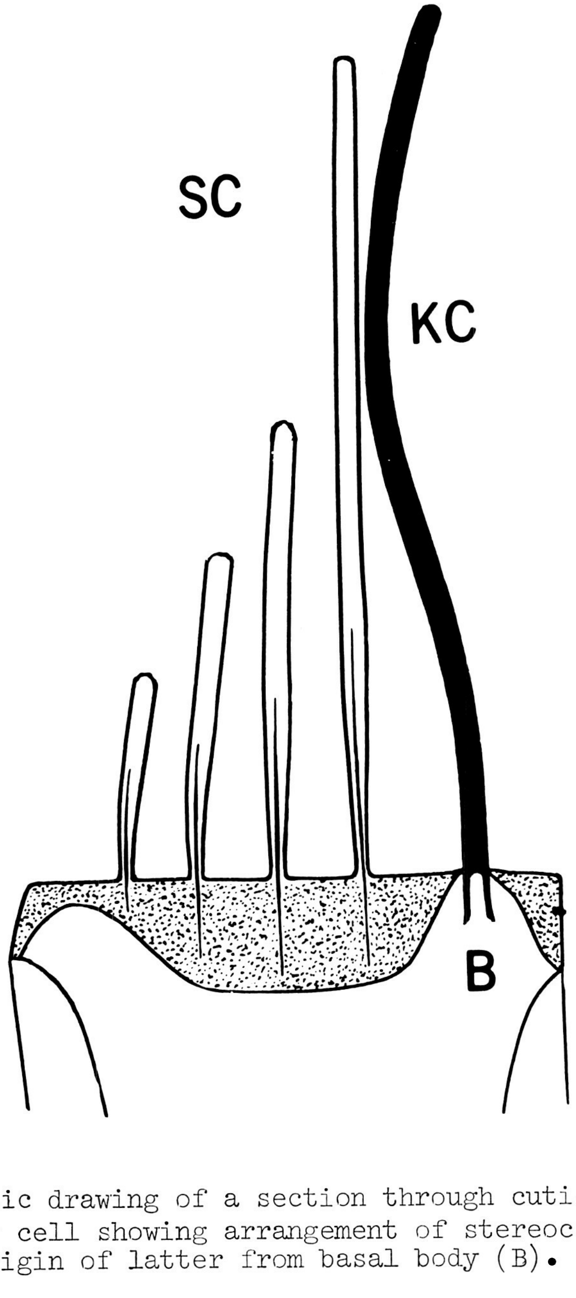


Figure 8. Schematic drawing of a section through cuticular region of a vestibular sensory cell showing arrangement of stereocilia (SC) and kinocilium (KC) and origin of latter from basal body (B). (Ades, H. W., <u>op</u>. <u>cit</u>.)

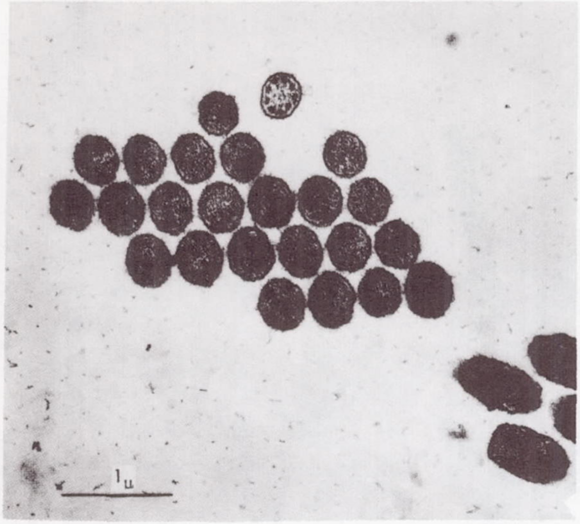


Figure 9a. Cross section of a bundle of sensory hairs at some distance above the surface of the censory cells (From Wersäll, J.; and Lundquist, P.: Morphological Polarization of Mechanoreceptors of the Vestibular and Acoustic Systems. Second Symposium on the Role of the Vestibular Organs in the Exploration of Space, NASA SP-115, Jan. 1966, pp. 57-72)

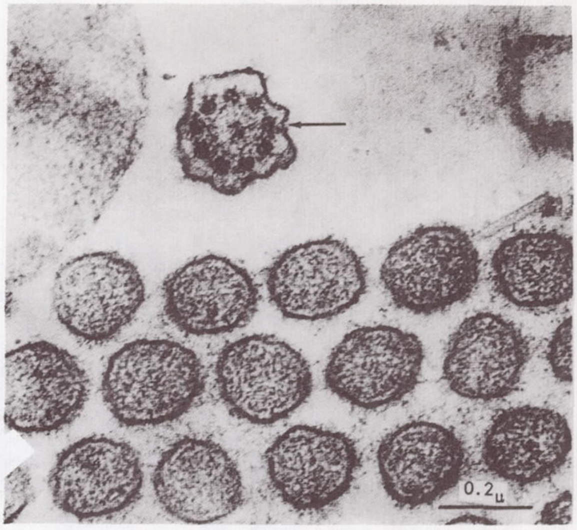


Figure 9b. Cross section of part of a hair bundle with a kinocilium (arrow) demonstrating the regular arrangement of the nine peripheral double tubules (Wersäll, J., and Lundquist, P., op. cit.)

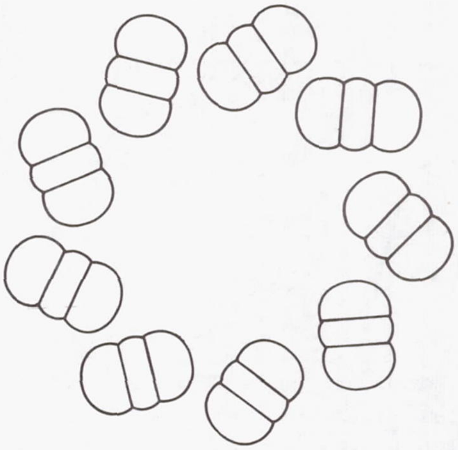


Figure 9c. Schematic representation of cross section through basal body of kinocilium showing spiral arrangement of triple tubular filaments

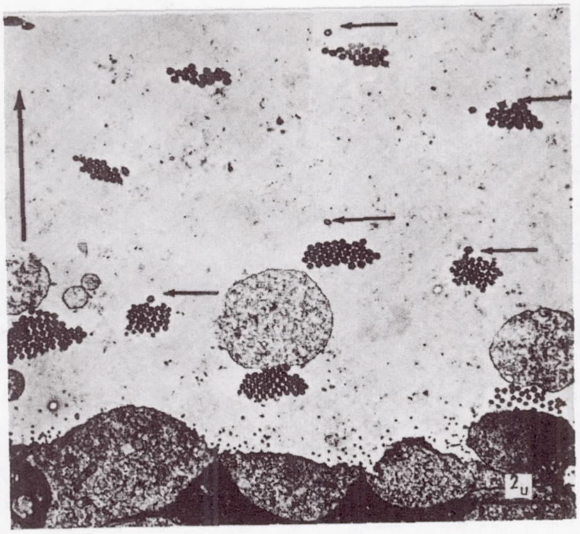


Figure 10. Cross section through a number of hair bundles from the horizontal crista ampullaris of a guinea pig, demonstrating the orientation of the hair bundles, indicated by the thick arrow to the left. The kinocilia (thin arrow) are observed on the utricular side of the hair bundles. (Wersäll, J., and Lundquist, P., op. cit.)

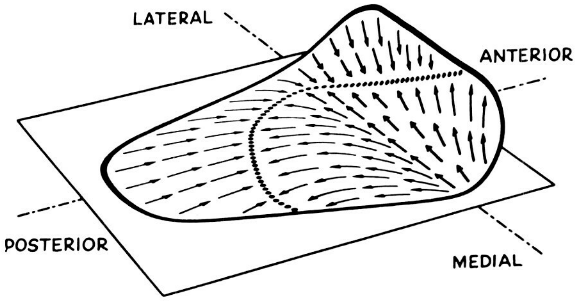


Figure 11a. Schematic representation of polarization pattern of sensory cells in utricular macula of guinea pig. Arrows indicate the direction of polarization showing how it spreads fanlike from one side of macula up to a certain line beyond which polarization is reversed. Kinocilia on either side of this dividing line are facing each other. (From Spoendlin, H. H.: Ultrastructural Studies of the Labyrinth in Squirrel Monkeys. Symposium on the Role of the Vestibular Organs in the Exploration of Space, NASA SP-77, Jan. 1965, pp. 7-22)

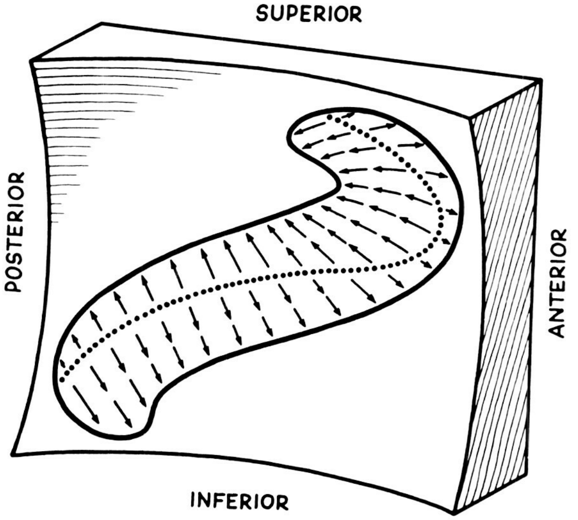


Figure 11b. Schematic representation of polarization pattern of sensory cells in saccular macula of guinea pig. Here polarization is again reversed along a certain line going through entire macular surface (indicated as dotted line). In contrast to macula utriculi kinocilia on either side of this boundary line are not facing each other but facing away from each other. (Spoendlin, H. H., op. cit.)

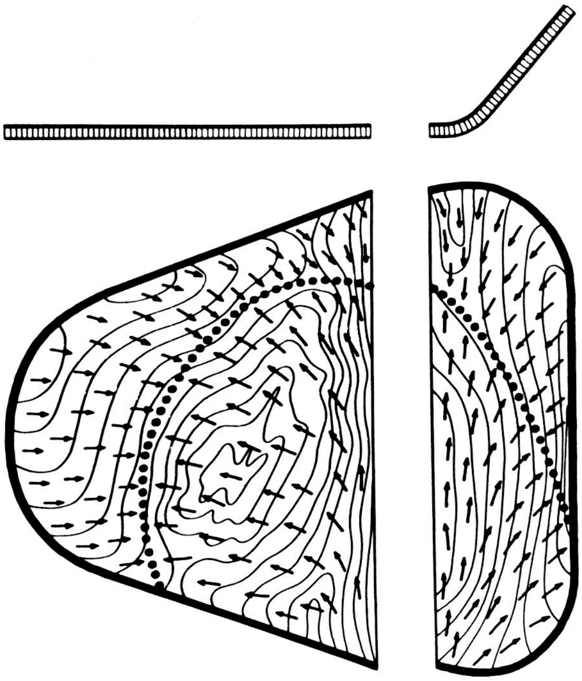


Figure 12. Schematic drawing showing how reconstruction of surface of utricular macula of squirrel monkey was done with serial sections of horizontal and inclined part of macula. Since surface of the macula utriculi is not entirely flat, each section of the serial sections hits actual surface of the sensory epithelium along a certain line which is indicated in this drawing by the fine curved lines. Arrows indicate direction of polarization of kinocilium as evaluated in each section with aid of phase contrast microscopy. (Spoendlin, H. H., op. cit.)

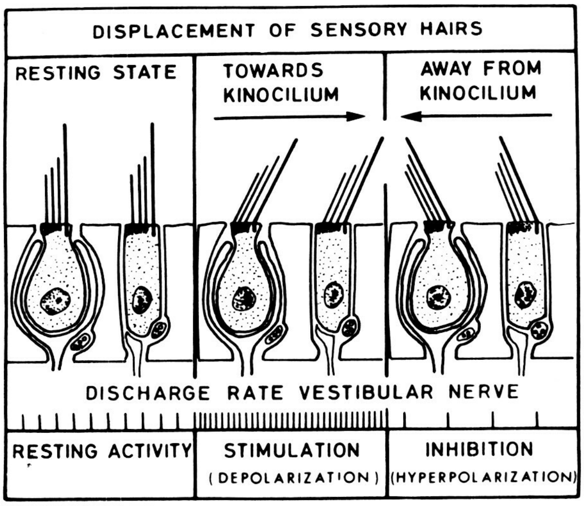


Figure 13. Electrical discharge rate of the hair cells as a function of displacement of the sensory hairs. (Wersäll, J., and Lundquist, P., op. cit.)

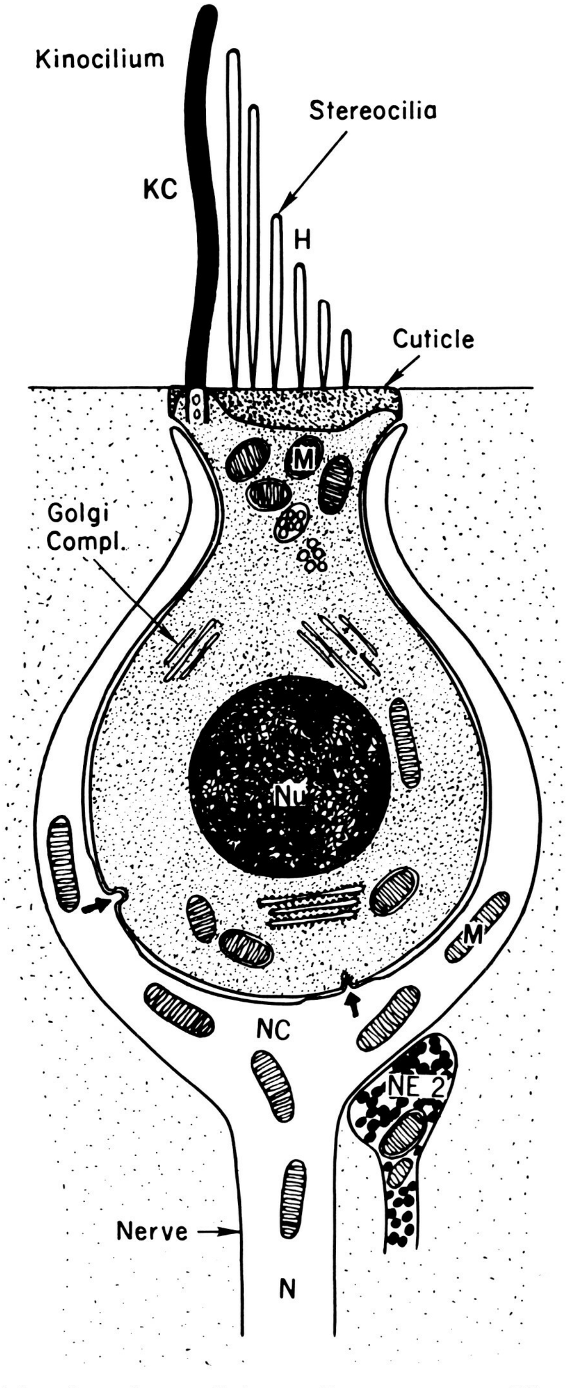


Figure 14. Schematic drawing of type I sensory cell showing its nucleus (Nu), mitochondria (M), and two types of hairs (H and KC). Surrounding nerve calyx (NC) shows two synaptic areas (arrows). Applied to outer surface of calyx can be seen a granulated, presumably efferent, nerve ending (NE 2). (Ades, H. W., and Engström, H., *op. cit.*)

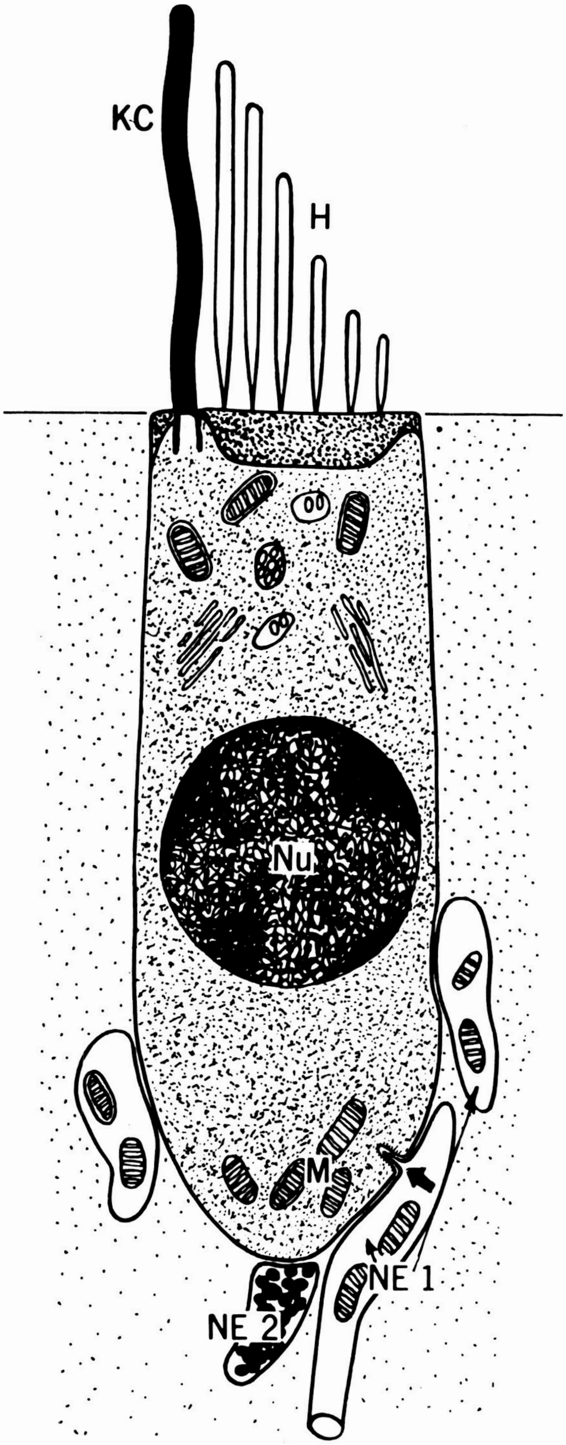


Figure 15. Type II sensory cell showing two kinds of nerve endings (NE 1 and NE 2), and two types of hairs (H and KC) (Ades, H. W., and Engström, H., op. cit.)

