Short Title:

VESTIBULARLY DRIVEN HEAD AND EYE MOVEMENTS

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Title: EXPERIMENTAL AND THEORETICAL INVESTIGATION OF VESTIBULARLY DRIVEN HEAD AND EYE MOVEMENTS.

ABSTRACT

This is a study of the vestibulo-ocular and vestibulo-collic reflexes, two neuromuscular control systems providing velocity stabilization of eye and head respectively, relative to space. As well as having a common role in visual image stabilization, the two systems share the same angular velocity sensor, the semicircular canal, and the responses of both are complicated by the occurrence of saccades, or quick re-positioning flicks which permit intermittent velocity stabilization (between flicks), even during movements whose amplitude exceeds the limits of eye or head excursion respectively. In the vestibulo-collic system further complexity arises because of direct mechanical feedback of the canal signal. Detailed study of these interrelated dynamic systems requires mathematical analysis, with careful consideration of possible dynamic properties of system components.

Accordingly, three major themes are developed, all to some extent based on control theoretical principles, i.e. critical analysis of previous work, theoretical studies, and experimental investigations.

1. Previous anatomical and physiological investigations of relevant system components are examined in some detail with emphasis on their potential contributions as parts of a dynamic system.

2. Vestibulo-ocular and vestibulo-collic systems are examined theoretically as control systems. In the case of the former, for which a working mathematical model exists, the work described (a) has demonstrated some further implications of this model, and (b), using a modified model, has shown that observed irregularities in saccade amplitude and frequency are very probably strategically determined to optimize performance. In the

latter case, the vestibulo-collic system, theoretical analysis clarifies the nature of the system, yields predictions as to system performance (experimentally confirmed in a later section), and suggests specific experimental approaches.

3. Study of vestibulo-collic system response in man has demonstrated that significant that significant nystagmoid head stabilization can occur. In the pigeon, functional characteristics of closed loop vestibulo-collic response have been studied quantitatively and summarized mathematically; the level of arousal, presumably affecting loop gain, emerges as a major determinant of system response. Vestibulo-ocular response in pigeons has been examined as a means of estimating dynamic properties of the semicircular canal, and to this end a new method of analyzing this reflex response has been developed. In the pigeon, the vestibulo-collic system shows considerably better low frequency performance than the vestibulo-ocular system.

EXPERIMENTAL AND THEORETICAL INVESTIGATION OF VESTIBULARLY-DRIVEN HEAD AND EYE MOVEMENT

Experimental and Theoretical Investigation of Vestibularly-Driven Head and Eye Movement

by

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CHAPTER 1

INTRODUCTION

The vertebrate organism has evolved a powerful set of interlocking hierarchical control mechanisms for stabilization of the visual image on the retina of the eye. Major sources of afferent information for these reflex controls are visual, vestibular and kinaesthetic, the latter referring primarily to information arising in muscle and joint receptors. On the efferent side of the reflex arc, visual stabilization is achieved through compensatory and tracking movements of the eyes and head, and to a lesser extent through adjustments of body position and posture. The subsystems involved in control of these three effector platforms are closely related, utilizing sensory information arising in many cases from the same sources, and sharing many neural transmission and processing facilities. In addition these systems are all to some extent concerned in posture and in the subjective awareness of body orientation and of the disposition of body parts, a fact which further emphasizes their close functional relationships with one another.

The principal theme of this thesis is the role of semicircular canal information in the stabilization of the head and eyes during body rotation in the horizontal plane. In order to obtain an overall perspective, it is appropriate to consider briefly the major reflex systems involved in head and eye movement, and their role in the larger question of postural control. These considerations are largely confined to systems active during rotation in the horizontal plane, mainly because rotation in any other plane complicates the issue by introducing additional influences due to rotation of the gravitational vector relative to the head.

Reflex tracking movements of the head and eyes may result from visual stimulation alone, the well-known optokinetic or "train" nystagmus being a particular manifestation of these reflexes. Head movement control under these circumstances has not been extensively studied, but ocular tracking has received considerable attention. Young (1962) and others have suggested that purely visual tracking depends on position and velocity information derived from the visual input, with corrections applied to the eye's tracking velocity and position at discrete intervals of time, in addition to continuous velocity correction. However there appears to be velocity saturation, so that the maximum target velocity which the human eye will track under visual control alone is considerably less than the maximum velocity of the tracking eye movements which occur in response to vestibular stimulation. Moreover tracking fails for inputs having frequency components in excess of about one cycle per second.

Information from both linear and angular labyrinthine motion sensors is involved in the vestibular control of eye movement. In the better-known rotational case, significant eye stabilization relative to space is achieved, even in the absence of vision, by the "vestibulo-ocular system", which produces compensatory eye movement whose velocity is approximately proportional to the canal signal, itself closely related to head angular velocity under normal circumstances. This system provides stabilization at higher input frequencies than does the visual tracking system, and is clearly of considerable importance during rapid head movements, as in running over rough terrain, or during travel in some man-made vehicles; for example, low-level flight at high speed in turbulent air, or land vehicles moving over rough terrain. However there is apparently little correction for errors in the semicircular canal signal such as occur during rotation with slowly changing angular velocity. The loss of visual acuity in these circumstances is some times very disturbing to man when he exposes himself to motions which fall outside the normal physiological range of operation of this system, as frequently occurs for example during normal rotational manoeuvers in flight and space, or during underwater activities.

Vestibular stabilization of the head is known to be important in birds and small animals, and is potentially significant in any animal having efficient vestibular sensors and a suitably mobile head. The possible functional difference between this mode of visual-image stabilization and that achieved through the vestibulo-ocular system is considerable and has not previously been considered in detail. Considering again only the horizontal rotation case, it is apparent that eye movement must slavishly follow the canal signal, whereas head movement modifies it, compensatory head movement tending to null the canal signal which produced it. Such direct mechanical feedback could theoretically result in a radical difference between the dynamic behaviour of this system and that of the vestibulo-ocular system, despite the fact that both utilize the same sensor, the semicircular canal. In particular there exist the possibilities of greater precision and a wider frequency range of efficient operation. In addition, of course, the introduction of compensatory head movement reduces the required excursion and speed of eye movements, a fact which may be important in bringing the velocity of eye movement within the range in which the visual tracking system can operate effectively.

There are a number of subsidiary mechanisms which affect the operation of the three major systems already mentioned. These include orienting responses to auditory and tactile stimuli, and reflexes based on information from muscles and joints, the latter being of particular interest in the present context. Proprioceptive reflexes originating in the neck muscles are well known to have significant effects on eye movement and probably play an important role in head stabilization. In any detailed study of combined head and eye stabilization it would be necessary to consider the interrelated effects of such reflexes originating in eye muscles as well as neck muscles.

Vestibular stabilization of the head obviously has a primary postural function in addition to its role in visual image stabilization. Man and higher vertebrates appear to rely heavily on vision as an information source for postural control, but the use of visual information for this purpose requires accurate assessment of the disposition of the body and its parts. Such assessment may be made on the basis of information from muscle and joint receptors, supplemented by those sensations of touch and pressure which can be related to the direction of gravity. In precisely the same way, vestibular information about angular and linear head movement probably contributes also to the assessment of body motion and position. However for this assessment to be related to surroundings fixed in space, some sort of reference must be provided, such as vision or a relatively stationary gravitational field. The problem of distinguishing linear translational movements of the head (and body) from changes in the orientation of the head with respect to the gravitational field is considerable in the absence of other sensory information, although Mayne (1969) has recently suggested specific ways in which this could be achieved using information from linear and angular motion sensors only. Alternatively, angular stabilization of the head relative to space, which is potentially realizeable through semicircular canal mechanisms, could in principle provide a model of the fixed inertial coordinate system and thus obviate the need for other references, at least for short intervals. This is of course the principle of the gyro-stabilized platform in inertial guidance systems, and it is tempting to speculate that the evolution of particularly efficient vestibular head stabilization in avian species may have been influenced by special navigational requirements in the airborne environment.

In this thesis, vestibular head stabilization and vestibular eye stabilization during horizontal plane rotation are regarded as functions of two semi-independent neuro-muscular control systems, here called the vestibulo-collic and vestibulo-ocular system respectively. The investigation, both experimental and theoretical, of these dynamic systems draws heavily on the philosophy and methodology of control systems theory. Experimental studies to be described are largely concerned with vestibular stabilization of the head in pigeons and man, a topic which has received little previous attention, but which is of considerable practical and theoretical interest. Dynamic response characteristics of the pigeon vestibulo-ocular system have also been examined experimentally, for the first time. Theoretical studies are concerned with both vestibulo-collic and vestibulo-ocular systems, but particularly the latter.

In the course of these theoretical studies, which tend to encourage careful evaluation of the various components in the systems involved, it has become apparent that while there exists in the vestibular afferent pathway considerable potential for information processing, few attempts have been made to characterize the nature of such processing. Precise dynamic understanding of these processes is naturally of great significance for any attempts at detailed modelling of visual and postural stabilization systems, particularly if such modelling is to be sufficiently realistic to seriously advance our understanding of the nature of neural control structure and form a firm theoretical basis for rational medical diagnosis and treatment. Consequently in the review of current knowledge of the vestibular sensory system which forms the first main portion of this thesis, careful attention is given to the potential for information processing which exists at each stage of the afferent pathway.

The thesis is divided into three main parts, whose content may be roughly summarized as Historical, Theoretical and Experimental. In Part I there is first an outline of the anatomy of the labyrinth and the microscopic anatomy and physiology of the sensory epithelia (Chapter 2). Next, in Chapter 3, the functional characteristics of the semicircular canals are reviewed. Theories of the hydromechanical operation of the canals are followed from their infancy in the late nineteenth century to the emergence of the overdamped second-order "torsion pendulum" model, and the more recent detailed examinations of the validity of this widely-used approximation. The problem of estimating the dynamic parameters of the canal model is considered in some detail, since the approximate nature of some of the methods in common use, and of the model itself, must be taken into account in evaluating vestibular reflex systems. The vestibular afferent pathway is the topic of Chapter 4, in which, as mentioned above, emphasis is placed upon the potential for information processing in this sensory path. Commonly held assumptions about semicircular canal thresholds are re-examined, a recent model for adaptation effects is considered, and a possible mechanism for low-pass filtering of canal information in the vestibular nuclei is proposed for the first time.

Part II is an account of theoretical studies in the vestibulo-ocular system, and contains two chapters. Chapter 5 begins with a detailed description of the mathematical model of this system proposed by Sugie and Jones (1966), but contains in addition new analytical results which offer possible explanations for some previously unexplained phenomena, and suggest several avenues for future investigation. In Chapter 6 an account is given of a collaborative theoretical study, involving Mr. U. Wettstein and the author, of the optimal occurrence-times and amplitudes of the saccadic flicks of eye position which are so characteristic of the vestibulo-ocular response. The results of this study, which is based on a modified version of the Sugie-Jones model, suggest that observed variations in saccade amplitude and inter-saccadic interval are very nearly optimal from the point of view of minimizing the velocity of retinal image slip.

Experimental investigations of vestibulo-collic and vestibulo-ocular responses in pigeons and man are the principal topics of Part III, but the first chapter of this part, Chapter 7, is devoted to consideration of historical, anatomical and theoretical aspects of the vestibulo-collic system. Chapter 8 describes experimental apparatus and methods, including a highly satisfactory electromagnetic method for recording angular head movement. Human experiments described in Chapter 9 have shown for the first time that vestibularly-driven nystagmoid head movements occur in man, and suggest that the vestibulo-collic reflex may have a significant role in visual image stabilization despite the large mass of the human head. More detailed studies of the vestibulo-collic system, using pigeons, are described in Chapter 10. From these experiments, variations in slow-phase head velocity recorded in response to sinusoidal and step changes in table angular velocity, have been analyzed to provide for the first time a quantitative description of the functional characteristics of the head stabilization system. Chapter 11 describes experiments in which the dynamic response characteristics of the pigeon vestibulo-ocular system have been evaluated for the first time, yielding a new and more realistic estimate of the long time constant of the pigeon semicircular canal. A new method of evaluating vestibulo-ocular response, based on the Sugie-Jones model, is also described. Responses of the vestibulo-ocular and vestibulo-collic systems in the pigeon are shown to be qualitatively and quantitatively different, as expected on theoretical grounds, but saccadic (quick-phase) mechanisms in the two systems appear to be closely related.

Results of these experimental and theoretical studies are summarized in Chapter 12.