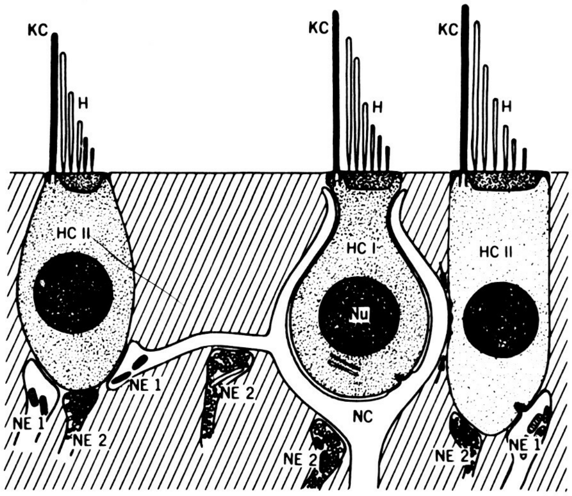
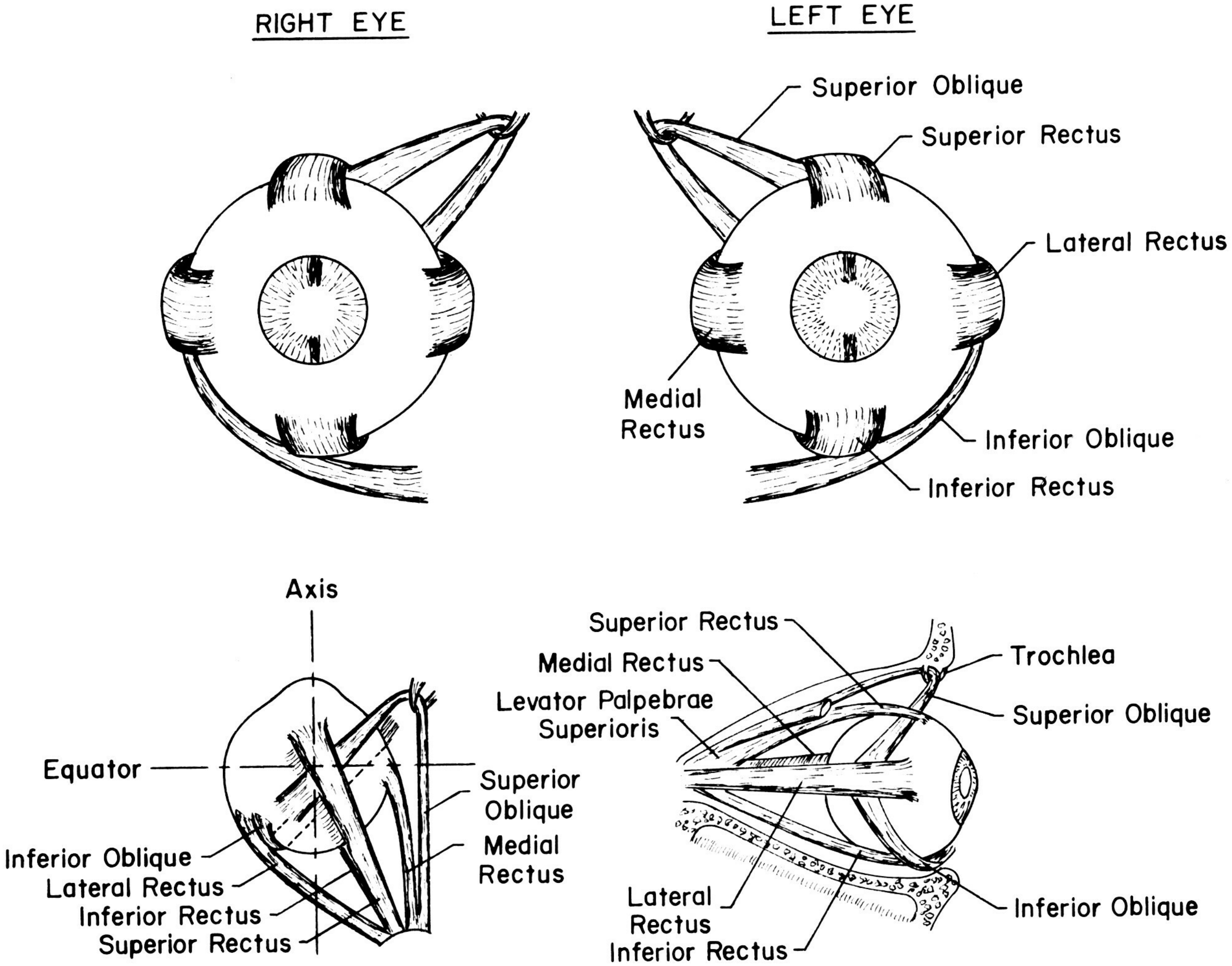
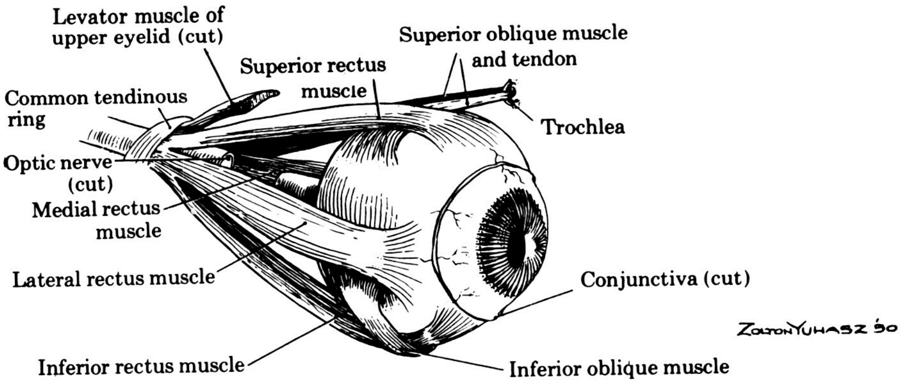


Figure 16. Schematic drawing of vestibular sensory cells of Type I (HC I) and Type II (HC II), showing complexity of neural interconnections which may be found in vestibular sensory epithelia. Hair cells of both types may have contact with the same nerve calyx (NC). A side branch from a nerve calyx may course for some distance to make contact with a Type II cell. Various ways in which both type 1 (NE 1) and type 2 (NE 2) nerve endings may terminate are shown. (Ades, H. W., op. cit.)



TOP VIEW

SIDE VIEW



(From Dorland, op. cit.)

Figure 17. The extrinsic ocular muscles seen from various angles

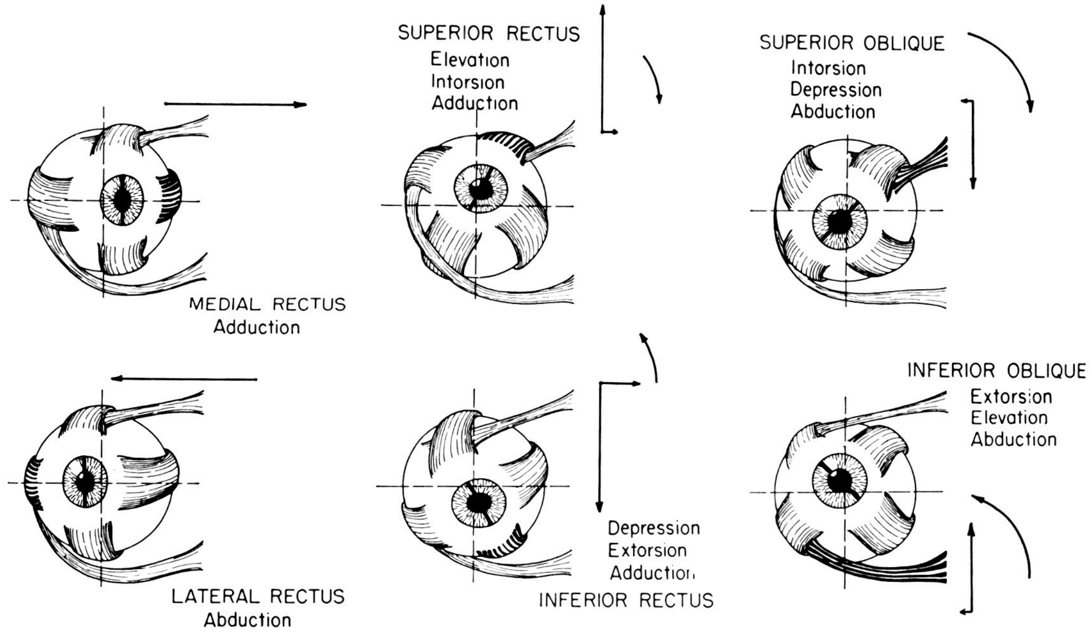
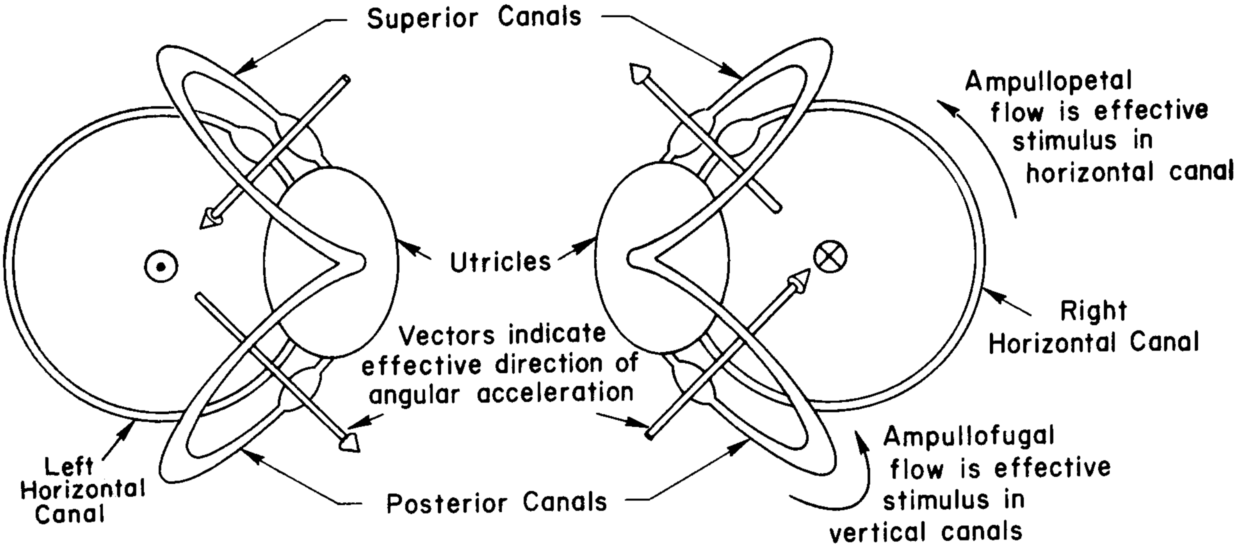


Figure 18. Action of the three pairs of antagonistic eye muscles (From Adler, F. H.: Physiology of the Eye. Fourth ed., The C. V. Mosby Co. (St. Louis), 1965)



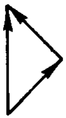
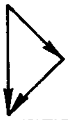
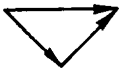
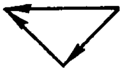
ACCELERATION OF THE HEAD	ACCELERATION VECTOR AND COMPONENTS	SENSITIVE CANALS	COMPENSATORY EYE MOVEMENT EVOKED
Roll right		Right superior Right posterior	Roll left
Roll left		Left superior Left posterior	Roll right
Pitch up		Left posterior Right posterior	Down
Pitch down		Left superior Right superior	Up
Yaw right	⊗	Right horizontal	Left
Yaw left	⊙	Left horizontal	Right

Figure 19. Compensatory eye movements evoked by acceleratory stimulation of the semicircular canals

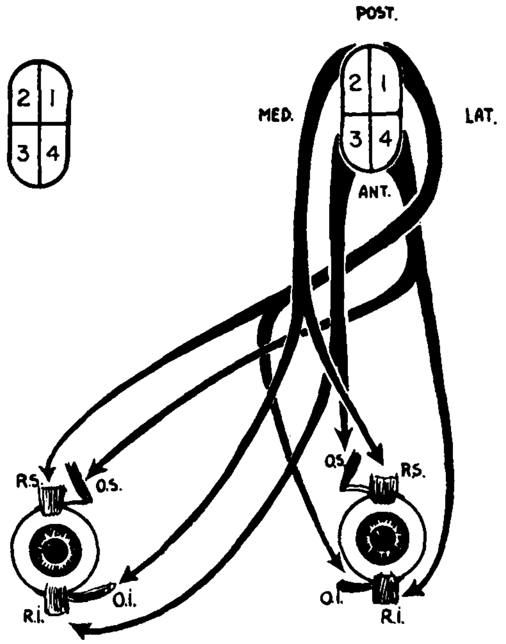


Figure 20. Quadrant theory of connections of utricular sensory cells with the vertical recti and obliques. The reflex connections of the two sides are of course symmetric (mirror images of each other). The assumption is made that bending of the otolithic hairs during gliding, or better only a tendency to glide, of the otolithic membrane toward the interior part of the macula increases discharge frequency of the majority of receptors. (From Szentagothai, J.: Pathways and Synaptic Articulation Patterns Connecting Vestibular Receptors and Oculomotor Nuclei. The Oculomotor System. M. Bender, ed., Harper and Row (New York), 1964, pp. 205-223)

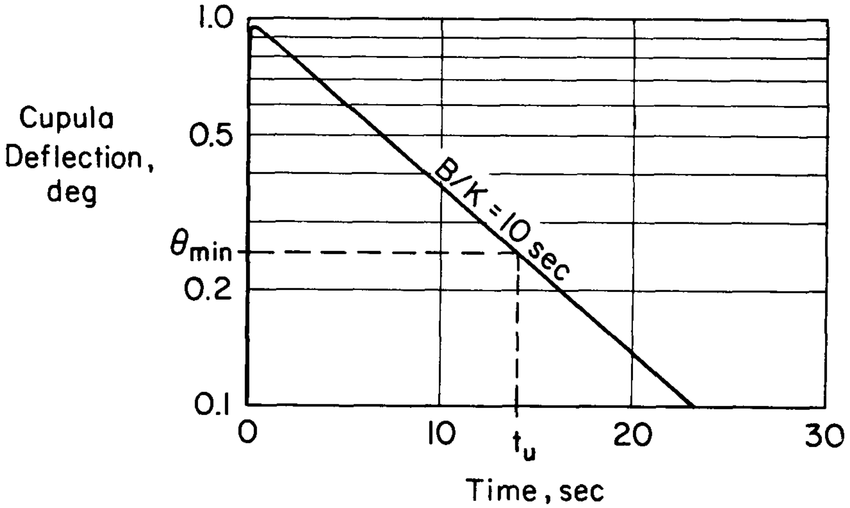


Figure 21. Cupula deflection following a step change in angular velocity of γ = 10 deg/sec ordinate logarithmic (From Van Egmond, A. A. J.; Groen, J. J.; and Jongkees, L. B. W.: The Mechanics of the Semicircular Canal. J. Physiol., 110, 1949, pp. 1-17)

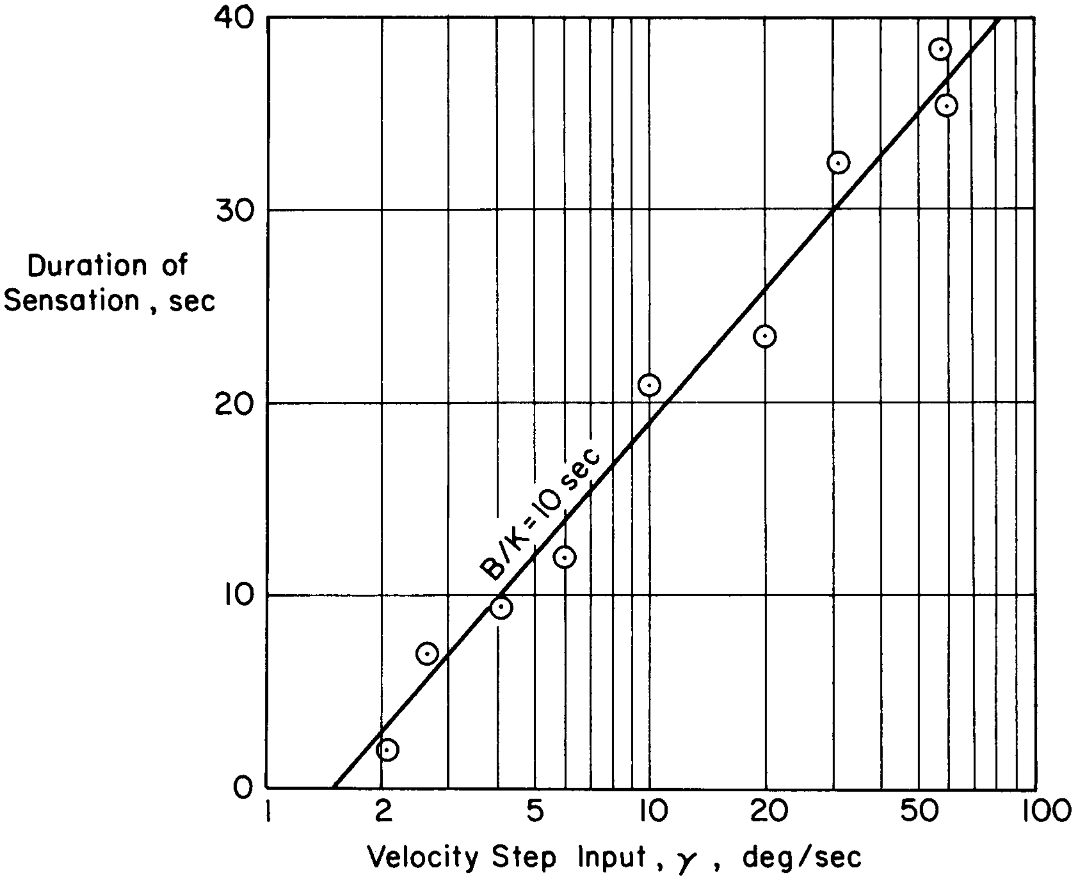


Figure 22. Subjective cupologram showing duration of sensation versus velocity step input (Van Egmond, A. A. J., Groen, J. J., and Jongkees, L. B. W., op. cit.)

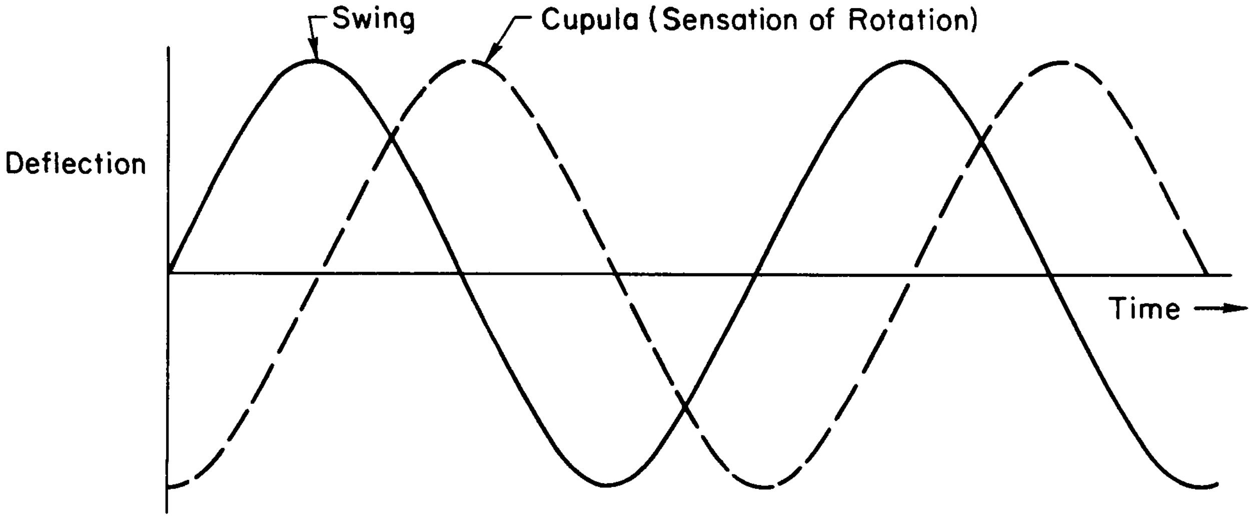


Figure 23. Phase relationship between torsion swing and cupula deflection (sensation of rotation) at resonance

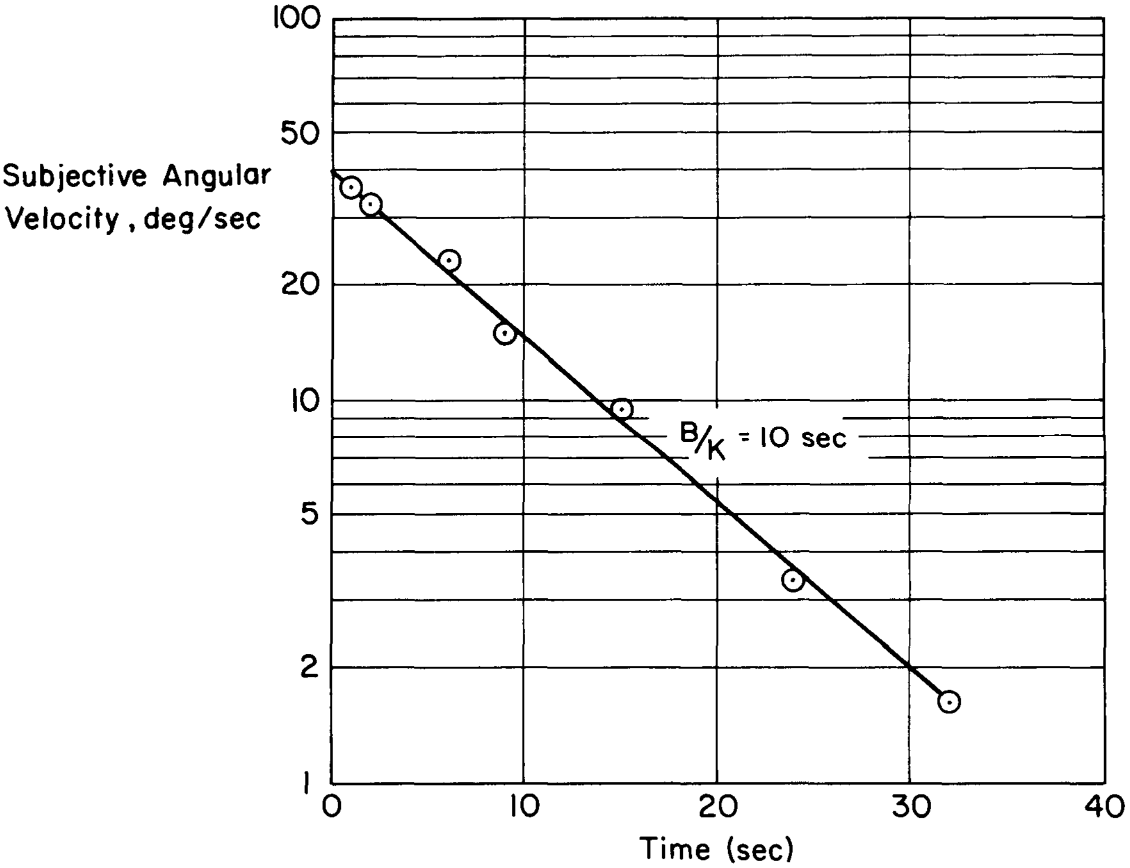


Figure 24. Subjective angular velocity following a velocity step input of 40 deg/sec (Van Egmond, A. A. J., Groen, J. J., and Jongkees, L. B. W., op. cit.)