PART I

THE VESTIBULAR SENSORY SYSTEM

CHAPTER 2

ANATOMY AND PHYSIOLOGY OF THE LABYRINTHINE RECEPTORS

2.1 GROSS ANATOMY

The vestibular receptors are located within the bony labyrinth of the middle ear and represent the phylogenetically older portion of the labyrinthine complex. The bony labyrinth is a system of cavities and canals in the petrous portion of each temporal bone, consisting of three parts, vestibule, semicircular canals and cochlea. It contains a clear fluid, the perilymph, which serves in part to support the membranous labyrinth lying within it. The vestibular receptors are contained in the vestibule and the connecting semicircular canals. In contrast to the cochlea, the vestibular portion of the labyrinth is remarkably similar in its basic structure in nearly all vertebrates. Hence the mammalian labyrinth will be described and minor differences in other species will be mentioned as necessary. Descriptions of the bony anatomy are taken largely from Johnston, Davies and Davies (1958).

The bony labyrinth consists of denser bone than that surrounding it and hence may be dissected out intact. This is particularly true in birds in which the surrounding bone is extensively aerated. The vestibule is a relatively large bony cavity containing the utricule and saccule of the membranous labyrinth. The three semicircular canals make connection with it posteriorly and the cochlea anteriorly. Inferiorly the aqueduct of the vestibule, carrying the endolymphatic duct, extends to the posterior surface of the petrous temporal bone.

The so-called semicircular canals in fact each describe about two thirds of a circle in man, and more or less in other species. Each canal lies roughly in one plane, the three planes on each side of the head being approximately orthogonal. The two lateral or horizontal semicircular canals are approximately in the same plane, tilted backwards in man about 30° from the classical anatomical horizontal plane of the skull. It seems probable that in most species the plane of the horizontal canals corresponds to the plane which is normal to the earth's gravitational vector when the head is in the posture usual for locomotion in the particular species (de Beer, 1947). The two vertical canals on each side lie in diagonal planes approximately at right angles to each other and to the horizontal canal, so that the plane of the anterior vertical canal on one side is parallel to the plane of the posterior vertical canal on the other (Fig . 2-1).

At one end of each canal is a dilation or ampulla, which is approximately twice the diameter of the bony canal itself. The ampullae of the horizontal and anterior vertical canals are at the anterior ends of these canals and are situated close together, where they communicate with the superior end of the utricle. The ampulla of the posterior canal is inferior and posterior, where this canal communicates with the lower end of the utricle. The two vertical canals on each side of the head join posteriorly to make a common communication with the vestibule, while the posterior end of the horizontal canal makes a separate communication.

The membranous labyrinth (Gray, 1907; de Burlet, 1920; Johnston et al., 1958; Ades & Engström, 1965; Spoendlin, 1965; Engström, Lindeman & Ades, 1966; Igarashi, 1966) is considerably smaller than the bony labyrinth, and consists of the sac-like utricle and saccule lying within the vestibule, the three membranous canals (semicircular ducts) and the cochlear duct. All parts of the membranous labyrinth contain endolymph and are in communication with each other. The space between bony wall and membranous labyrinth is in part occupied by perilymph, and in part by trabeculae of connective tissue. The membranous canals are particularly well supported, being closely adherent on their outer curvature to the bony canal (Engström, Lindeman & Ades, 1966). Utricle and saccule are anchored to the bone in the regions of their respective maculae (de Burlet, 1920; Engström et al., 1966).

The utricle is the larger of the two vestibular sacs and occupies the upper posterior part of the vestibule, where it communicates with the three membranous canals. Its upper anterior wall forms a pouch lying in a bony recess and carrying on its anterior wall and floor (Spoendlin, 1965) the sensory epithelium of the utricular macula. Lower down on the anterior wall of the utricle a fine canal leads to the endolymphatic duct and the saccule. The saccule also lies in a bony recess and on its lateral wall (Spoendlin, 1965) is found another small patch of sensory epithelium, the saccular macula. From the lower part of the saccule a fine connection passes

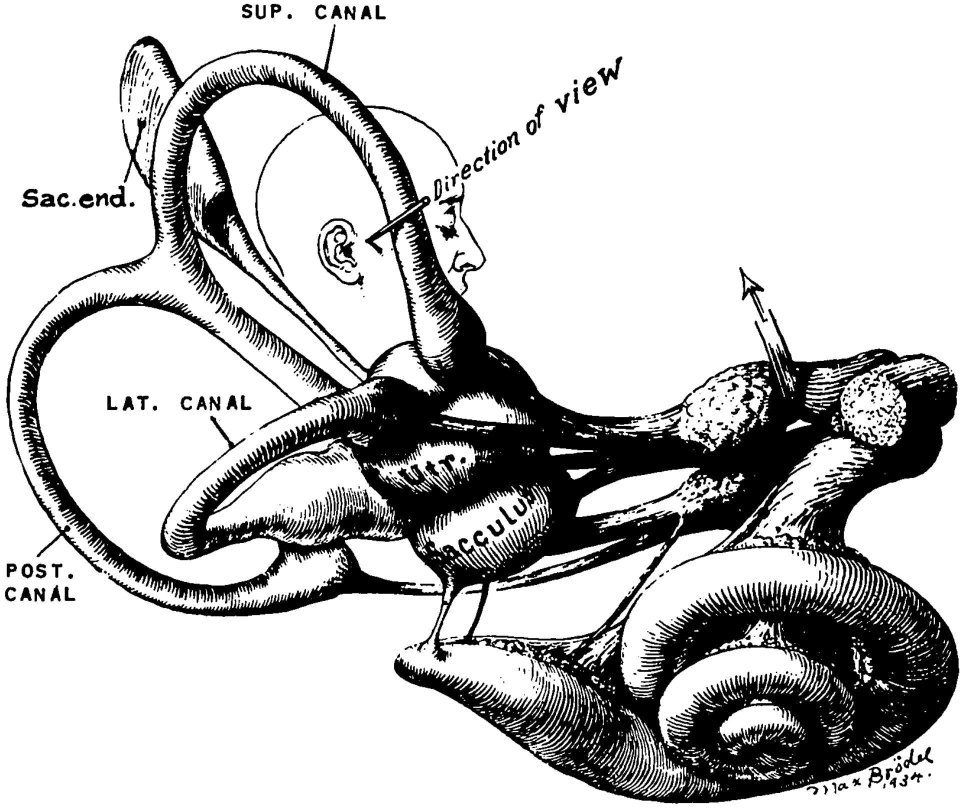


Fig. 2-1 SEMI-DIAGRAMATIC DRAWING OF THE HUMAN VESTIBULAR APPARATUS (From M. Hardy, Anat. Rec., 59:412, 1934

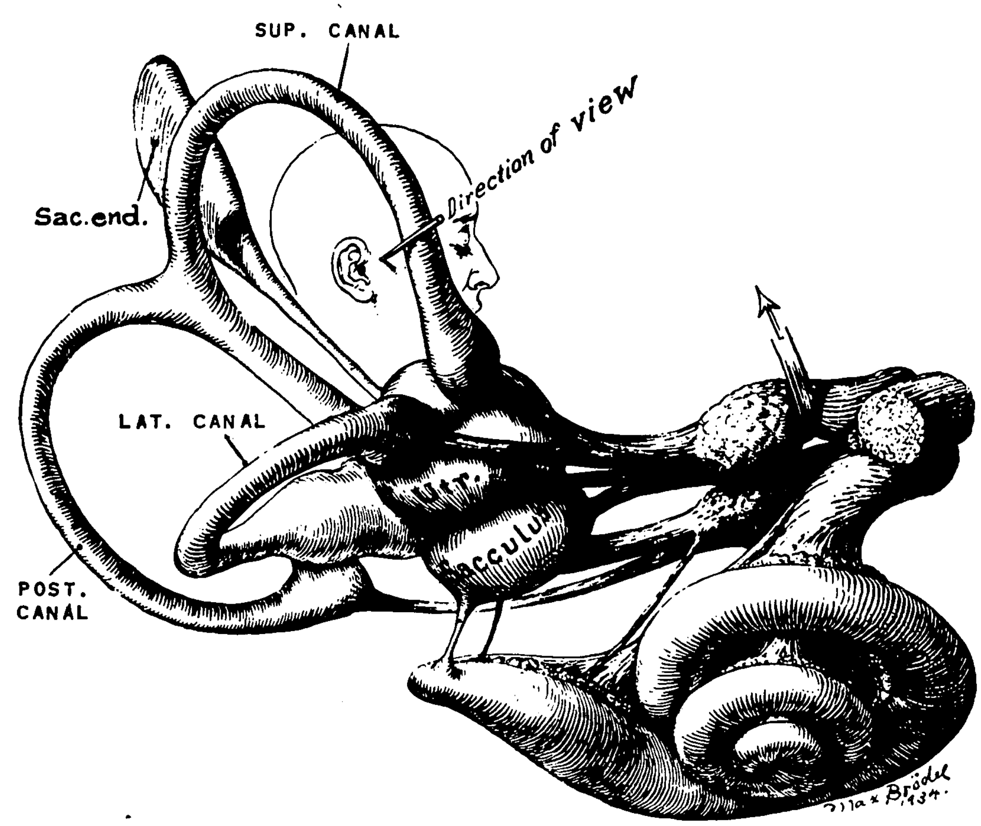


Fig. 2-1 SEMI-DIAGRAMATIC DRAWING OF THE HUMAN VESTIBULAR APPARATUS (From M. Hardy, Anat. Rec., 59:412, 1934

down to join the cochlear duct.

The sensory epithelium of the vestibular portion of the labyrinth is found in the three ampullae of the semicircular canals and in the maculae of the utricle and saccule, and is similar in all locations to the epithelium of the lateral-line organ of fish, which appears to be the evolutionary forerunner of the labyrinth system. The epithelium is supplied by the posterior or vestibular division of the eighth cranial nerve. The nerve cells are bipolar with cell bodies in Scarpa's ganglion, which lies on the trunk of the nerve in the internal auditory meatus. Distally the nerve splits into seven branches, one to the ampulla of each semicircular canal, one to the utricle, two to the saccule and one to the cochlea. The saccule also receives a small nerve from the cochlear division.

The specialized sensory epithelium consists in each case of a patch of columnar cells with cilia projecting into a mass of gelatinous material lying in the endolymphatic cavity over the surface of the epithelium. In the semicircular canals the epithelium is thrown into a transverse crest, the crista ampullaris, lying across the ampullary dilation away from the center of curvature of the canal. The gelatinous cupula is usually described as a flap extending from the crest and sides of the crista to the uniformly curved opposing wall of the ampulla. Dohlman's observations (1961, 1967) suggest that in life the cupula is much broader and more rounded in cross section than it is usually depicted. It is of homogeneous gelatinous structure containing fine canals into which protrude the sensory hairs, which may extend almost to the top of the cupula (Dohlman, 1961). Steinhausen (1927) and Dohlman (1935) have shown that the cupula forms a water-tight barrier across the ampulla, and can be made to move by changing the pressure in the endolymph on one side.

The macular epithelium of utricle and saccule is also curved, and each macula is covered by a fibrillo-gelatinous mass of quite distinctive structure (Johnson & Hawkins, 1967). Relatively few macular sensory hairs project far into the substance of the respective otolithic membrane, which consists according to these authors of a gelatinous ground substance containing a fine branching fibrillar network, carrying on its surface an accumulation of calcareous crystals. It seems clear that the otolithic receptors respond to linear acceleration, being sensitive to tangential shearing forces (Trincker, 1957-62) because the calcareous otoconia are more dense than the surrounding endolymph.

2.2 MICROSCOPIC ANATOMY OF THE SENSORY EPITHELIA

The microscopic anatomy of the vestibular sensory epithelium has recently been under intensive study (Wersäll, 1956; Flock, 1964; Lowenstein, Osborn & Wersäll, 1964; Ades & Engström, 1965; Engström, Lindeman & Ades, 1966; Wersäll & Lundquist, 1966; Spoendlin, 1965, 1966). The sensory areas of maculae and ampullae are composed of columnar hair cells, which are the mechano-neural transducers, and supporting cells. In fish and frogs the hair cells are all simple cylindrical cells innervated by myelinated nerve fibers making connection at the base of the hair cells (Lowenstein, Osborn & Wersäll, 1964). In mammals and birds there are two types of hair cell (Wersäll, 1956). Type I hair cells are flask-shaped, and surrounded by nerve terminals in the form of a chalice, while Type II cells are cylindrical with a rounded base to which small nerve endings make contact.