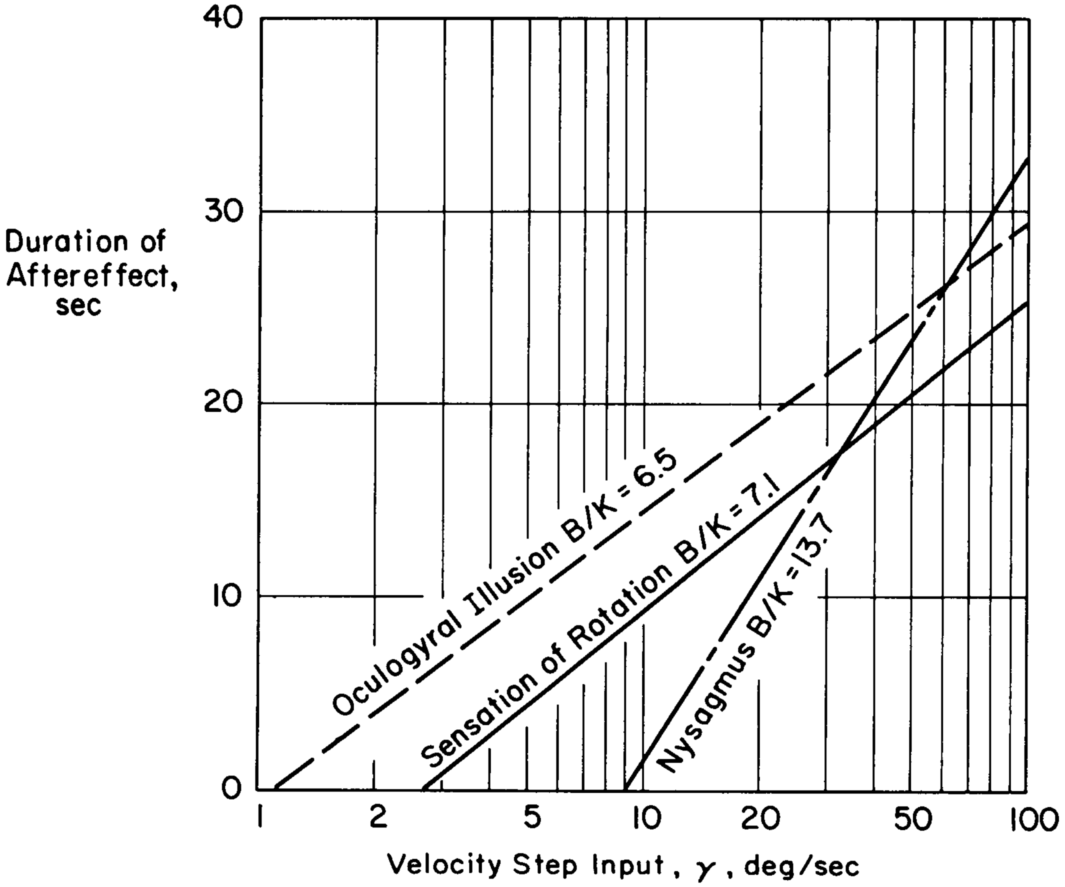


Figure 25. Averaged cupulograms showing nearly identical slopes for the oculogyral illusion and subjective sensation cupulograms but not for that of nystagmus (From Howard, I. P.; and Templeton, W. B.: Human Spatial Orientation. John Wiley and Sons (New York), 1966, and Van Dishoeck, H. A. E.; Spoor, A.; and Nijhoff, P.: The Opto-gyral Illusion and its Relation to the Nystagmus of the Eyes. Acta Oto-Laryng., 44, 1954, pp. 597-607)

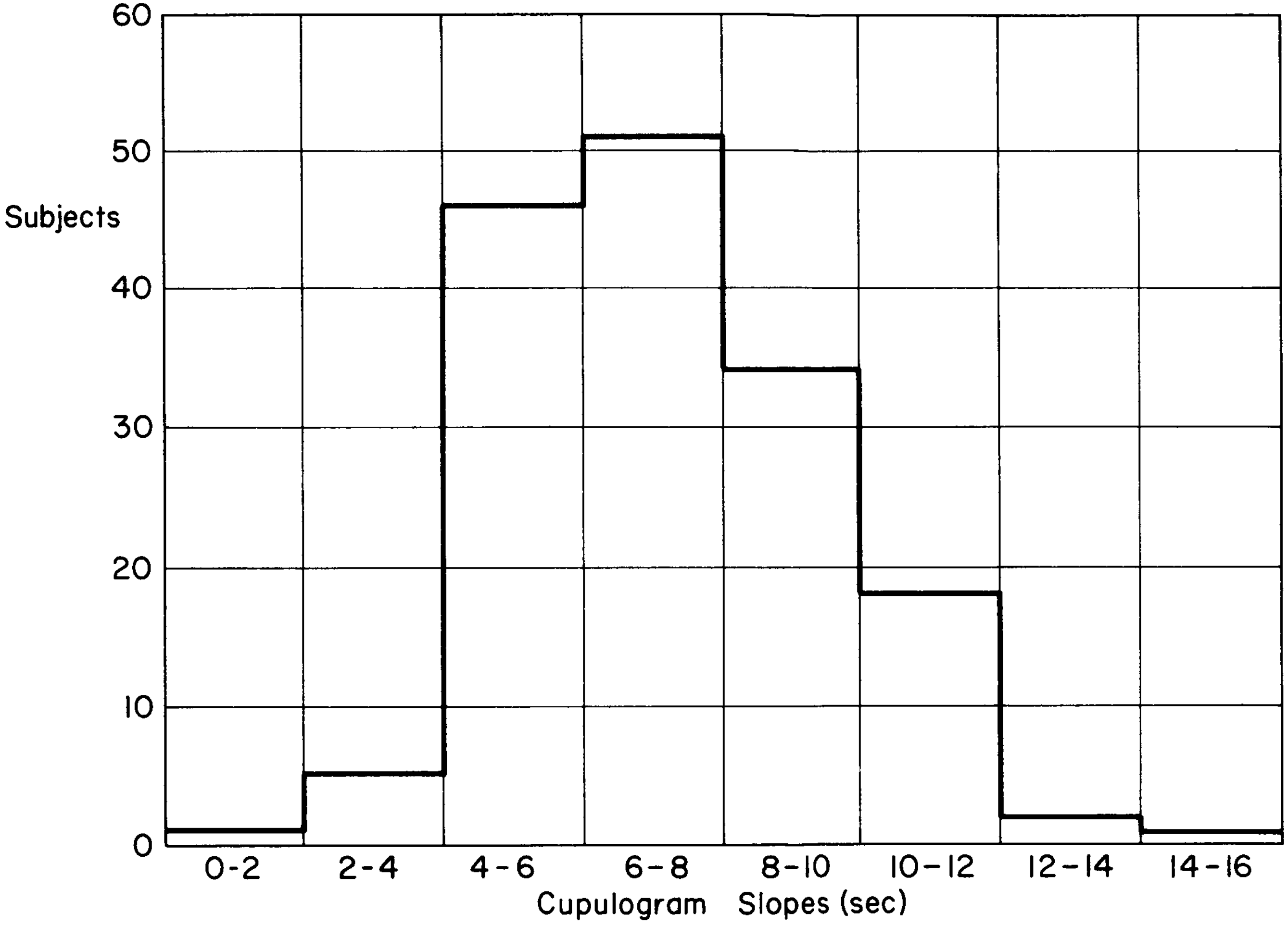


Figure 26. Frequency distribution of oculogyral cupulogram slopes for 158 student pilot subjects (From Dobie, T. G.: Motion Sickness During Flying Training. AGARD Conference Proceedings Series No. 2, Sept. 1965, pp. 23-32)

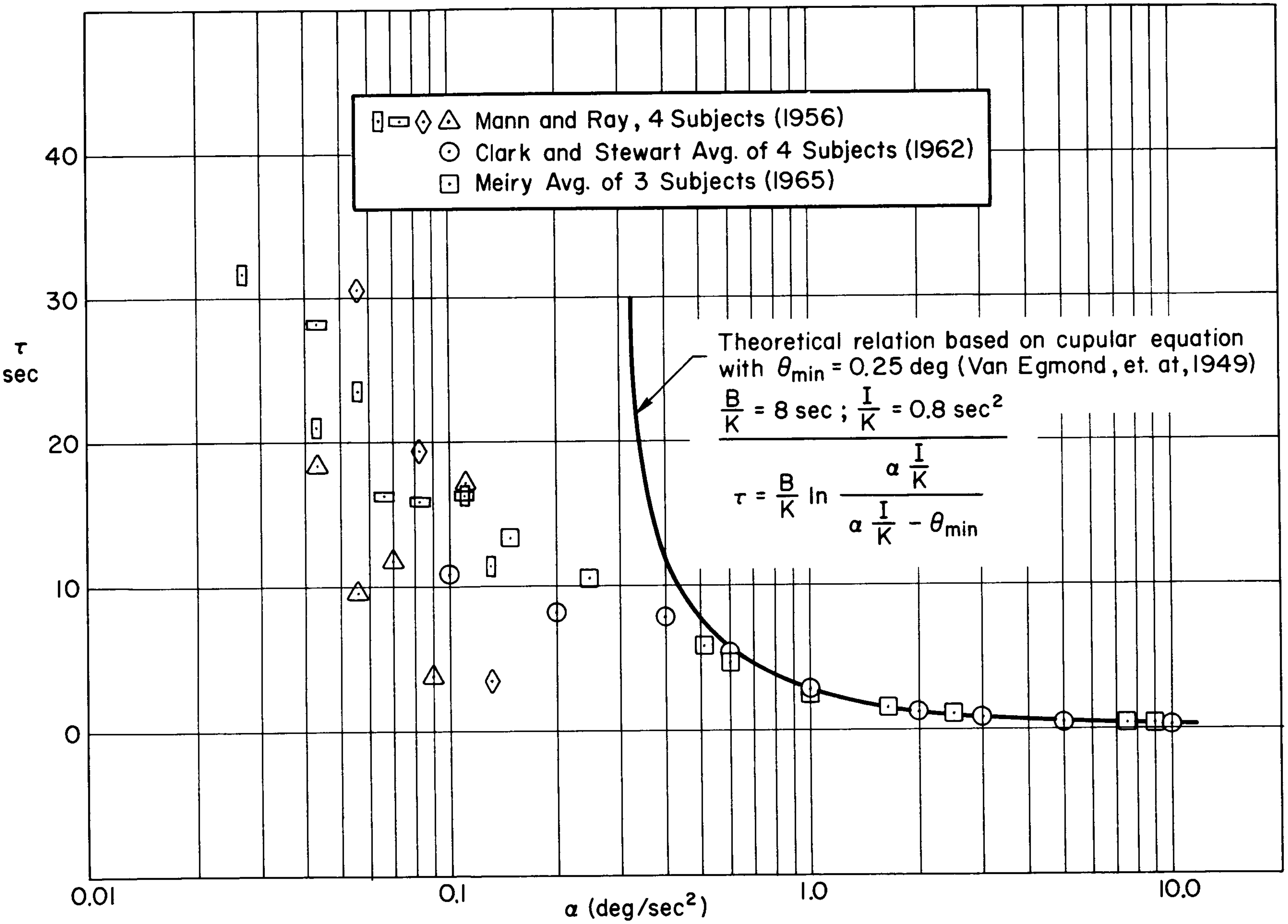


Figure 27. Latency time for perception of angular acceleration about vertical axis

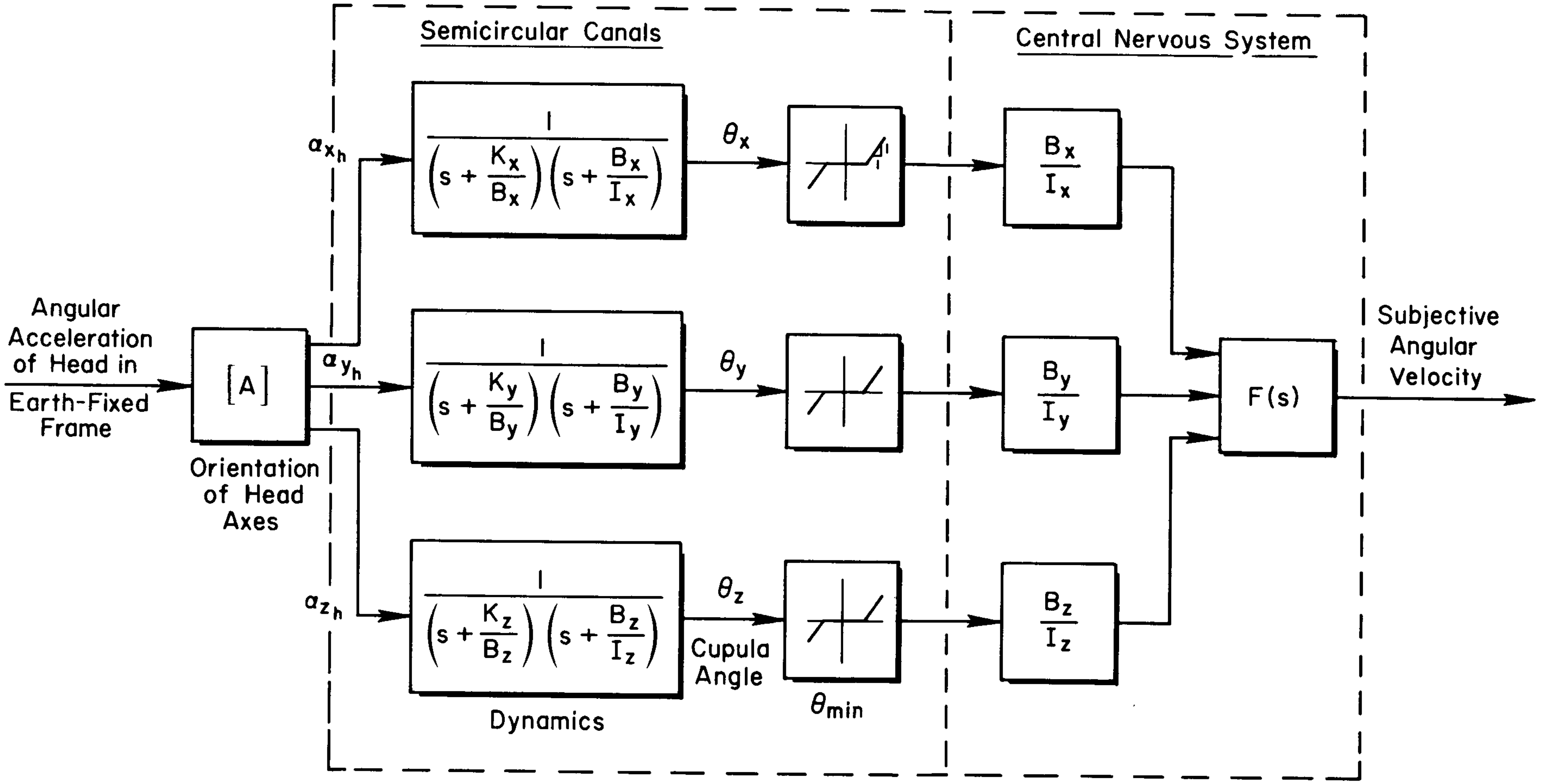


Figure 28. Mathematical model of semicircular canal function (Meiry, J. L., *op. cit.*)

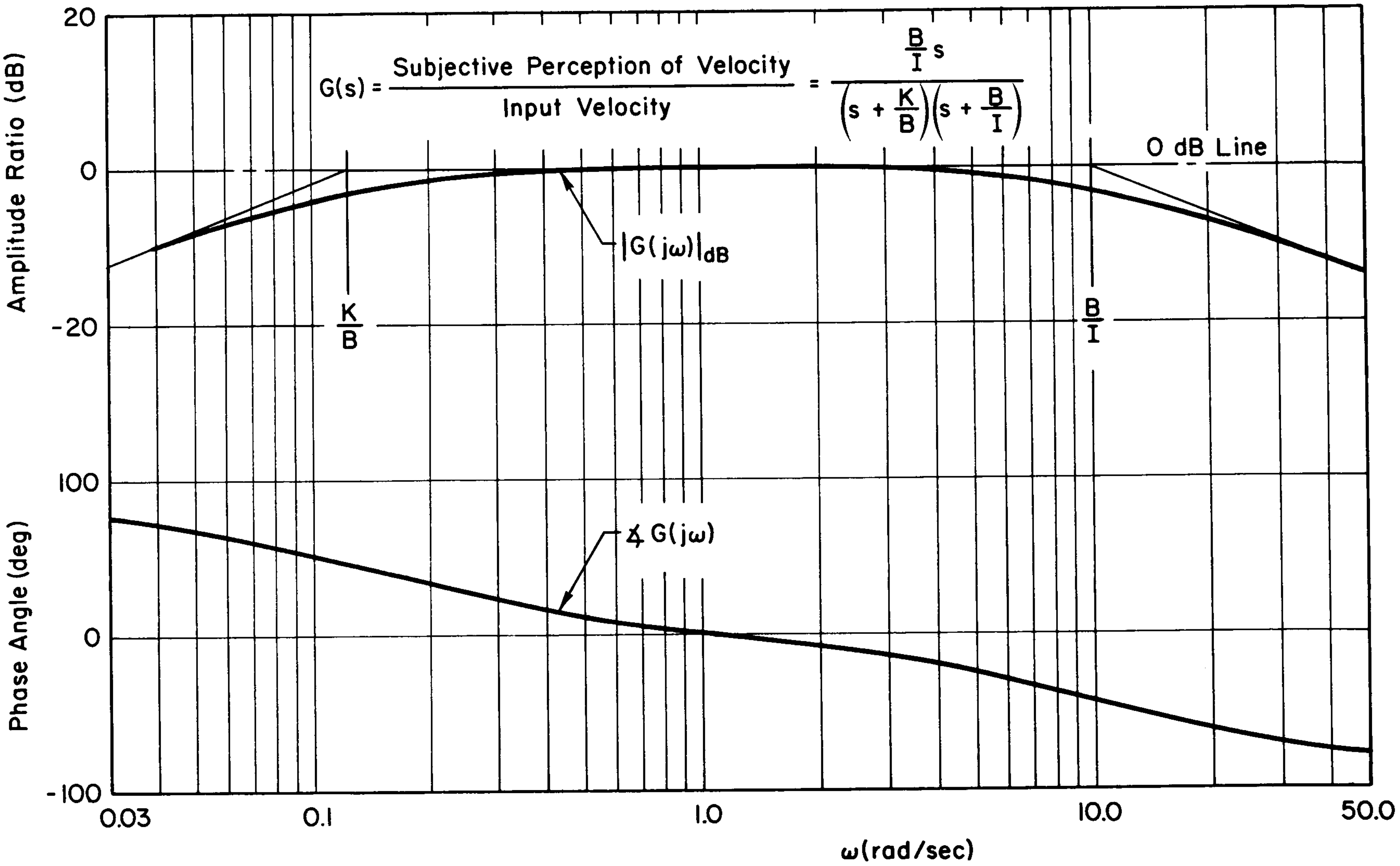


Figure 29. Frequency response of subjective perception model of semicircular canals

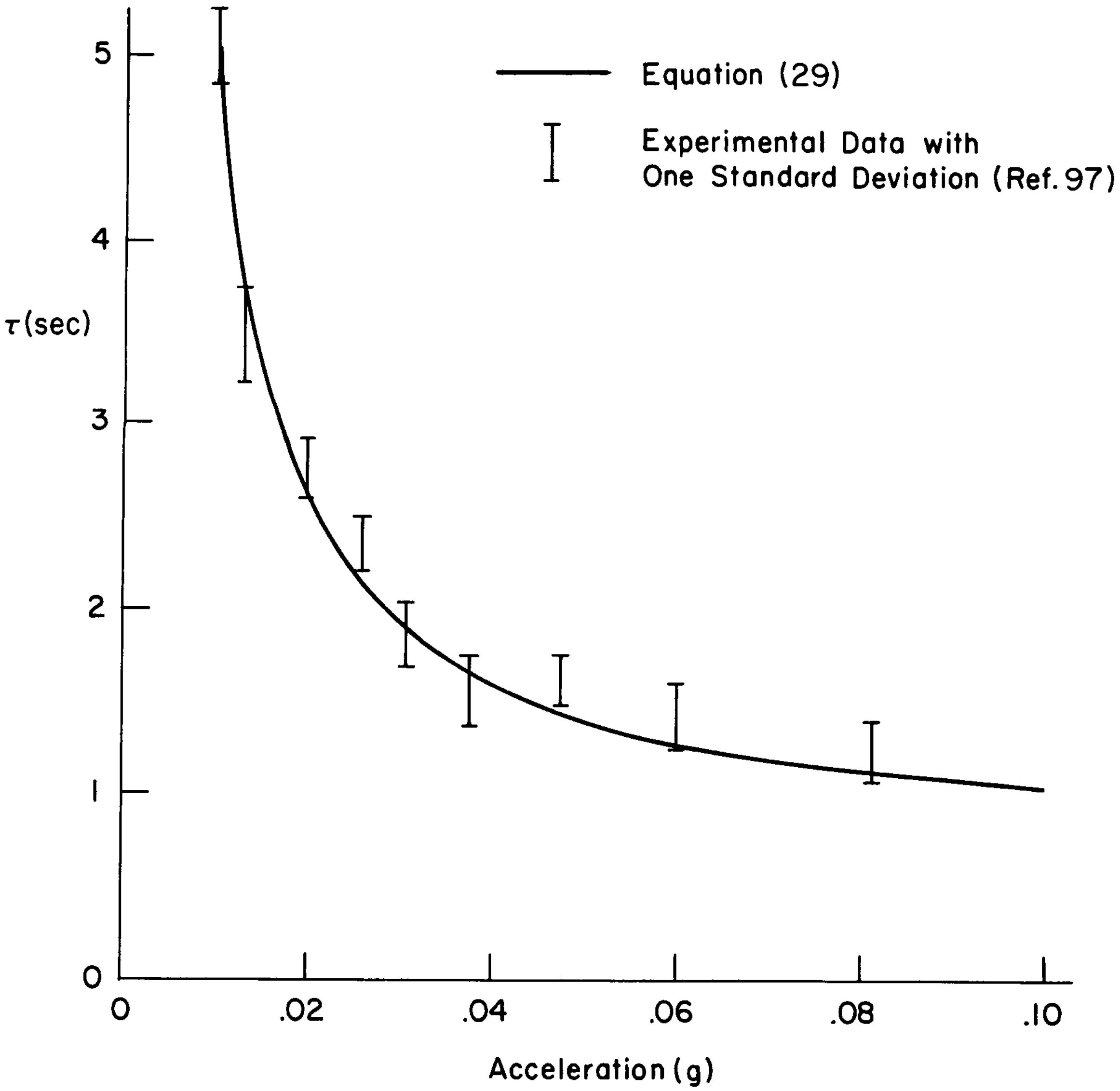


Figure 30. Latency times for perception of acceleration along the head vertical axis with subject supine (Meiry, J. L., _op. cit._)