On the cell surface there are two types of hair processes, each cell having one kinocilium located at the periphery of the hair bundle, and 60 - 100 stereocilia. The latter are arranged in a regular pattern and are graded in height, the longest being on the side of the cell nearest the kinocilium and the shortest away from it. In each of the cristae the kinocilia of the sensory cells are almost all oriented the same direction. In the crista of the horizontal canal the kinocilia all face the utricle, whereas in the vertical canals the hair cells all have kinocilia facing away from the utricle (Lowenstein & Wersäll, 1959). This morphological polarization of the sensory cells may have important functional significance since, as these authors point out, the different orientation of kinocilia in horizontal and vertical canals corresponds to the direction of cupula deflection which produces increased frequency of firing in the ampullary nerves. Cupula deflection towards the utricle ("utriculopetal") excites the receptors of the horizontal canals, and "utriculofugal" deflection excites in the vertical canals. In both cases the excitatory deflection is one in which the hair processes are deflected towards the side of the cell which bears the kinocilium.

The Type I sensory cell makes very close contact with its nerve chalice at several locations, and it seems possible that neural transmission at these junctions may be electrical (Spoendlin, 1966). At the Type II sensory cells there are two types of small nerve ending making direct contact. A sparsely granulated type of ending similar in appearance to the nerve chalice surrounding the Type I sensory cell is most numerous, and is thought to represent the afferent nerve terminal. A second type of ending is filled with vesicles and is presumed to be an efferent presynaptic terminal. A few of these vesiculated endings are also seen in association with Type I sensory cells but in this situation they make contact not with the sensory cell itself, but with the outer surface of the chalice-like structure of the afferent nerve terminal. The more common arrangement of the sensory cells and nerve terminals is seen in Fig. 2-2, taken from the publication by Ades and Engström (1965).

2.3 MECHANO-NEURAL TRANSDUCTION IN LABYRINTHINE RECEPTORS

Modern theories of the operation of the labyrinthine receptors, including the cochlea, depend on the assumption that the nervous impulse is somehow generated by deflection of the hair processes of the sensory cells as a result of movement of the overlying gelatinous mass, cupula, otolithic membrane or tectorial membrane as the case may be, and much intensive study has been devoted to finding out how this comes about. Before going into this problem it is necessary to review briefly what is known of the neurophysiology of the receptor cells. The subject has been reviewed by Trincker (1962).

As in other mechanoreceptor cells, various potentials may be recorded from the labyrinthine sensory cells. The first to be observed was the cochlear microphonic or "Wever-Bray effect" recorded by these authors in 1930. This was originally described as an alternating potential of low amplitude produced at the hair-bearing surface of the sensory cells in response to sound stimulation and at the same frequency. Von Bekesy (1951) has shown that the cochlear microphonic is a function

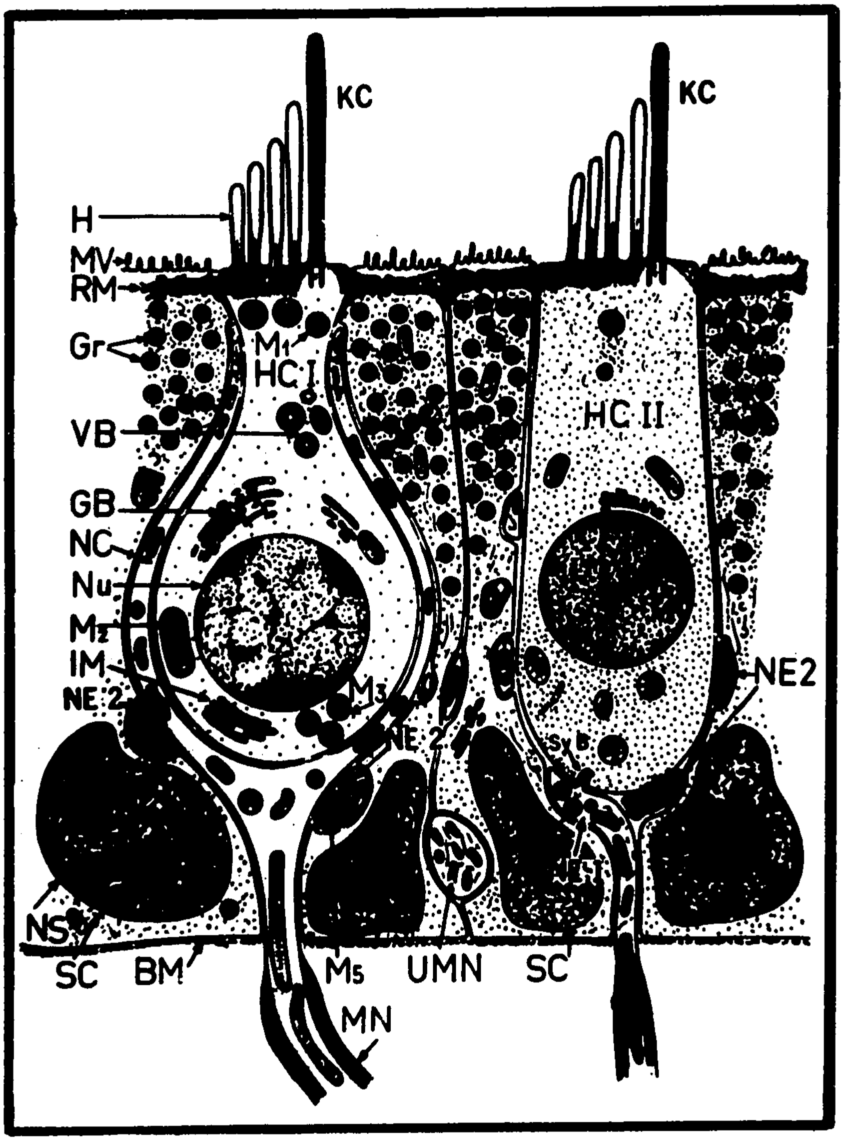
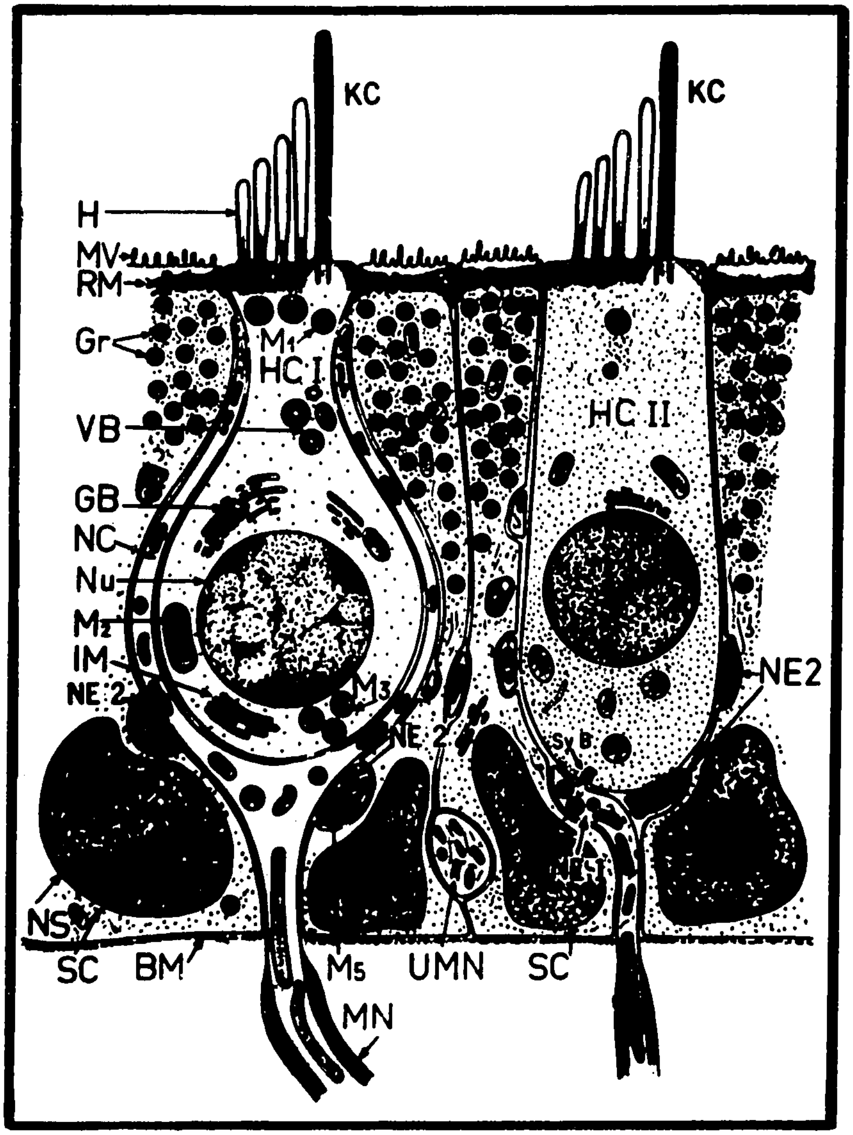


Fig. 2 - 2 DRAWING OF TWO TYPES OF VESTIBULAR SENSORY CELLS (from Ades & Engstrom, 1965)

HC I, HC II - sensory cells, types I and II; NC - nerve calyx around type I cell; NE2 - granulated nerve endings (probably efferent); NE1 - sparsely granulated nerve endings (probably afferent); H - stereocilium; KC - kinocilium.



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of the displacement of the tectorial membrane and is maintained steady during steady displacements. Associated with the cochlear microphonic is the "Summating Potential", a steady potential across the hair cells (endolymph negative) which occurs during moderate to strong acoustical stimulation. This potential also seems derived from the hair cells and may be a result of some sort of mechanical rectification process (Davis, 1960). Finally in addition to the action potential and the DC polarization of the interior of the hair cells there is a steady DC potential in the endolymph of about 80 mv. positive relative to the perilymph. This potential appears to arise in part from secretory cells in the stria vascularis of the cochlea (Davis, 1960).

The situation in the vestibular receptors of the labyrinth has obvious parallels with the situation in the cochlea although precise relationships are not clear. As in the case of the cochlea the generator potential was first observed in the form of "microphonics", i.e., alternating potentials in response to a rapidly oscillating stimulus (Ashcroft & Hallpike, 1934). In the otolith organs such microphonics can be produced by mechanical vibration (Ashcroft & Hallpike, 1934), and in the cristae of the semicircular canals by sound (Tullio & Storti, 1938). In the latter case it is necessary to provide a fistula in the bony wall of the canal to permit the fluid vibrations set up at the oval window to reach the cristae. Ampullary microphonics were recorded by several investigators in a number of different experimental animals (de Vries & Bleeker, 1949; van Eyck, 1949; Trincker & Partsch, 1957), and appeared to have the same characteristics as cochlear microphonics including the absence of latency, refractoriness and fatigue. Trincker and Partsch (1959) found that ampullary microphonics could reach frequencies of 120,000 Hz.

Trincker (1957, 1959) subsequently recorded a DC potential in the canal endolymph, positive with respect to the perilymph. He found a potential of about 120 mv. across the hair cell layer which could be varied by manoeuvers producing cupula deflection. Utriculopetal deflection in the horizontal canal and utriculofugal deflection in the anterior vertical canal produced greater negativity within the crista, and deflection in the opposite direction reduced negativity. The curve relating potential to cupular deflection is sigmoid (Fig. 2-3) but the plateau in the excitatory direction is higher than in the inhibitory direction. The measured potential changes appear large compared to the microphonics, which are of the order of 100 microvolts in amplitude. However, Trincker used large cupula deflections (± 60°) in these experiments and there is evidence to suggest that in the normal operation of the semicircular canals the actual cupula deflections are much smaller (see below). Trincker (1959a, 1961) has also recorded DC potentials from the utricular macula, which vary with artificial tangential movement of the otolithic membrane in both directions.

The precise mechanism of hair cell stimulation remains a highly controversial question and much remains to be elucidated. According to an early hypothesis, rejected by most authors, hair cell distortion produced a potential by a piezoelectric mechanism. Davis (1957) suggested for the cochlea that the hair cell membrane might act as an electrical resistance varying with deformation. Current flow due to the potential across the membrane would thus vary with the bending or shearing of the hairs.