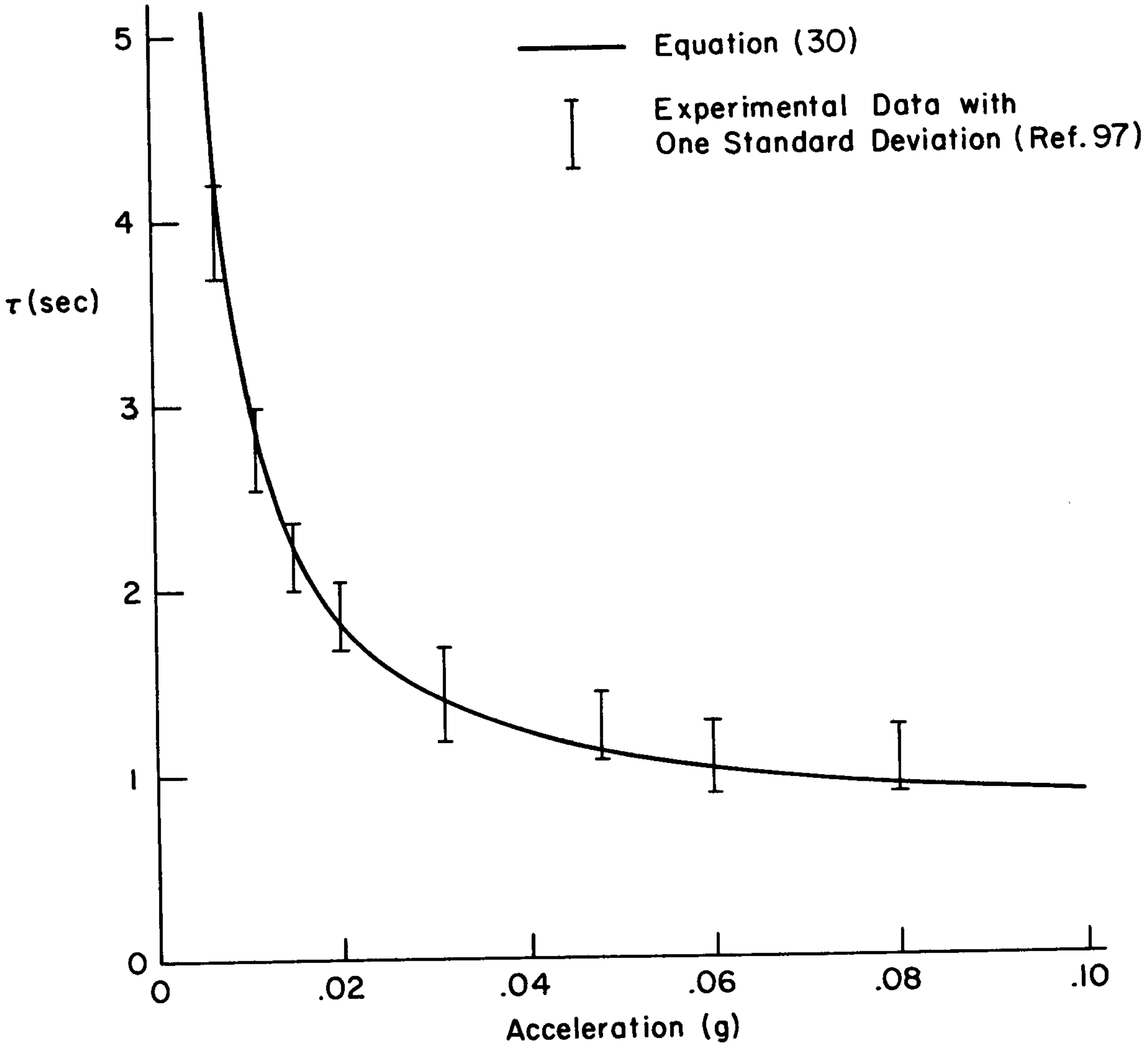


Figure 31. Latency times for perception of acceleration along the sagittal axis with the head upright (Meiry, J. L., op. cit.)

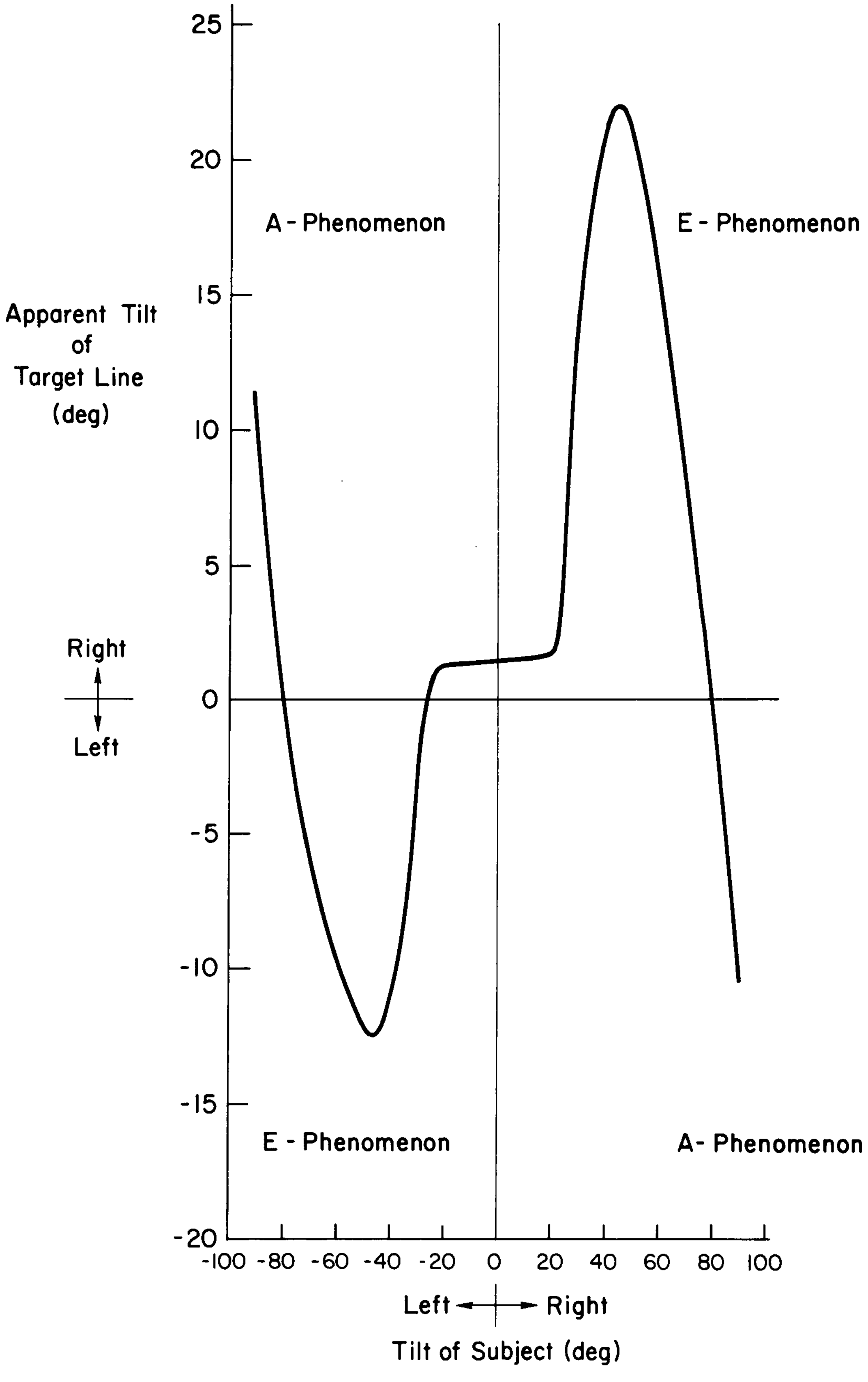


Figure 32. Typical mean curve of egocentric visual localization of the horizontal showing E- and A-Phenomena (From Graybiel, A.: Orientation in Aerospace Flight. Spec. Rept. 66-6, Naval Aerospace Medical Institute, 10 Oct. 1966)

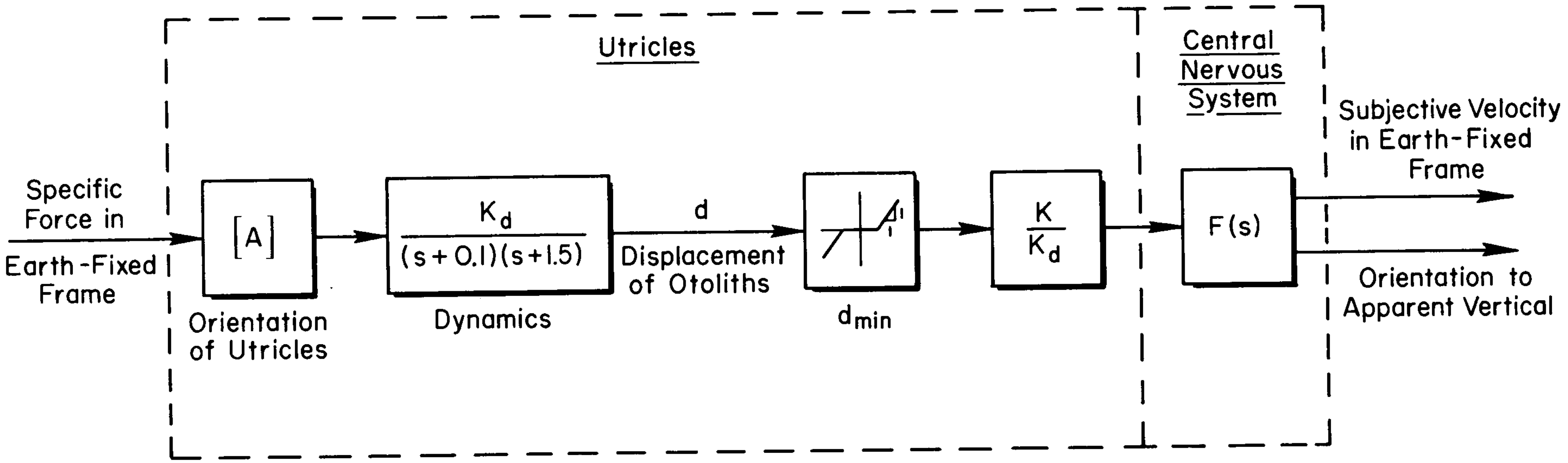


Figure 33. Subjective perception model of the utricles (Meiry, J. L., *op. cit.*)

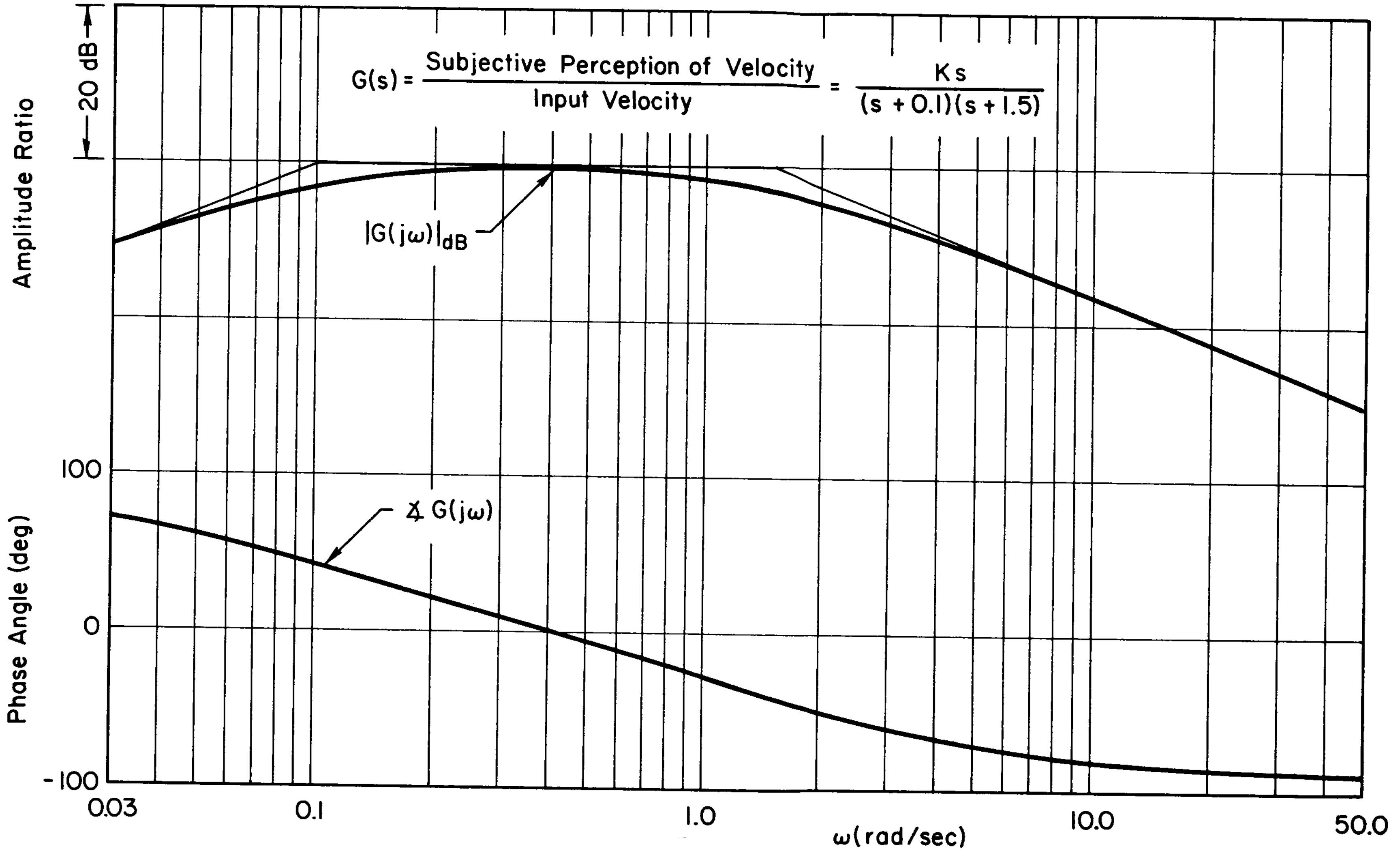


Figure 34. Frequency response of subjective perception model of utricles (Meiry, J. L., *op. cit.*)

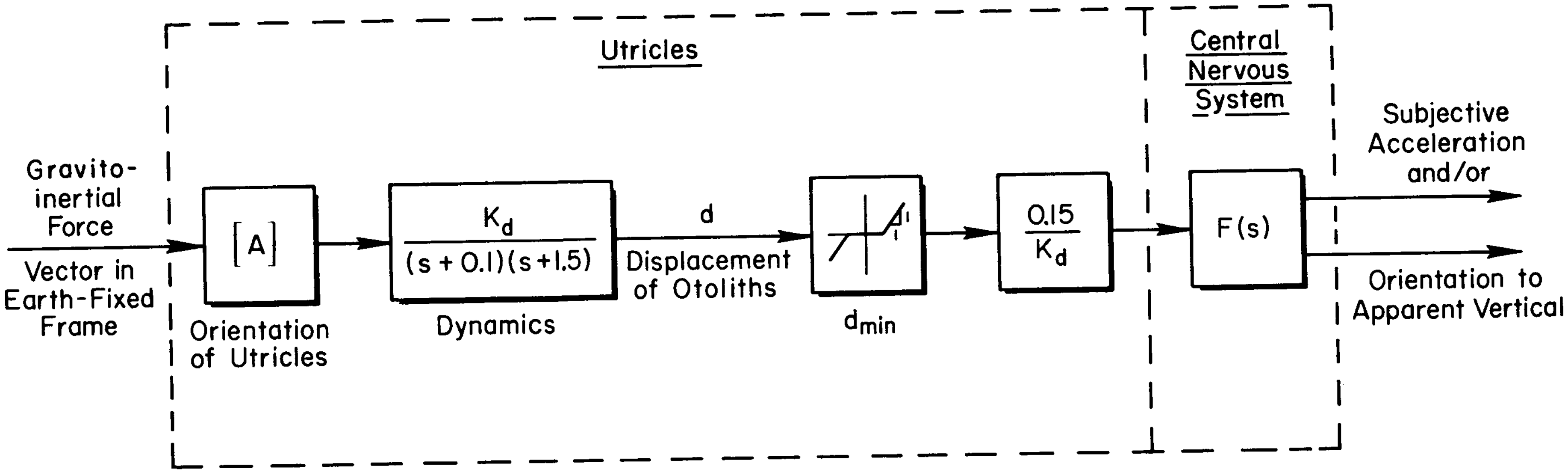


Figure 35. Proposed subjective perception model of the utricles (Based on author's interpretation of data in Meiry, J. L., _op_. _cit_.)

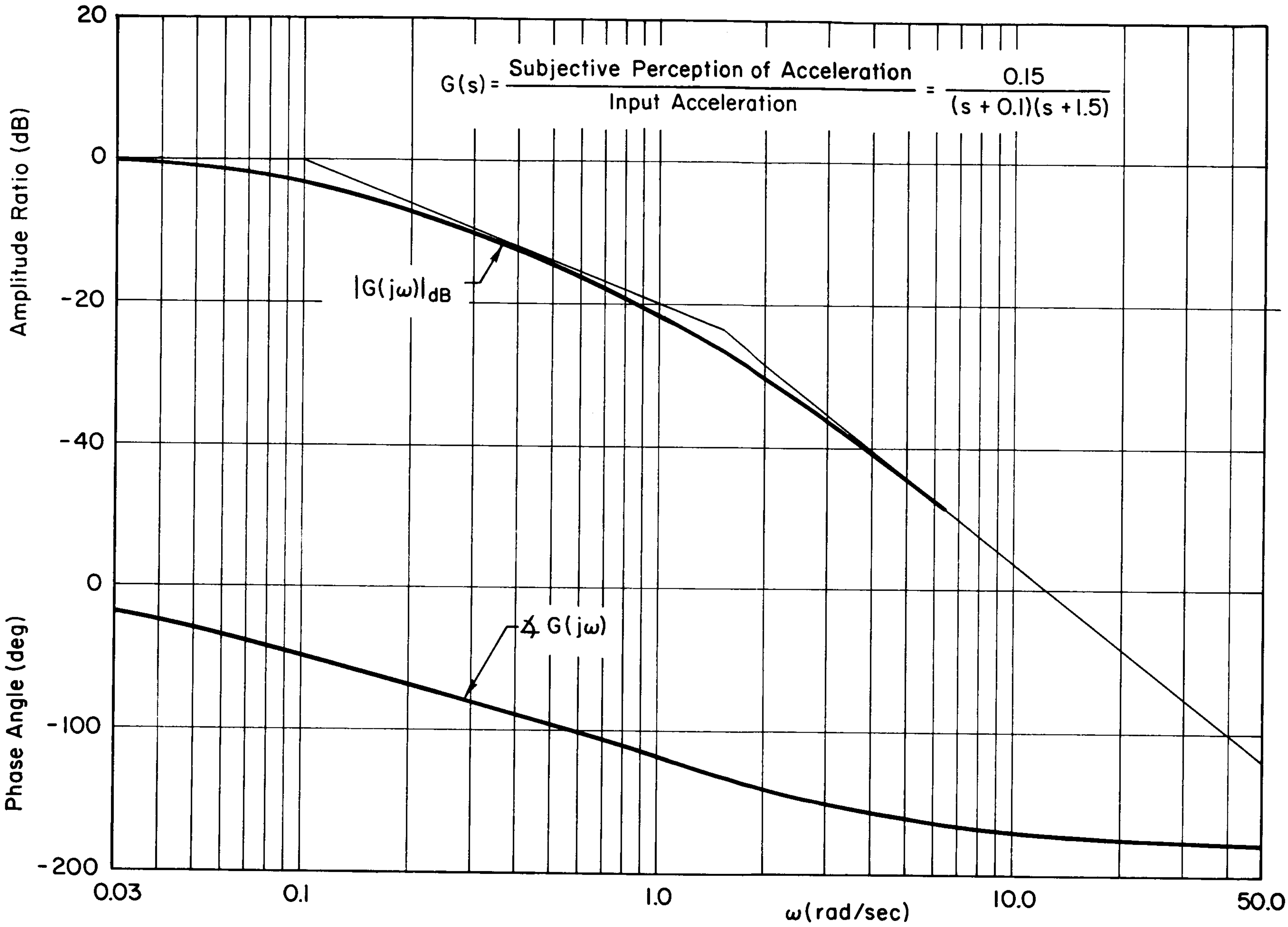


Figure 36. Frequency response of proposed subjective perception model of utricles

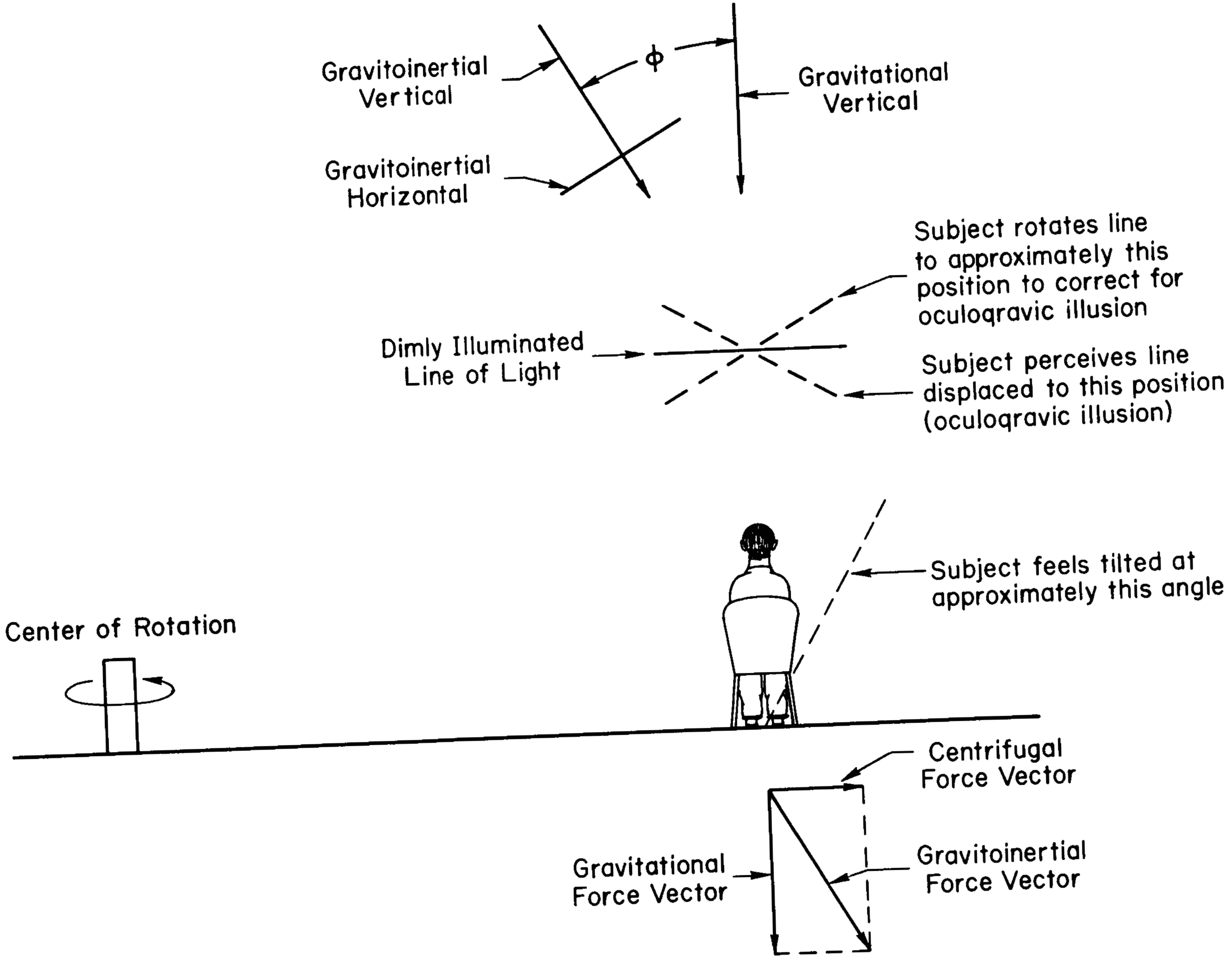


Figure 37. Schematic representation of the oculogravic illusion in the frontal plane (Adapted from Clark, B.; and Graybiel, A.: Factors Contributing to the Delay in the Perception of the Oculogravic Illusion. Rept. 120, Naval School of Aviation Medicine, 13 Aug. 1965)

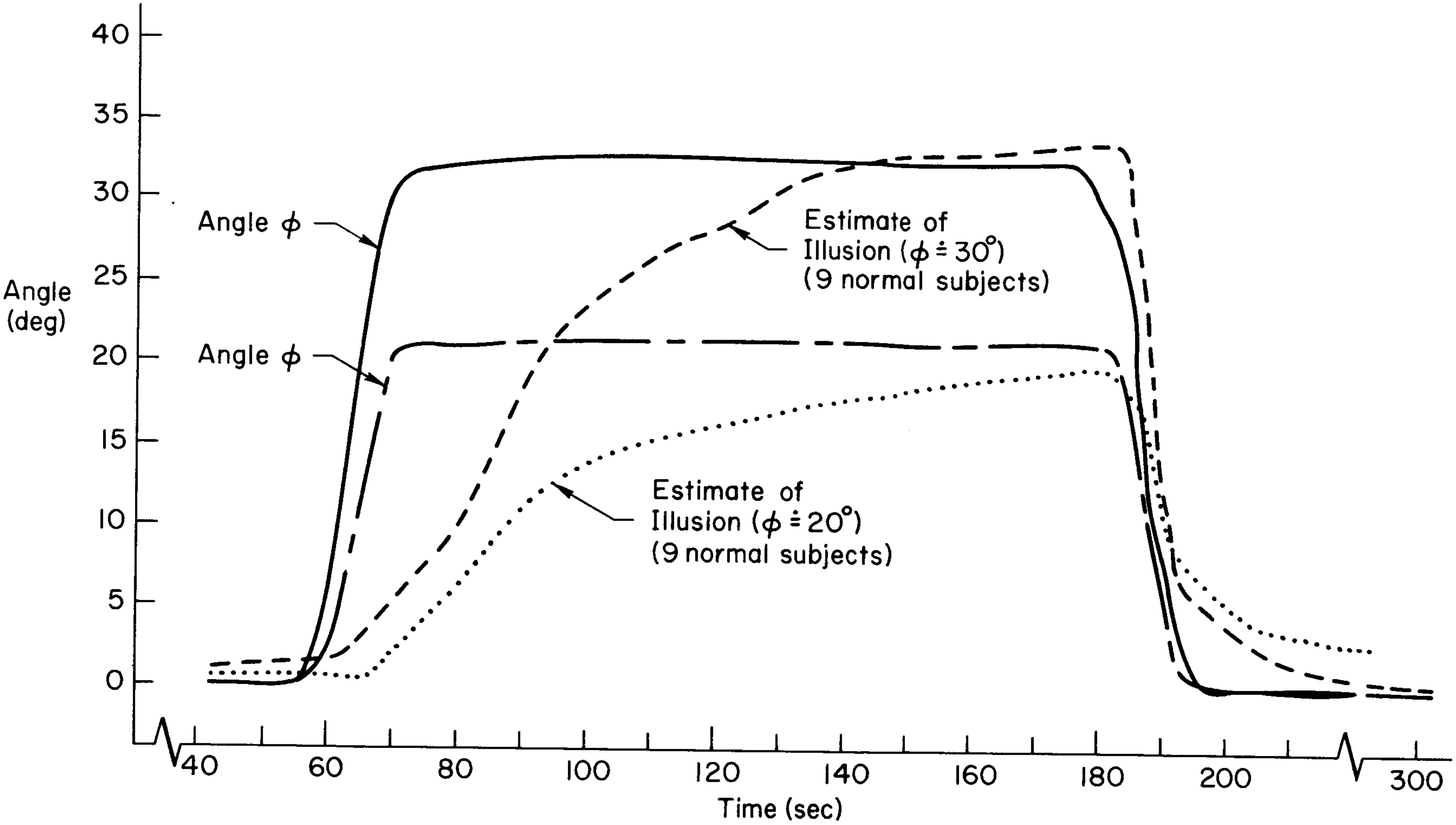


Figure 38. Time course of subject's rotation of target line compared with change in direction φ of G vector (Adapted from Graybiel, A.; and Clark, B.: The Validity of the Oculogravic Illusion as a Specific Indicator of Otolith Function. Rept. No. 67, Naval School of Aviation Medicine, 17 Feb. 1962)

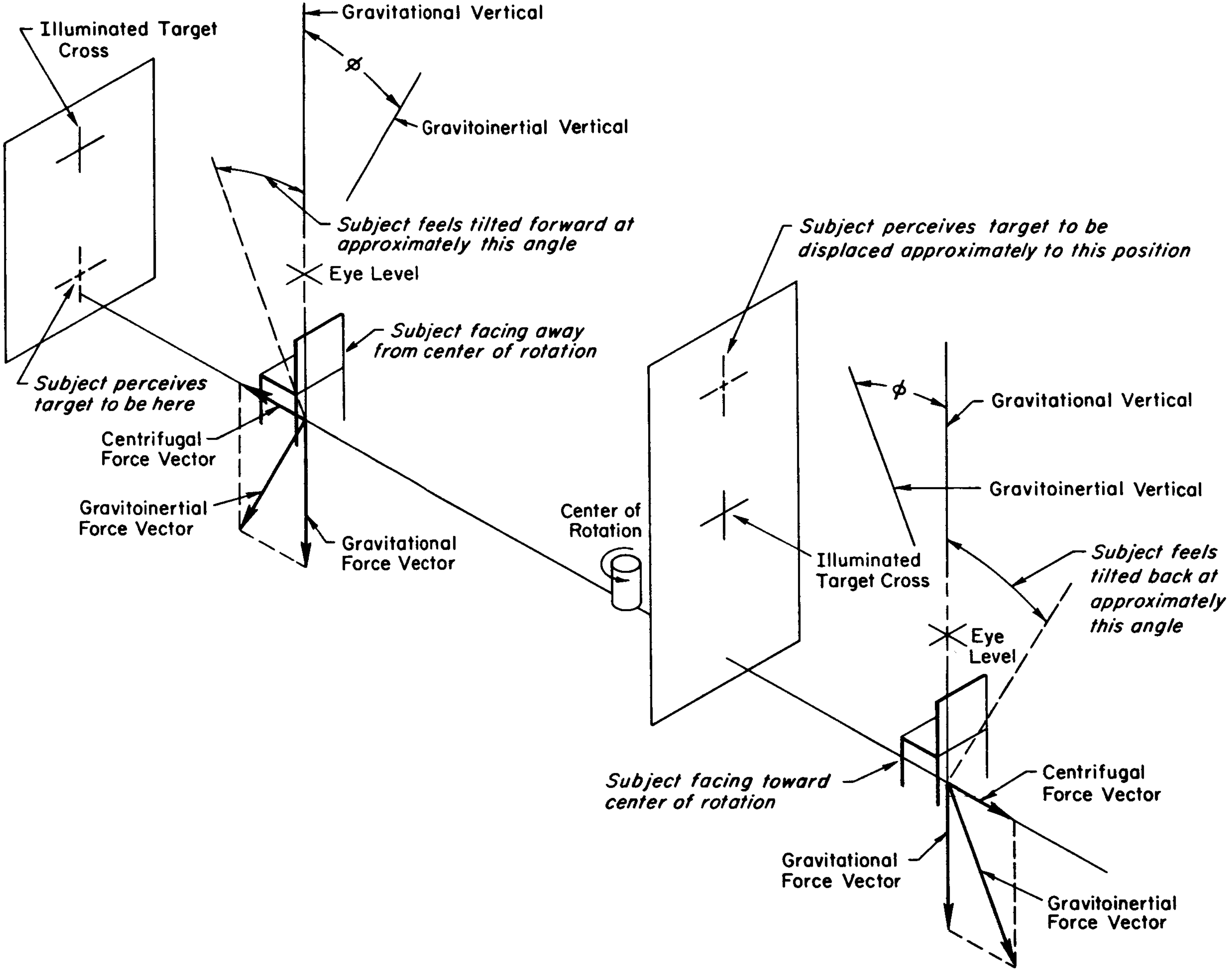


Figure 39. Schematic representation of the oculogravic illusion in the sagittal plane

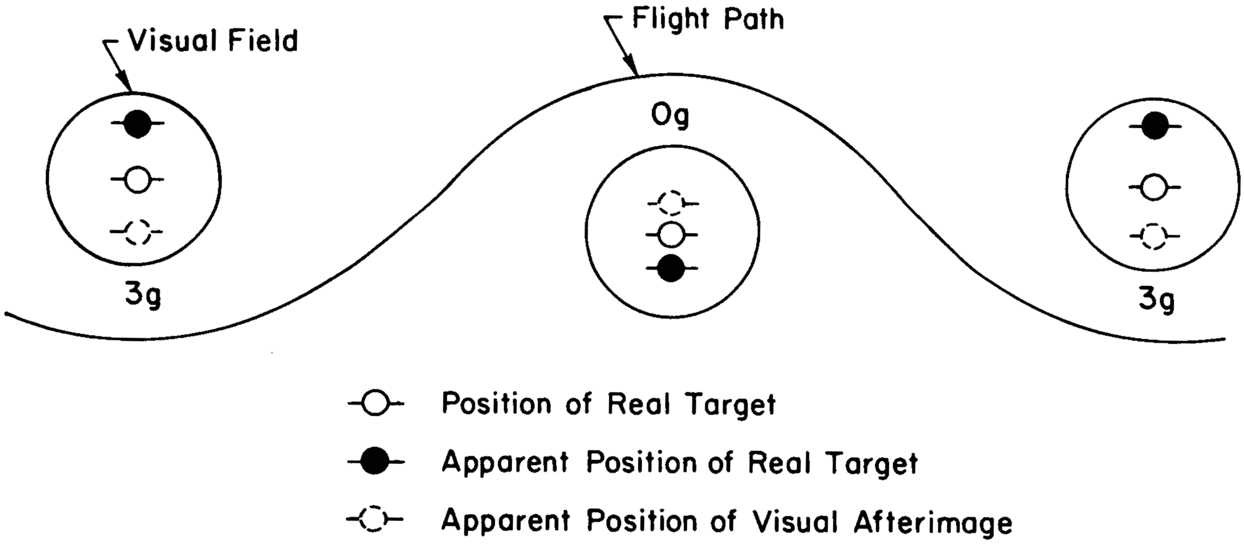


Figure 40. Appearance of the elevator illusion during a parabolic maneuver (Adapted from Clark, B.: Visual Space Perception as Influenced by Unusual Vestibular Stimulation. Human Factors, vol. 5, no. 3, June 1963, pp. 265-274)

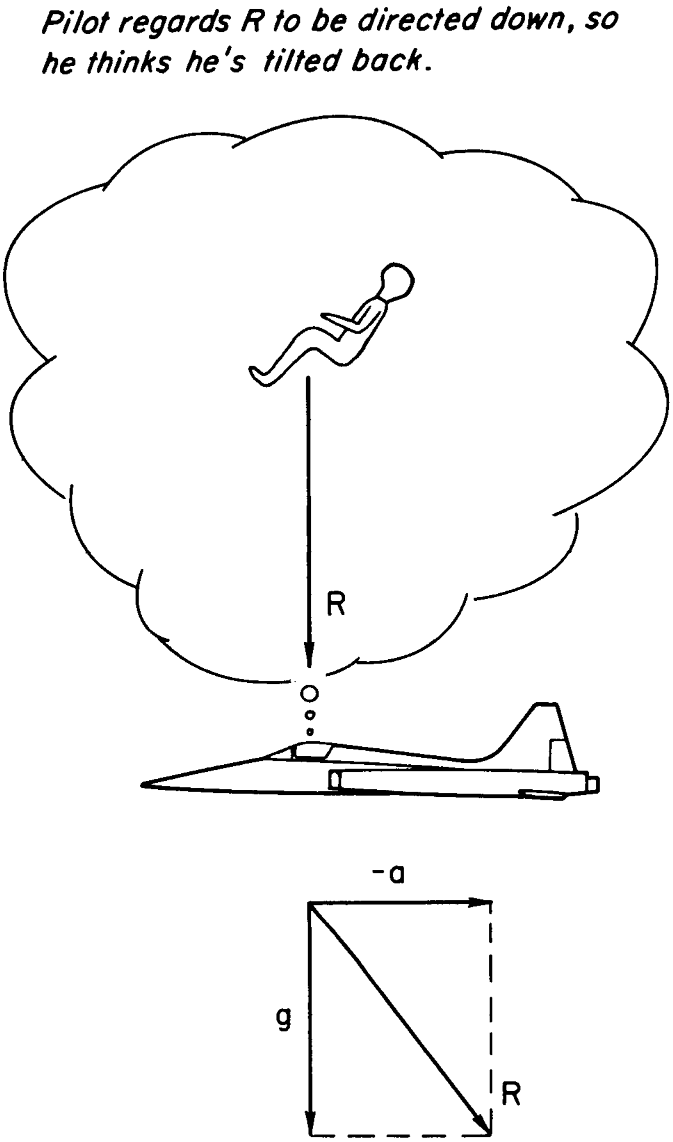
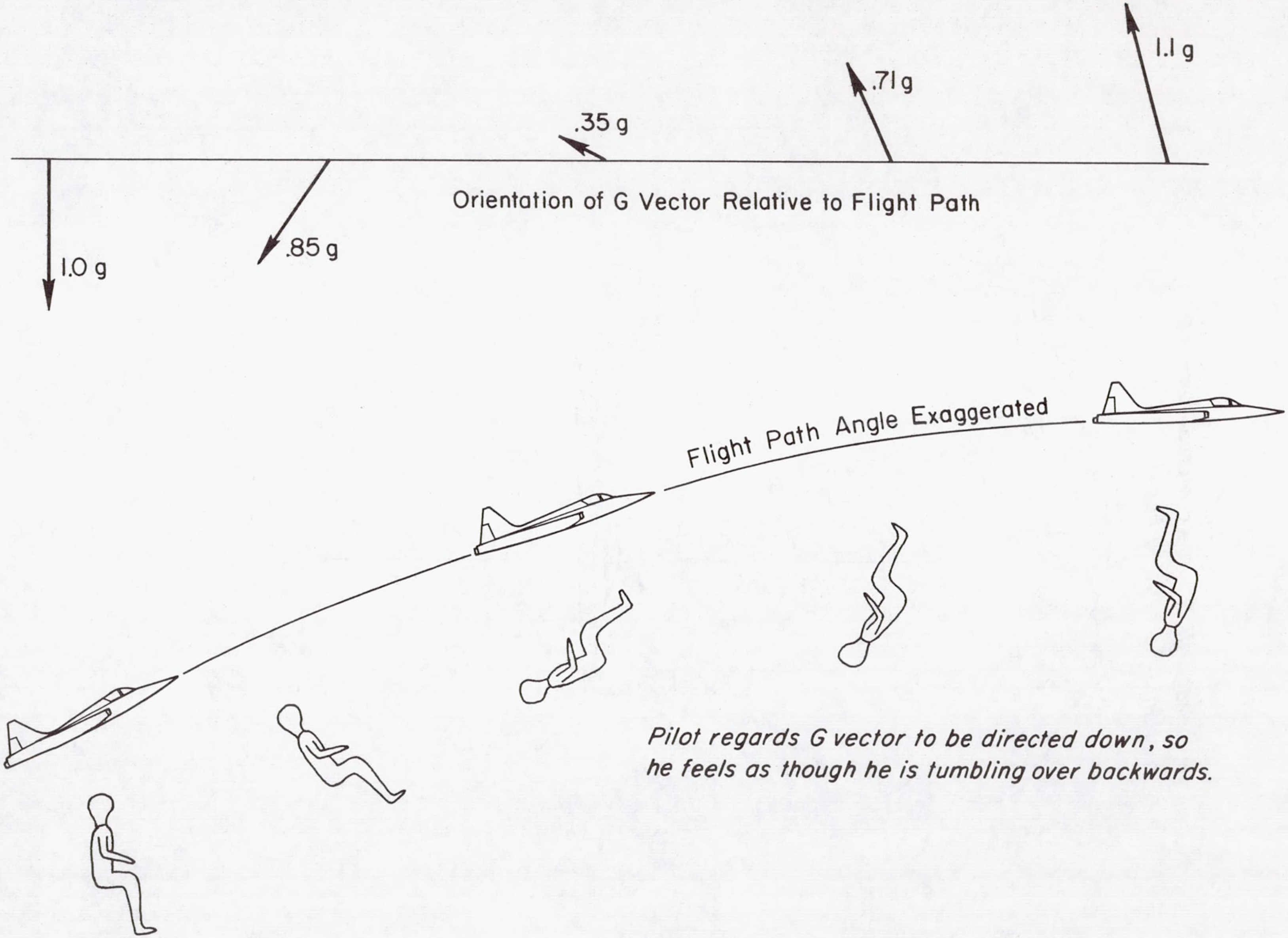


Figure 41. Sensation of nose-high attitude during takeoff



Pilot regards G vector to be directed down, so he feels as though he is tumbling over backwards.