Dohlman (1960) argued against current flow as the origin of the potential on the grounds that (a) the microphonic shows no latency, refractoriness or fatigue, and (b) endolymph is similar in composition to intracellular fluid and contains a high concentration of potassium (Smith, Lowry & Wu, 1954; Citron, Exley & Hallpike, 1956; Rauch & Koestlin, 1958). With the endolymph 120-150 mv. positive with respect to the anterior of the cell, and a large ciliated cell surface in contact with endolymph, the cell would be flooded with potassium if the membrane were permeable. He therefore suggested that the hair bearing membrane is impermeable and functions as the dielectric in a capacitor with static charge built up on either side. Such a charge might explain the apparent stiffness of the cilia in the living preparation, compared to their limp appearance after death. He suggested that the resting endolymph potential is produced by the polarization of active secretory areas, the stria vascularis in the cochlea and in the vestibular system the planum semilunatum. This is an area on the side of the crista which shows a rapid secretion of sulfated

AMPULLARY POTENTIAL

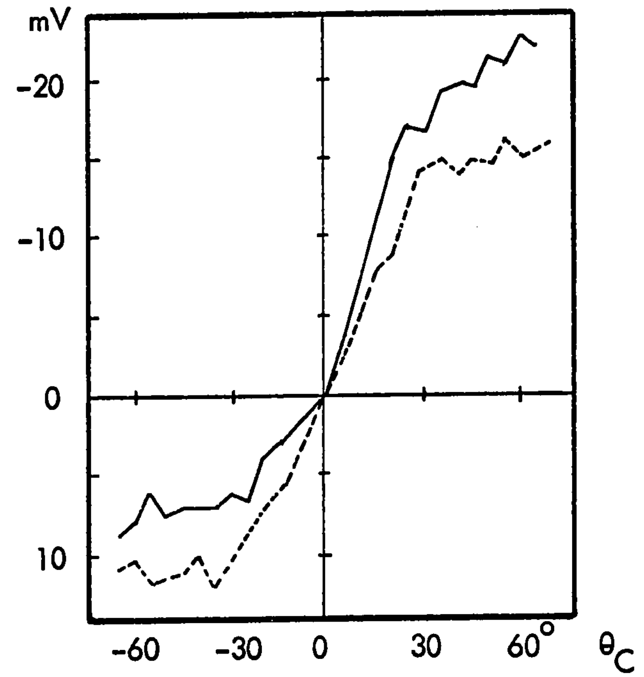


Fig. 2-3 CHANGES IN DC POTENTIAL IN THE CRISTA AMPULLARIS DUE TO STATIC CUPULAR DEFLECTIONS IN THE GUINEA PIG (From Trincker, 1962)

Potentials recorded inside the hair-cell layer of the horizontal semicircular canal. Utriculo-petal deflections positive.

mucopolysaccharides (Dohlman & Ormerod, 1960) which are taken up by cupula and endolymph. Vilstrum and Jenssen (1961) showed in vitro that movement of such mucopolysaccharide substances produced "displacement potentials" in the axis of movement. Dohlman (1960) and Christiansen (1961) suggested that a film of polysaccharide molecules covering the cilia might be the cause of the generator potentials.

Finally, Lowenstein and Wersäll (1959) were led by the similarity of the kinocilium to motile cilia, to suggest that they might act as a "mobile cilium in reverse", a view supported by Trincker (1960) and Groen (1961). However, as Lowenstein (1966) subsequently pointed out, there are no clearly distinguishable kinocilia in the cochlear hair cells. Moreover, such a mechanism would again require some cell functions involving ionic movements and Dohlman's arguments (1960) regarding latency, refractoriness and fatigue would again apply.

2.4 EFFERENT INNERVATION OF VESTIBULAR RECEPTORS

It is now well established that there is a descending system of neurones from the auditory cortex to the cochlea (Rasmussen, 1955). At the level of the VIIIth nerve this efferent system consists mainly of the olivo-cochlear bundle extending from the contralateral olive to the cochlea, but in addition there is an uncrossed pathway from the olive (Rasmussen, 1960). The function of this system remains uncertain despite intensive investigation. Recent work, reviewed by Filigamo, Candiollo and Rossi (1967) and Fex (1967) indicates a powerful inhibitory action by efferent fibers, with crossed and uncrossed components having rather different peripheral connections and effects.

Wersäll (1956) and Engström (1958) suggested on morphological grounds that the vesiculated nerve endings seen in the vestibular sensory epithelia were efferent terminals. At about the same time Petroff (1955) observed the disappearance of a system of fine nerve fibers in these regions following eighth nerve section and following a midline incision in the floor of the fourth ventricle. In 1958 Dohlman, Farkashidy and Salonna demonstrated acetycholinesterase activity in the sensory epithelium and this activity was subsequently found to disappear following section of the VIIIth nerve (Ireland & Farkashidy, 1961). Rasmussen and Gacek (1958) and Gacek (1960a) reported anatomical investigations demonstrating the existence of a myelinated efferent vestibular pathway with fibers extending into the five vestibular sensory areas (three cristae and two maculae), but they were only able to follow them as far as the basement membrane of the neural epithelium. In contrast to Petroff they found no crossed fibers, and felt that the fibers originated from the homolateral lateral vestibular nucleus. Rossi (1964) and Rossi and Cortesina (1965) described three efferent pathways, all uncrossed, originating from the lateral vestibular nucleus, from a small adjacent group of cells, and from the pontine and bulbar reticular formation near the midline. Carpenter (1960) however reported investigations indicating that uncrossed efferent fibers originate mainly in the medial and superior vestibular nuclei, and that in addition there are efferent vestibular fibers, mainly crossed, arising in the fastigial nuclei. Recently Llinas, Precht and Kitae (1967a, 1967b) have demonstrated a direct monosynaptic projection from Purkinje cells in the auricular lobe of the frog cerebellar cortex to the vestibular sensory epithelium, in addition to monosynaptic and disynaptic connections from the sensory epithelium to the Purkinje cells.

Little is known about the precise mode of termination of cerebellar and other vestibular efferent fibers. Gacek (1960b) reported that the VIIIth nerve in the cat contains about 12,000 vestibular fibers but only about 200 efferent fibers. Engström, Lindeman and Ades (1966) have pointed out that the number of vesiculated efferent nerve terminals in the vestibular epithelia is far greater than 200. They suggest that some of the efferent terminals may originate as branches of afferent fibers feeding back to the sensory cells.

Physiological investigation of the efferent systems has been sparse. Schmidt (1963) recorded in the proximal ends of cut ampullary and macular nerves. He found no resting activity but recorded action potentials on stimulating the contralateral ampullae. Sala (1962, 1963, 1965) stimulated Deiter's nucleus and recorded activity occurring after a long latency (22-32 msec.) in the vestibular portion of the contralateral VIIIth nerve. He also studied the effects on the DC potential in the crista ampullaris, and found that caloric stimulation of one ear produced depolarization in the ipsilateral crista and hyperpolarization contralaterally. Electrical stimulation in the region of Dieter's nucleus produced hyperpolarization bilaterally.