Figure 42. Sensation of nose-high attitude or inversion during pushover from a climb to level flight (Adapted from Martin, J. F.; and Jones, G. M.: Theoretical Man-Machine Interaction Which Might Lead to Loss of Aircraft Control. Aerospace Med., vol. 36, no. 8, Aug. 1965, pp. 713-716)

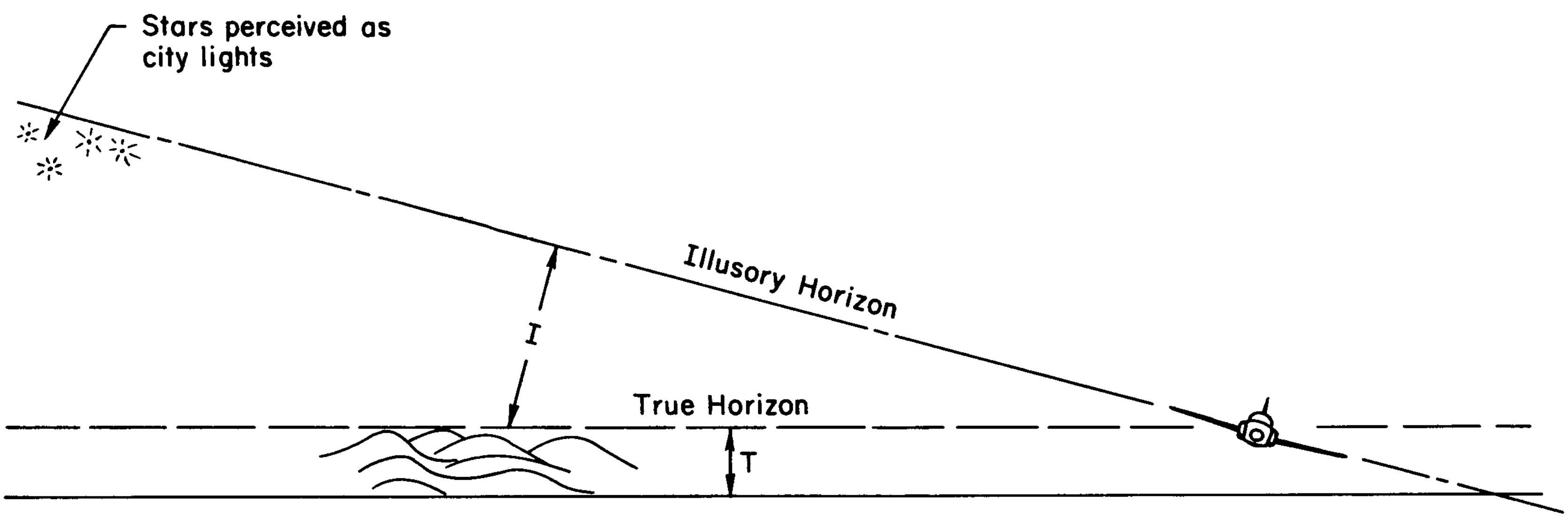
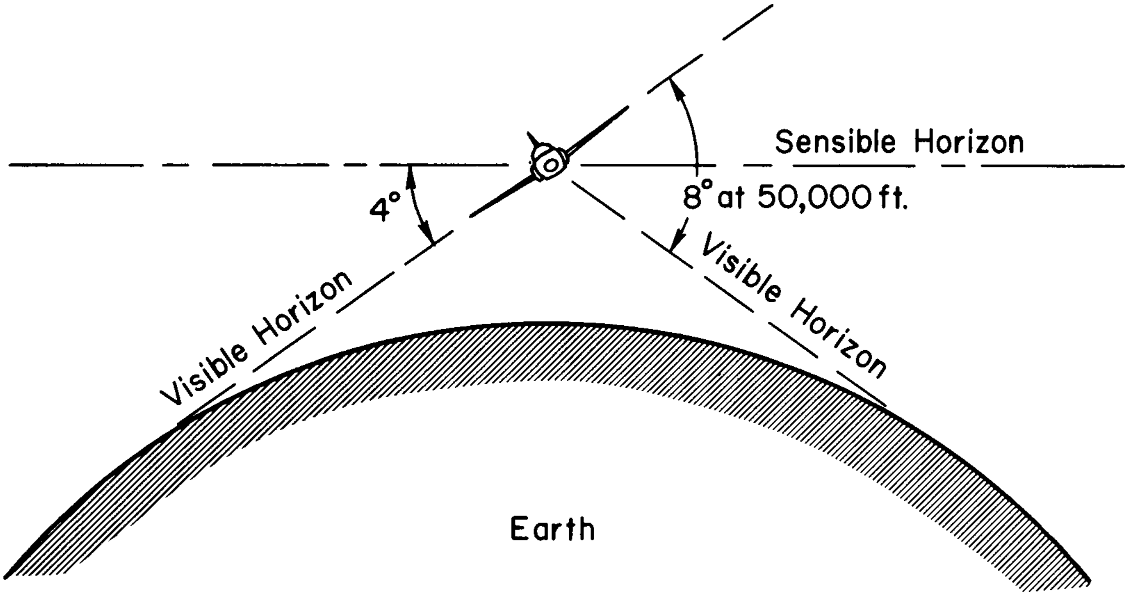
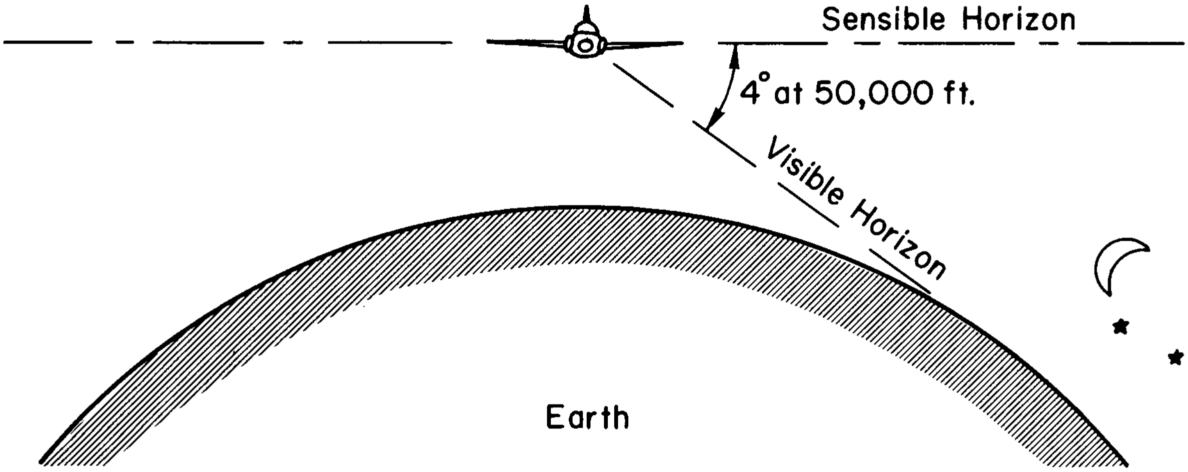


Figure 43. Aircraft aligned with fictitious horizon caused by perceiving stars as city lights (Pilot believes altitude to be I when it is really T.) (Adapted from Clark, B.; and Graybiel, A.: Disorientation: A Cause of Pilot Error. Res. Rept. NM 001 110 100.39, Naval School of Aviation Medicine, 2 Mar. 1955)



a) Bank Angle Developed Using Horizon Reference on One Side



b) Celestial Bodies Seen Below Horizon at Night

Figure 44. Depression of horizon at high altitude (Adapted from Benson, A. J., op. cit., by permission of Her Britannic Majesty's Stationery Office)

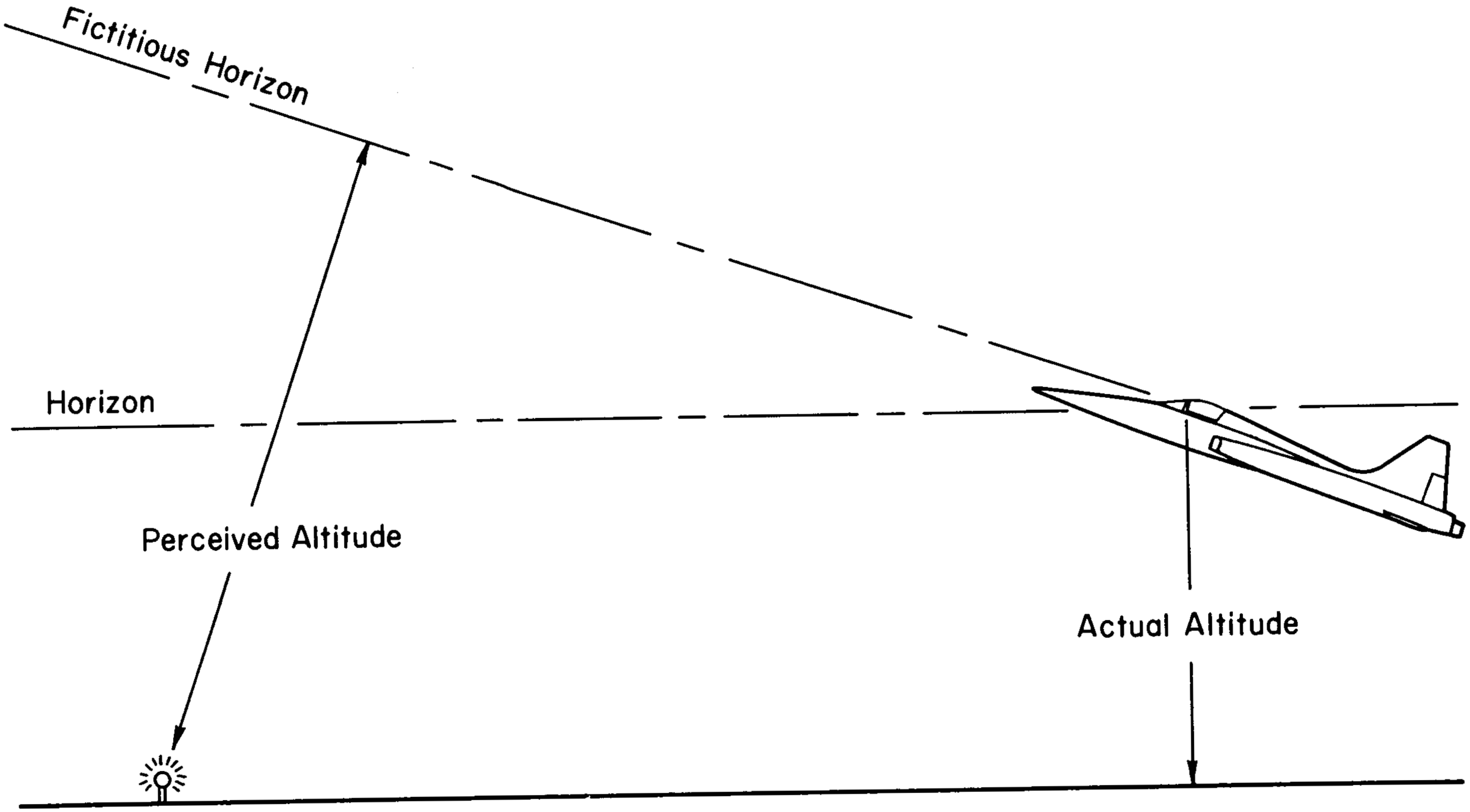
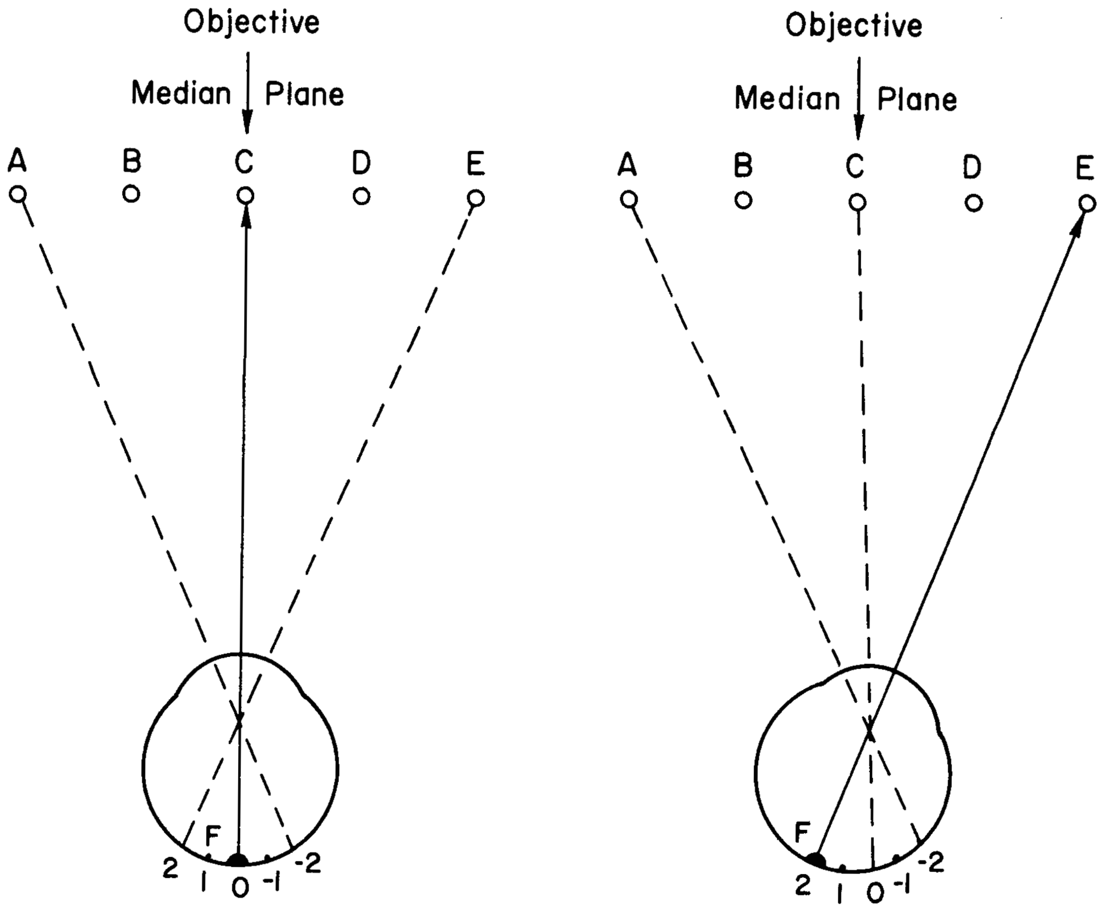


Figure 45. False perception of altitude due to flying with an unperceived error in attitude



(a) Eye in Primary Position

(b) Eye Turned Voluntarily to the Right

Figure 46. Concept of retinal space values (Adapted from Bruell, J. H.; Albee, G. W.: Notes Toward a Motor Theory of Visual Egocentric Localization. Psychol. Rev., vol. 62, no. 5, 1955, pp. 391-400)

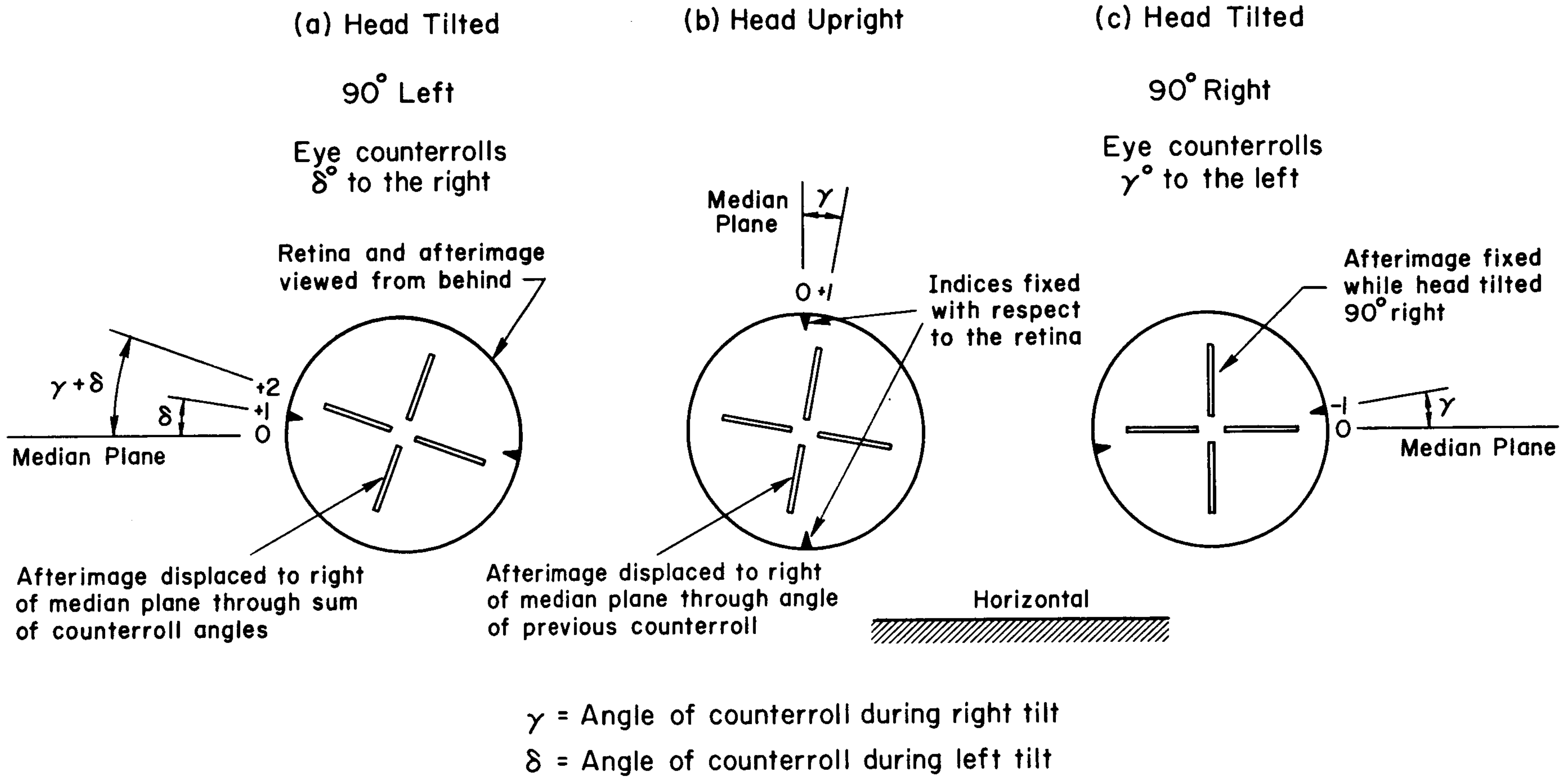


Figure 47. Change of retinal space values caused by counterrolling (an involuntary reflex) of the eye

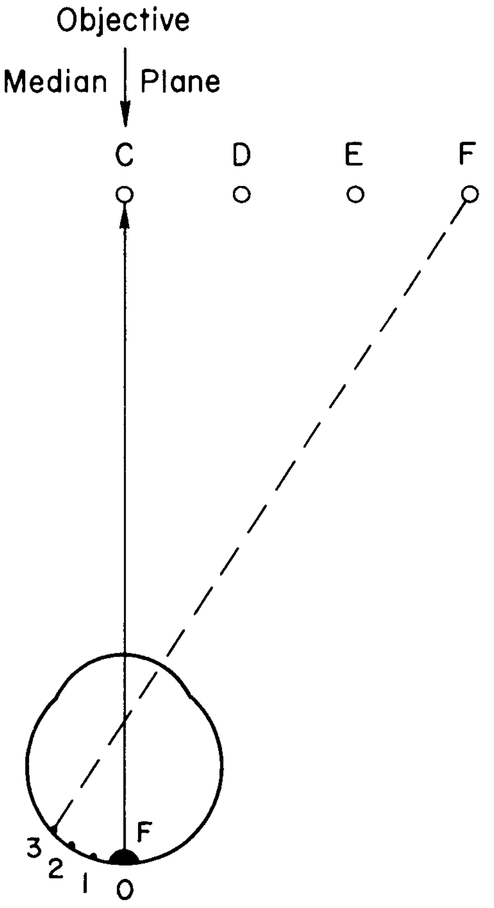


Figure 48. Visual field extending to the right of the object of regard (Adapted from Bruell, J. H.; and Albee, G. W., *op. cit.*)

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APPENDIX A

ANALYSIS OF THE CORIOLIS ILLUSION

Two approaches are taken in this appendix to describe mathematically the angular accelerations responsible for the Coriolis illusion. In the first approach an analysis is made of the motion of endolymph in an idealized semicircular canal as the head is tilted with respect to a coordinate system rotating at constant velocity, ω. It is shown that the flow of endolymph through the semicircular canal can be expressed completely in terms of Coriolis forces. It should be understood that the Coriolis force is a mathematical entity which allows us to account for the motion of bodies in a rotating coordinate system. A particle or system of particles moving in a straight line relative to an inertial frame appears to move in a curved path relative to a rotating coordinate system. To an observer in the rotating coordinate system the particle or system of particles appears to be acted upon by some mysterious force producing the curved path. In essence the Coriolis force accounts for this apparently spurious motion.

Coriolis forces thus account mathematically for the acceleration of endolymph in the semicircular canals as the head is tilted in a rotating environment. The physical process which takes place is that when the orientation of the head is changed in a rotating environment the direction of rotation of the head changes accordingly, but the endolymph in the semicircular canals continues to move as before by virtue of its own inertia. A Coriolis force analysis is one way of deriving an expression for the relative motion thus produced.

In the second approach to the problem, the flow of endolymph through the semicircular canal is derived in terms of vector components. The constant rotation vector, ω, is resolved into components normal to the plane of each canal. As the orientation of the head is changed relative to the rotation vector, ω, the components of ω normal to the plane of each canal change and thus give rise to the sensations known as the Coriolis illusion.

The two methods of analysis yield identical results since they merely represent two approaches to the same problem, the representation of motion in a rotating coordinate system. The component vector method is the more straightforward of the two approaches and is, perhaps, more readily interpreted physically.

1. Coriolis Force Analysis

The velocity of a particle in space may be represented (ref. 50) as:

$$v_S = v_R + \omega \times R \tag{A-1}$$

where the rotating axes have no linear velocity or acceleration relative to the space axes.

v_S = velocity of particle relative to space axes

v_R = velocity of particle relative to rotating axes

ω = rotation rate of rotating axes, assumed to be constant

R = radius vector from origin of rotating axes to particle

The time rate of change of v_S is given by

$$\left(\frac{dv_S}{dt}\right)_S = a_S = \left(\frac{dv_S}{dt}\right)_R + \omega \times v_S$$

$$= a_R + 2(\omega \times v_R) + \omega \times (\omega \times R) \tag{A-2}$$

where a_S = acceleration of the particle relative to the space axes

a_R = acceleration of the particle relative to the rotating axes

The equation of motion of the particle in inertial space is $F = ma_S$ and, in the rotating coordinate system, is

$$F - 2m(\omega \times v_R) - m\omega \times (\omega \times R) = ma_R \tag{A-3}$$

To an observer in the rotating coordinate system, the particle appears to move under the influence of an effective force, F_{eff}:

$$F_{eff} = F - 2m(\omega \times v_R) - m\omega \times (\omega \times R) \qquad (A-4)$$

The third term in equation A-4 is the familiar centrifugal force. It is a vector of magnitude $m\omega^2R$, orthogonal to ω, and directed away from ω. The second term in equation A-4 is the Coriolis force, a vector of magnitude equal to $2m\omega v_R \sin \alpha$, orthogonal to both ω and v_R, and pointing in a direction opposite (due to the minus sign) that determined from the advance of a right-handed screw turned from ω toward v_R through the angle α, the smaller of the angles between the two vectors.

Now let us consider how these equations of motion may be applied to determine the stimulation of the semicircular canals during motion of the head which elicits the Coriolis illusion. The situation which evokes the illusion is a tilting of the head while the head is rotating about another axis ω not aligned with the tilt axis. We might think of a subject in a centrifuge which rotates with constant speed ω. The rotation rate of the centrifuge is the rotation rate of the rotating coordinate system.

The problem will be simplified by considering the endolymph flow induced in a single semicircular canal which is idealized as a ring of endolymph as shown in figure A-1. In this figure the tilt axis of the canal lies in the plane of the canal, and in the plane of rotation, and is orthogonal to ω.

Initially, the canal is upright and is then tilted at a rate $d\varphi/dt$. The velocity, v_R, of a particle in the endolymph ring produced by the tilting motion of the canal is given by

$$v_R = r \sin \beta \frac{d\varphi}{dt} \qquad (A-5)$$

where β is the angular displacement of the particle relative to the tilt axis as shown in the sectional view of figure A-1

r is the radius of the endolymph ring

The change in centrifugal force on the endolymph ring as the ring is tilted does not induce flow in the ring, because of the symmetry of forces about the $\beta = \pm 90$ deg line. However, as we shall see, the Coriolis force does induce flow. The Coriolis acceleration of a particle of endolymph is

$$-2(\omega \times v_R) = 2\omega v_R \sin \alpha \qquad \text{(A-6)}$$

where α is the angle between ω and v_R, and the vector $\omega \times v_R$ is directed out of the page in figure A-1.

The terms on either side of equation A-6 are of opposite sign to correspond with the sign convention adopted in the figures. Referring to figure A-2, the vector $-2(\omega \times v_R)$ is directed to the right as shown and represents the accleration of a particle of endolymph relative to the rotating coordinate system under the action of the Coriolis force. We wish to represent accelerations directed to the right in figure A-2 as positive, hence the difference in signs in equation A-6.

The tilt angle $\varphi = \alpha - 90$ deg, so that $\cos \varphi = \sin \alpha$, and equation A-6 becomes

$$-2(\omega \times v_R) = 2\omega v_R \cos \varphi \qquad \text{(A-7)}$$

We will now determine the flow in the endolymph ring produced by the Coriolis acceleration given by equation A-7. This can be done by integrating around the circumference of the ring the torque produced by the tangential component of the Coriolis force and dividing by the moment of inertia of the endolymph ring to get the circumferential acceleration of the endolymph. This approach is valid provided the torque is taken about an axis of symmetry of the endolymph ring. Referring to figure A-2, the Coriolis force on an elemental mass, Δm, of endolymph is

$$F_{cor} = -2(\omega \times v_R)\Delta m = 2\omega v_R \Delta m \cos \varphi \qquad \text{(A-8)}$$

The tangential component, F_t, of Coriolis force is

$$F_t = F_{cor} \sin \beta = 2\omega v_R \Delta m \sin \beta \cos \varphi \qquad \text{(A-9)}$$

The torque on the elemental mass is

$$rF_t = 2\omega v_R r \Delta m \sin\beta \cos\varphi \tag{A-10}$$

The elemental mass is given by

$$\Delta m = \rho A r \Delta\beta \tag{A-11}$$

where ρ = mass density of endolymph
A = cross-sectional area of endolymph ring

The torque on the endolymph is obtained by integrating the torque on the elemental mass around the ring. Thus, substituting equation A-5 for v_R and equation A-11 and Δm into equation A-10 and integrating around the ring, we get:

$$T = \int_0^{2\pi} 2\rho A r^3 \omega \cos\varphi \frac{d\varphi}{dt} \sin^2\beta \, d\beta \tag{A-12}$$

or

$$T = 2\pi\rho A r^3 \omega \cos\varphi \frac{d\varphi}{dt} \tag{A-13}$$

The moment of inertia I of the endolymph ring is

$$I = mr^2 = 2\pi\rho A r^3 \tag{A-14}$$

The instantaneous angular acceleration, α_R, of the endolymph ring about its center is given by T/I. Thus, α_R is obtained by dividing equation A-14 into A-13, giving

$$\alpha_R = \omega \cos\varphi \frac{d\varphi}{dt} \tag{A-15}$$

This angular acceleration expresses the stimulation on the endolymph in a semicircular canal produced by Coriolis forces arising when the head is tilted in a rotating field. The change in velocity of endolymph can be obtained from equation A-15. Thus,

$$\Delta\omega_R = \alpha_R \Delta t = \omega \cos\varphi \frac{d\varphi}{dt} \Delta t$$

or

$$\omega_R = \int_0^{\varphi} \omega \cos\varphi \, d\varphi = \omega \sin\varphi \tag{A-16}$$

The change in velocity of endolymph flow in a semicircular canal is thus equal to the product of the passive rotation rate, ω, and the sine of the tilt angle, and is independent of the rate at which the head is tilted, provided, of course, that friction characteristics in the canal have not had time to act effectively.

The relationships above were developed for a semicircular canal aligned in a particular fashion to both its tilt axis and the spin axis, ω. Let us see how these same relationships apply to the flow in canals oriented differently.

In the development above, the tilt axis was portrayed as passing through a diameter of the canal. Therefore, tilt of the head produced pure rotation of the canal and no translation. If the tilt axis were displaced from the plane of the canal, as it is during real tilts of the head, then translation would accompany rotation of the canal as the head is tilted. Translation during tilt would change the velocity of the canal as a whole, which would not produce a flow of endolymph. We are interested only in velocity changes which are asymmetrical relative to the symmetry axes of the endolymph ring and which, therefore, induce flow through the canal. Clearly, only rotations of the canal produce such asymmetrical velocities. Consequently, no generality is lost by not considering a tilt axis displaced from the center of the canal. We have only to consider various orientations of the tilt axis relative to the axis of constant rotation, ω, and to consider the case of the tilt axis which passes obliquely through the center of the canal.

Figure A-3 shows the idealized endolymph ring with its tilt axis still in the plane of rotation and in the plane of the ring, but at an arbitrary angle, ϵ, with respect to the normal to the spin axis, ω. The expressions for v_R and the Coriolis force, $-2(\omega \times v_R)\Delta m$, are the same as those given in equations A-5 and A-8, respectively. The orientation of the Coriolis force relative to the endolymph ring is the same as that in figure A-1 wherein the tilt axis is orthogonal to the normal to ω. The flow induced in the endolymph ring is thus independent of the orientation of the tilt axis relative to the radius vector R, provides the tilt axis lies in the plane of rotation and in the plane of the endolymph ring.

Next consider the situation portrayed in figure A-4 showing the endolymph ring tilted about an axis outside its own plane but still in the plane of rotation. The tilt axis is shown displaced through an angle γ from the normal to the plane of the endolymph ring. The tilt rate vector, $d\varphi/dt$, is resolved into components normal to the plane of the ring and parallel to the plane of the ring in the plane of rotation. The tilt rate vector normal to the ring produces rotation of the ring about its own center. Initially, no Coriolis forces are generated due to this rotation because the endolymph, by virtue of its inertia, does not rotate. As friction with the walls of the ring drag the endolymph around, Coriolis forces thus generated would act normal to the plane of the ring and not affect the flow of endolymph. On the other hand, the tilt vector component in the plane of the ring tilts the ring as in the case portrayed in figure A-3. The magnitude of the tilt vector component is $(d\varphi/dt) \sin \gamma$.

Accordingly, the Coriolis force generated in a semicircular canal tilted about an axis not in its own plane is proportional to the product of the tilt rate times the sine of the angle between the normal to the plane of the canal and the tilt axis, provided the tilt axis is orthogonal to the axis of constant rotation, ω. Thus, equations A-15 and A-16 are modified to account for a tilt axis oblique to the plane of the canal:

$$\alpha_R = \omega \cos \varphi \frac{d\varphi}{dt} \sin \gamma \qquad \text{(A-17)}$$

$$\omega_R = \omega \sin \varphi \sin \gamma \qquad \text{(A-18)}$$

Equations A-17 and A-18 express the angular acceleration and velocity, respectively, of endolymph flow in a semicircular canal which is tilted at a rate $d\varphi/dt$ through an angle φ about an axis in the plane of rotation displaced through an angle γ from the normal to the plane of the canal. It can be shown that the direction of angular acceleration, α_R, is specified by the vector component, normal to the plane of the endolypmh ring, of minus the vector product $\omega \times \left[(d\varphi/dt) \sin \gamma\right]$.

Let us now apply these equations to the situation in which a subject is seated upright in a centrifuge rotating counterclockwise with angular velocity ω. The subject is displaced from the center of rotation and faces the direction of motion. He is now tilted to the right through an angle φ. This situation corresponds to that of a pilot in a turn to the left and rolling his head to the right (provided we ignore the bank angle and constant pitch rate in the turn). A top view of the situation is portrayed in figure A-5. The endolypmh flow acceleration vectors are shown as arrows normal to the plane of each canal. According to equation A-17 the flow acceleration induced in each canal is $\alpha_R = \omega \sin \gamma \cos \varphi \, d\varphi/dt$. The flow acceleration vectors in orthogonal pairs of canals may be added vectorially to give an equivalent flow equal in magnitude to $\omega \cos \varphi \, d\varphi/dt$.

The flow acceleration induced in the canals is the same as that which would be induced in a nonrotating environment by a downward pitching acceleration equal to $dq/dt = -\omega \cos \varphi \, d\varphi/dt$, and is sensed accordingly. Using the notation for aircraft motions to denote motions of the head, as in Table XIII, the constant rotation rate, ω, of the centrifuge provides a negative yaw rate of the head. Thus $\omega = -r$. The equivalent pitching acceleration sensed when the head is rolled through the angle φ to the right while yawing to the left is given by:

$$\dot{q} = r \cos \varphi \frac{d\varphi}{dt} \tag{A-19}$$

After the head has tilted through the angle φ, the change in endolymph velocity (before friction slows it down) is given by equation A-18 as $\omega_R = \omega \sin \gamma \sin \varphi$. This change in endolymph angular flow rate is the same as that which would be induced in a nonrotating environment by a change in pitch rate of $q = -\omega \sin \varphi$. Substituting $\omega = -r$, the equivalent pitch rate sensed when the head is rolled to the right through an angle φ while yawing with velocity r to the left (r is negative) is given by

$$q = r \sin \varphi \tag{A-20}$$

While it may not be obvious from the foregoing, the equivalent pitch acceleration and equivalent pitch rate sensed by the subject represent actual pitching motions of the head. Even though the head does not appear to move about its pitch axis, when the head undergoes a rolling tilt while subject to a yaw rate, a component of the yaw rate is projected onto the pitch axis producing a pitch rate as expressed by equation A-20. This resolution of motions is examined more clearly in the following subsection.

2. Component Vector Analysis

Consider the situation portrayed in figure A-6. The rotation axis, ω, is initially aligned with the vertical axis, Z_h, of the head so that the planes of the vertical canals are parallel to the axis of rotation, and the vertical canals are unstimulated. The head is now tilted to the right through an angle φ. A component $\omega \sin \varphi$ of the rotation vector, ω, now lies in the horizontal plane and is aligned with the lateral axis, Y_h, of the head. This component represents a pitch rate of the head of magnitude $a = \omega \sin \varphi$ and stimulates the vertical canals accordingly. This vector is shown in figure A-6 resolved into components normal to the superior and posterior canals.

In this example the rotation vector, ω, is directed downward and hence represents a positive yaw rate, $\omega = r$. Thus, $q = r \sin \varphi$, which is in agreement with equation A-20 derived using an analysis of Coriolis forces.

As the head is tilted, the component of angular rotation along the vertical axis, Z_h, is reduced by an amount $\omega(1 - \cos \varphi)$. Thus, if the horizontal canals (not shown in fig. A-6) have equilibrated to the positive yawing rotation, ω, and the head is tilted to the right, the pilot would sense (in addition to the head tilt and pitch motion) a yawing motion to the left equal to the change, $-\omega(1 - \cos \varphi)$, in actual yawing velocity. While this finding was not a part of the Coriolis force analysis, it could have been made using that method. Such a change in the perceived constant rotation rate has been reported (ref. 114) during centrifuge tests.

In the example above, it is obvious that the sensation of pitch brought about by rolling the head while undergoing a constant yaw rate is truly representative of the angular motions undergone by the head and not a spurious sensation as suggested by some authors (ref. 49 and others).

Figure A-7 portrays a situation in which the rotation axis is initially aligned with the head vertical axis, and the head is then tilted backward through an angle θ. After the head is tilted, there is a component of angular velocity $\omega \sin \theta$ aligned with the sagittal axis, X_h. This component represents a rolling velocity of the head of magnitude $\omega \sin \theta$ and stimulates the vertical canals accordingly. The vector $\omega \sin \theta$ is shown in figure A-7 resolved into components normal to the planes of the superior and posterior canals. The angular velocity in yaw is reduced by an amount $\omega(1 - \cos \theta)$, and the horizontal canals, having equilibrated to the initial rate, ω, are stimulated by the change, giving rise to a sensation of yawing to the left.

The analyses above show two methods of examining the same physical entity. The stimulation of the semicircular canals resulting when the head is tilted about one axis while undergoing a continuous rotation about another axis can be analyzed using Coriolis forces or resolution of vectors. The two methods yield identical results, although the latter is more straightforward and more readily visualized.

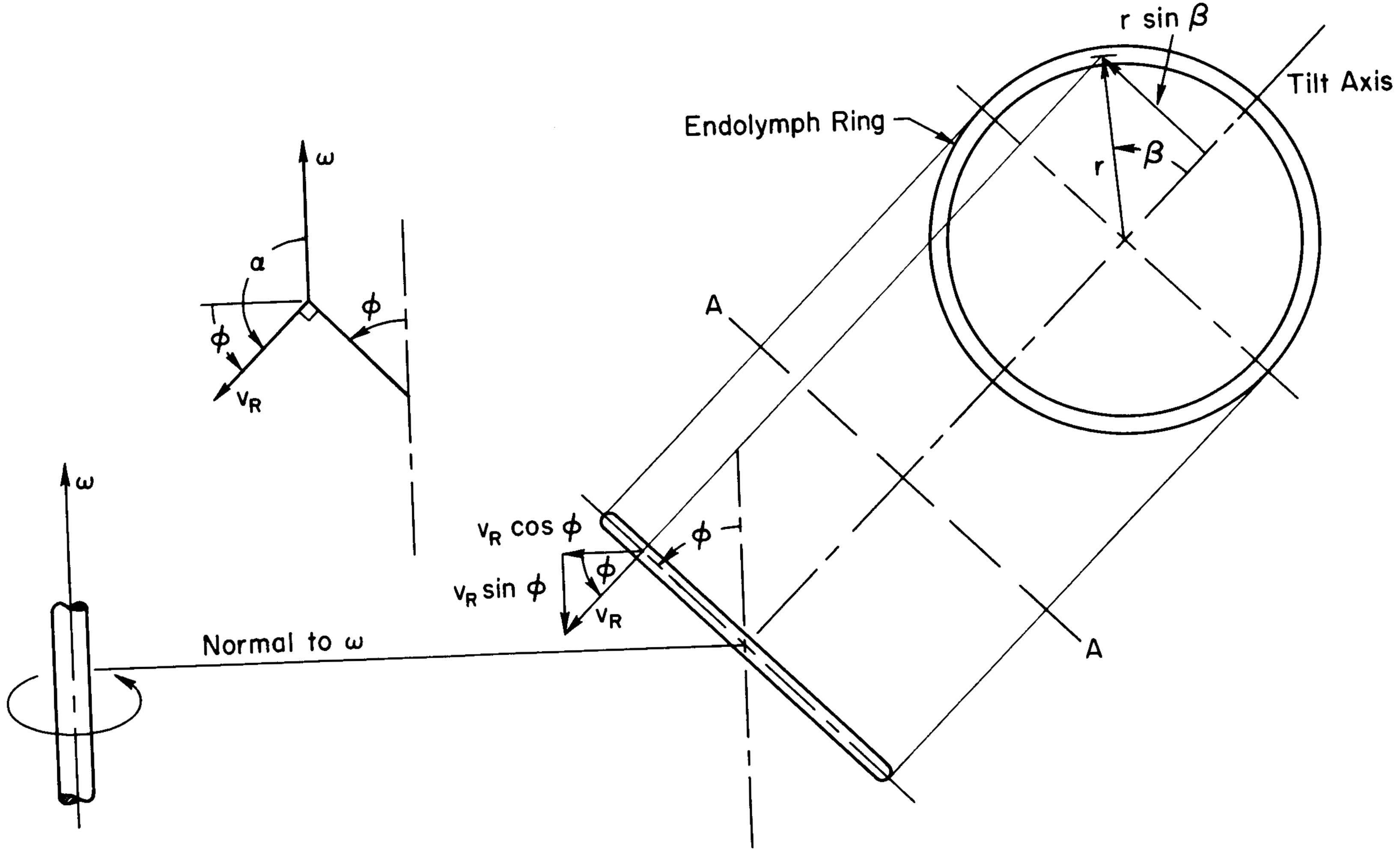


Figure A-1. Figure for calculation of v_R, the velocity of a particle of endolymph relative to the rotating set of axes as the endolymph ring is tilted

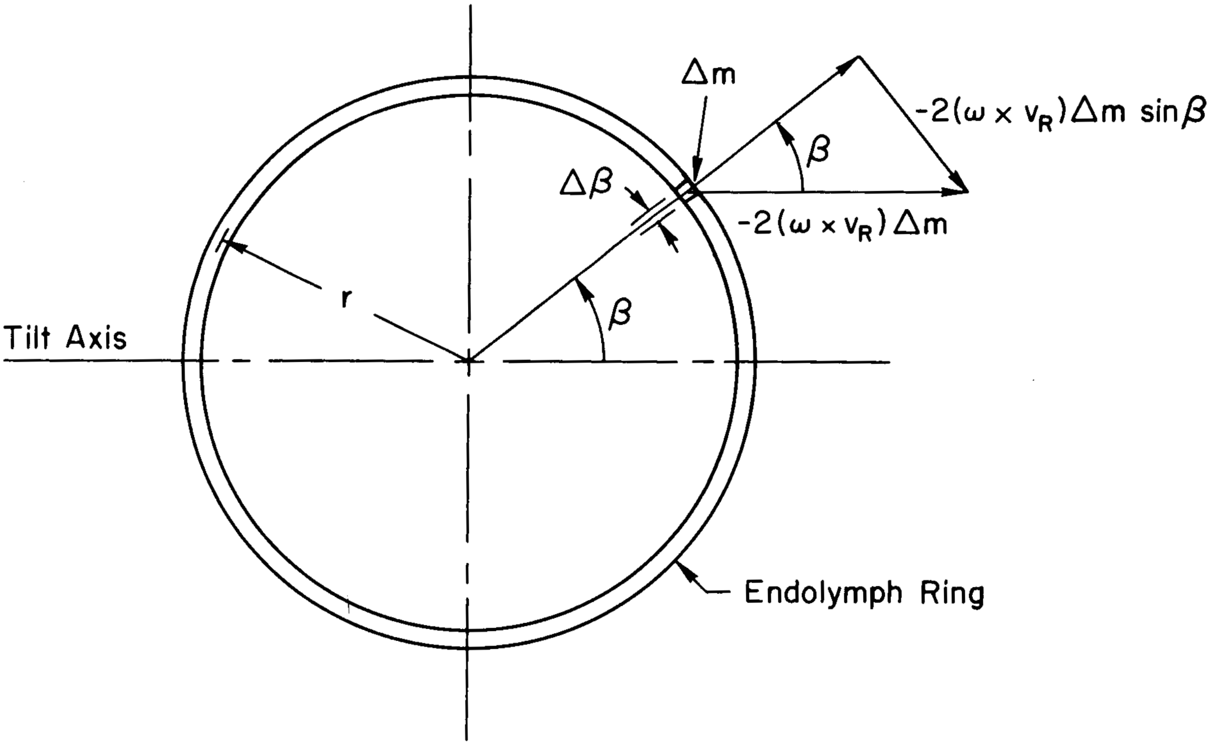
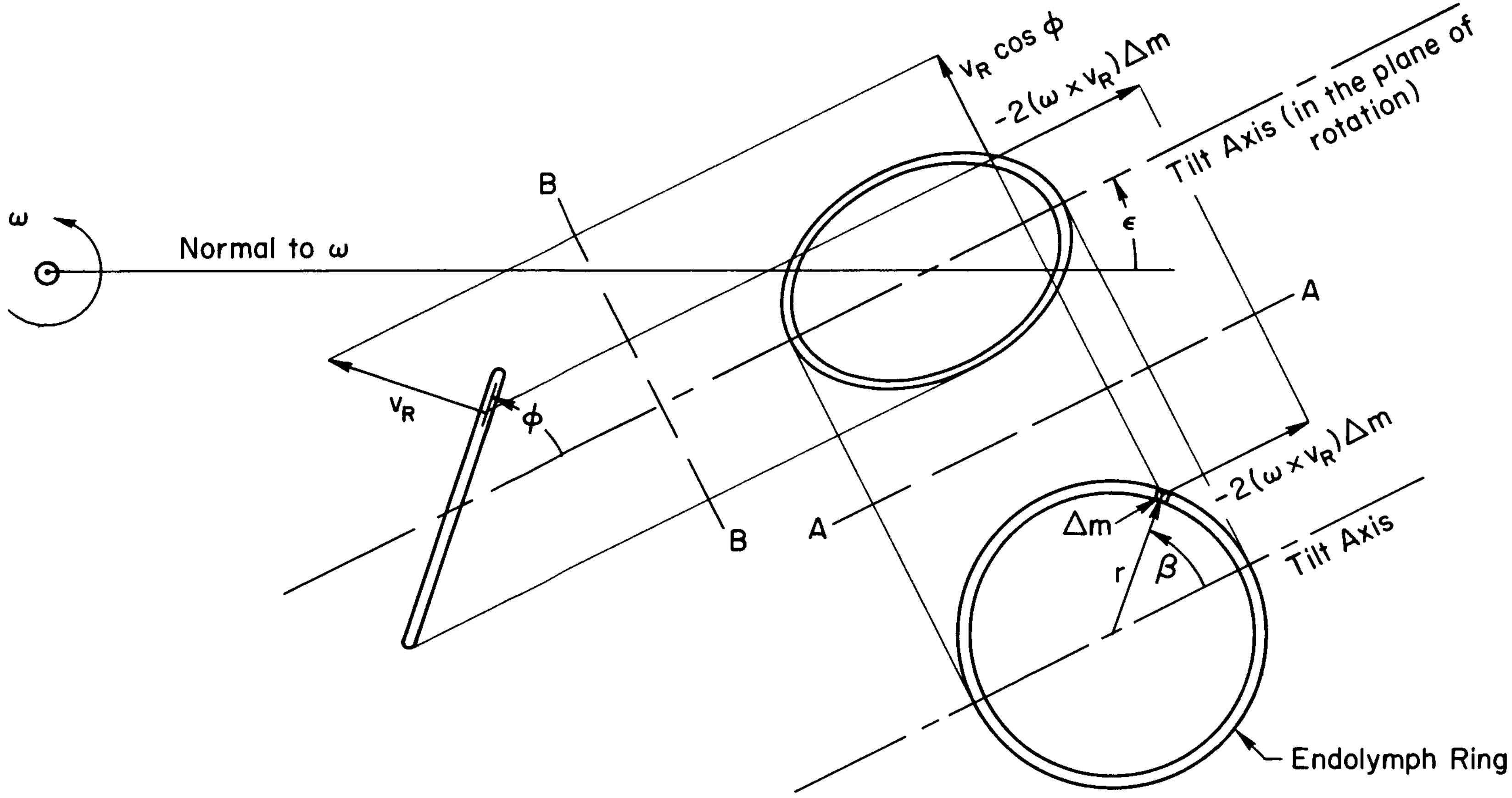


Figure A-2. Figure for calculation of tangential component of Coriolis force on endolymph ring



$$\text{Coriolis Force} = -2(\omega \times v_R)\Delta m = 2\omega r \Delta m \sin\beta \cos\phi \frac{d\phi}{dt}$$

Figure A-3. Figure showing Coriolis force on endolymph ring to be independent of orientation of tilt axis in plane of constant rotation

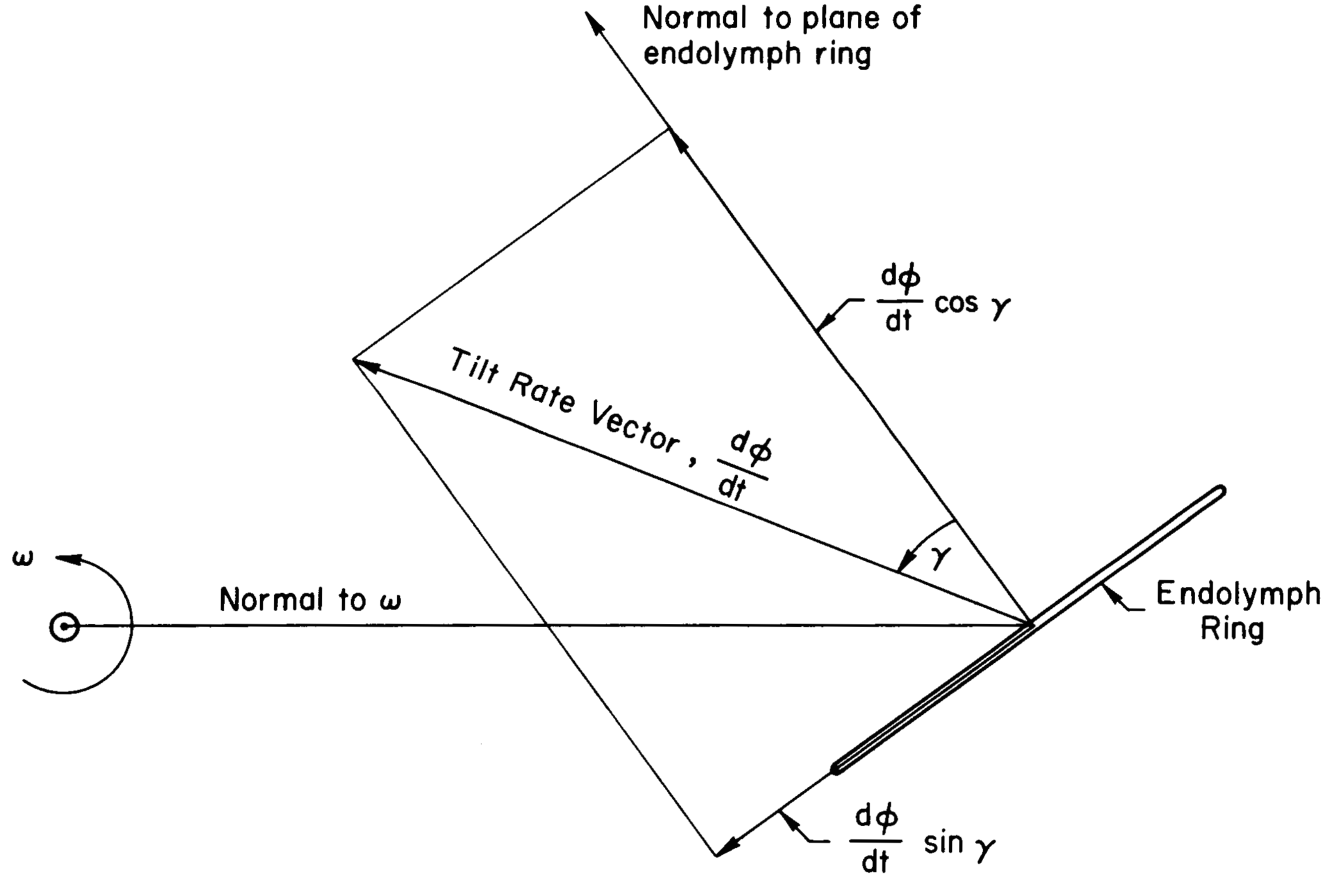


Figure A-4. Tilt of the endolymph ring about an oblique axis

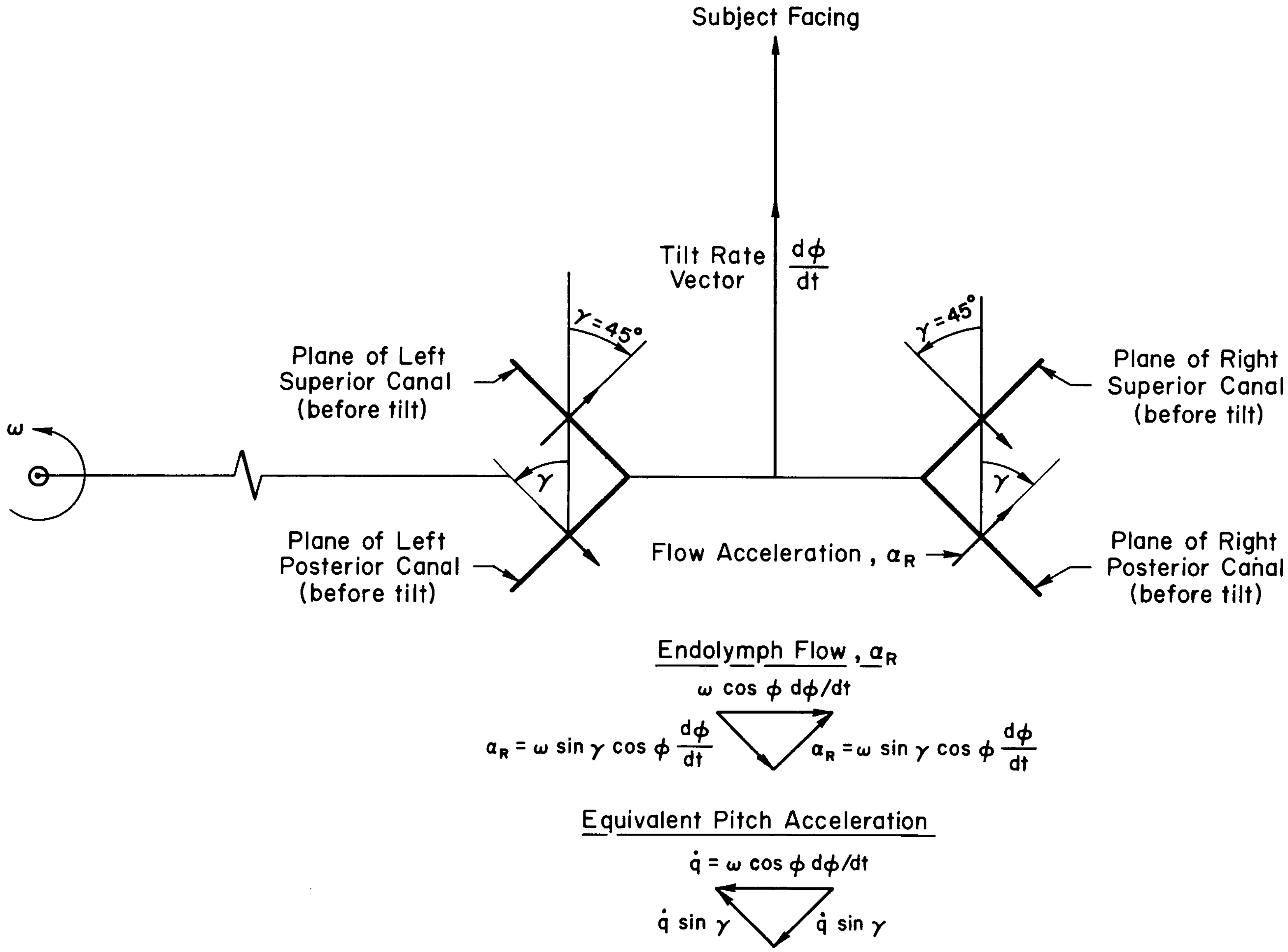


Figure A-5. Endolymph flow generated by Coriolis forces as head is rolled to the right during constant yaw rate to the left (γ = 45 deg)

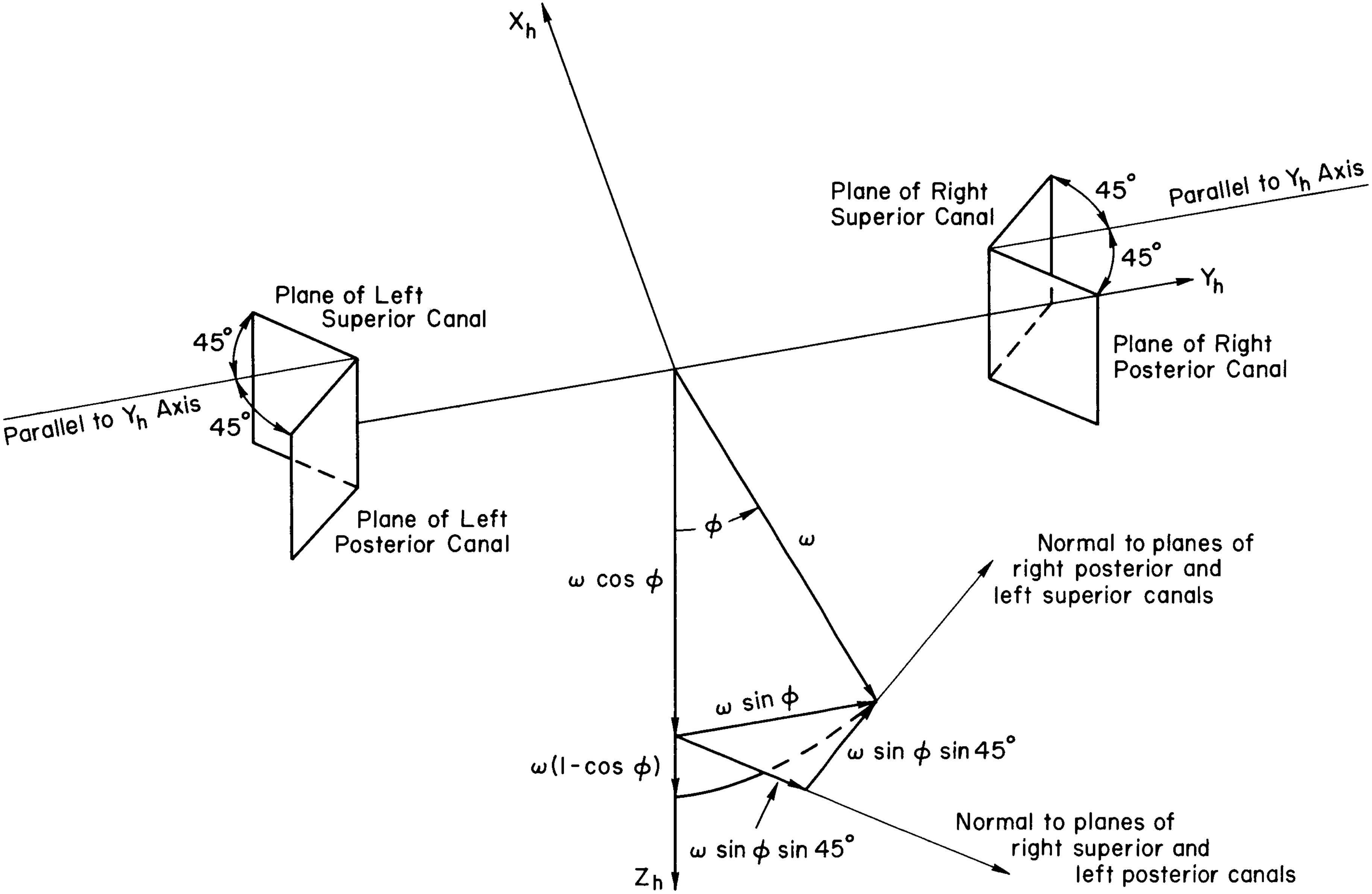


Figure A-6. Component vector analysis of a displacement of the head in roll

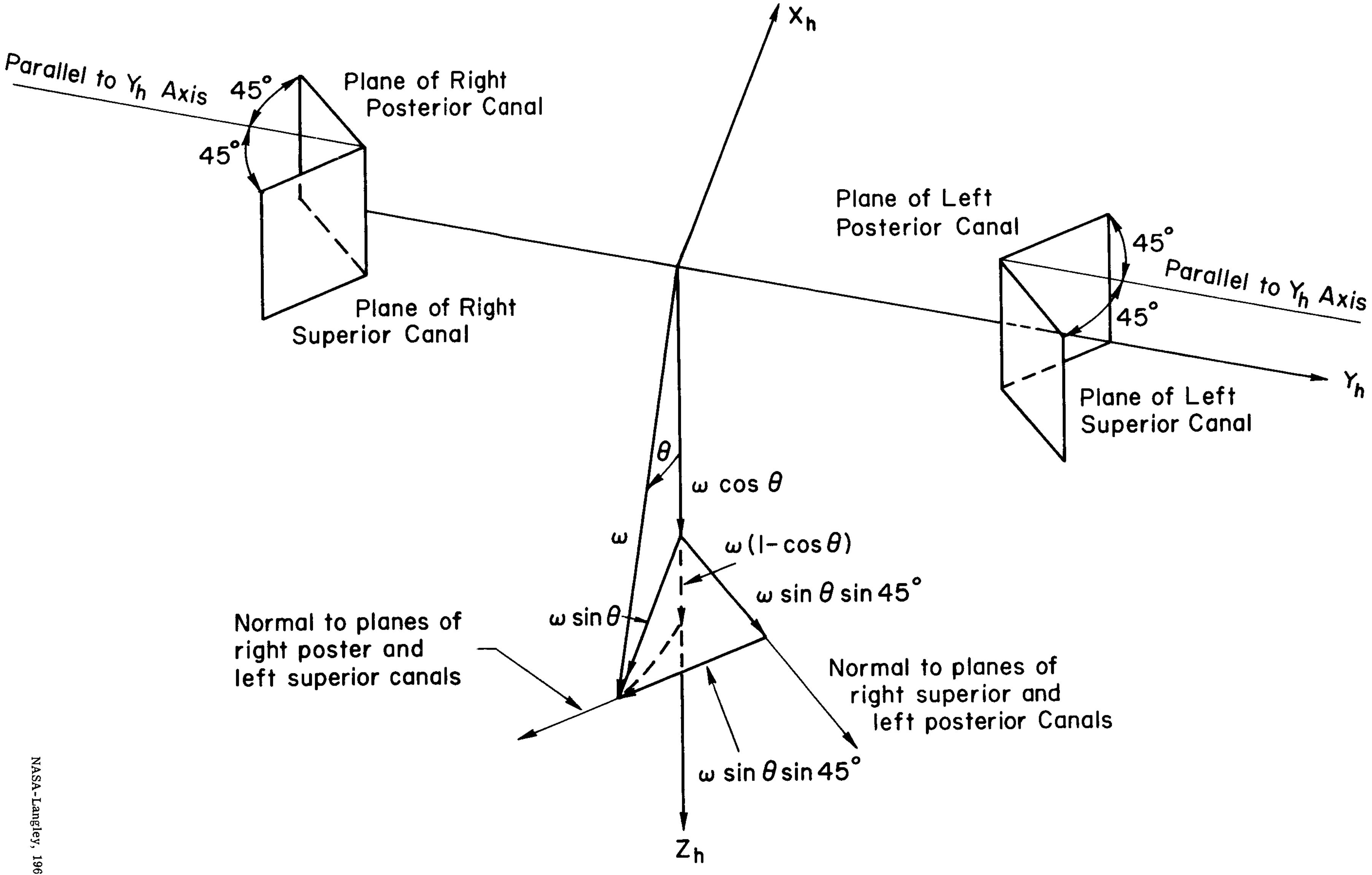


Figure A-7. Component vector analysis of a displacement of the head in pitch

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