These findings suggest an inhibitory function for the efferent pathway, as one might expect by comparison with other receptors and on theoretical grounds. Lowenstein (1966) has commented on the possibility of sharpening of contrast by a zone of inhibition around an area of excitation, a mechanism which seems to crop up again and again in peripheral information processing. Lowenstein (1966) has also suggested that a possible function of efferent control might be to bias a given sensory unit so as to change its operating range on its own s-shaped characteristic curve. Groen (1961) visualizes the possibility that the kinocilia are in effect motile and capable of changing their viscosity or elasticity under the influence of efferent fiber activity. Such a property might explain the apparent changes in the dynamic characteristics of the semicircular canals which sometimes seem to occur (see below).

CHAPTER 3

FUNCTIONAL CHARACTERISTICS OF THE SEMICIRCULAR CANALS

3.1 HISTORICAL DEVELOPMENT OF THEORIES OF THE OPERATION OF THE SEMICIRCULAR CANAL

The ear has been associated with the phenomenon of vertigo since the days of early Greek medicine, due presumably to the occurrence of vertigo in many pathological conditions of the ear. Around the turn of the nineteenth century, according to Camis (1930), a prominent school of throught grew up following the work of Autenrieth (1809), who believed that the canals were concerned with perception of the direction of sounds. This theory is reported by Camis to have motivated Flourens (1824) in his oft-quoted work on the effects of labyrinthectomy in pigeons. Goltz (1870) is credited with being the first to recognize that the canals were concerned with equilibrium, and felt that their prime function was to indicate the position of the head and thus aid in maintaining head posture.

In the 1870's three authors (Mach, 1875; Breuer, 1874; Crum Brown, 1874) proposed independently that the canals responded to rotational acceleration of the head, arguing that endolymph flow would occur due to the inertia of the fluid and in some way excite the hair cells. All three authors recognized that man has no true sense of uniform rotatory motion but only senses variations. They suggested that during an angular acceleration, as at the beginning of rotation, the endolymph would tend to remain at rest due to its inertia, while the skull moved around it. With continued rotation however, viscous forces would stop the relative movement and the fluid would assume the same velocity as the skull. Cessation of rotation would result in a relative movement of the fluid in the opposite sense. The slow rate of decay of sensation which occurs during and after a rotation at constant velocity was not explained except by Mach who suggested it was due to some neural phenomenon. Breuer (1874) and Stefani (1876) constructed physical models of the semi circular canals and were able to demonstrate fluid movements during angular but not linear accelerations.

Ewald (1887, 1892) appears to have been the first to demonstrate actual movements of the endolymph, achieved by artificially varying the pressure in the canals. This was followed by the work of Rossi (1915) who introduced lamp black into the horizontal canal of a shark and observed movement of the endolymph during angular accelerations. Maier and Lion in 1921 made a more detailed study of endolymph movements during natural stimulation. They used red blood cells as a contrast medium in order to detect fluid flow, and measured flow velocities of 1/2-1/20 mm/sec after stopping a prolonged rotation. However the fluid motion detected by them was only of short duration, and they were unable to explain the long duration of post-rotational nystagmus and sensation.

In 1922 the physicist Gaede was asked to clarify the situation, and presented the first-order differential equation describing to a first approximation the flow of a viscous fluid in a closed circular tube. He emphasized that in such a system a relative flow of fluid would only occur in response to angular acceleration, and that following a step change in the angular velocity of the tube, fluid flow would be of very short duration and would follow an exponential time course. He calculated that for a water-filled tube of natural dimensions the time constant would be 1/24 second. Schmaltz (1925, 1931) made a similar analysis. The results seemed to agree with the experimental impressions of most investigators.

Very shortly after this the first clear statement of the hydrodynamic theory of the canals as we now know it came from the work of Rohrer and Masuda (Rohrer, 1922; Masuda, 1922; Rohrer & Masuda, 1926). Masuda (1922) made a careful quantitative study of the duration of ocular nystagmus following various forms of rotational stimulation in guinea pigs. These authors felt that the observed phenomena were reflections of the mechanical behaviour of the cupula, which they argued must behave like a heavily damped pendulum, the cupula having a weak elastic restoring force and tending therefore to return towards its initial position after deflection by fluid movement. The return would be very slow because of the large viscous and small elastic effects.

This is precisely the current view of semicurcular canal function. To put the contribution of Rohrer and Masuda in perspective, however, it is necessary to explain the confusion existing at the time they were writing. First, owing to the well known artifact of histological fixation methods, it was believed that the cupula extended only part way across the lumen of the ampulla. This, however, was not the chief difficulty. It had been conceded by many authors since the time of Mach that the cupula might have an elastic restoring force owing to the structure of the hair processes. However, it was argued (e.g., Camis, 1930) that since the cupula had such a small mass, the action of even a small restoring force would cause it to return very rapidly to its resting position following a deflection. Rohrer pointed out that the return movement of the cupula would tend to move the endolymph as well, and this mechanical coupling between fluid and cupula would increase the effective inertia of the cupula. The undamped natural frequency of a simple pendulum is equal to the ratio of elastic to inertial forces, and thus for the cupula would be very low. Damping due to the viscosity of the endolymph would further reduce the frequency of free oscillations and with sufficient damping the response would become aperiodic.

Rohrer derived the theoretical expressions relating the duration of cupula motion following a stop to the velocity and duration of the preceding constant velocity rotation. By adjusting parameters in these expressions he was able to fit theoretical curves for both the underdamped and over damped cases to his experimental data. The parameter values obtained in this way were for the overdamped (aperiodic) case a time constant of 6.2 sec., and for the underdamped case a time constant of 12.5 sec., with a frequency of oscillation of 0.028 Hertz.

It will be noted that Rohrer did not assume that the cupula formed a water-tight barrier across the ampulla, as was shown subsequently in the work

Steinhausen (1927) and Dohlman (1935). However, this does not affect the validity of his conclusions, since he was able to show with a mechanical model that the existence of cupula leak does not significantly affect the situation unless fluid flow is so rapid as to cause turbulence, an extremely unlikely event in a system of these dimensions. These observations have subsequently been supported by theoretical considerations (Mayne, 1965; Spells, 1959).

Steinhausen (1927-39), in a series of papers, described techniques for direct visual observation of cupula motion in living animals during natural and artificial stiumulation. He showed that the cupula formed a watertight flap in the ampulla and described its slow return to its resting position following deflection caused by a brief acceleration. Dohlman (1935, 1941) made similar observations. The experiments of Ross (1936) and of Lowenstein and Sand (1940a, 1940b) who recorded the activity in single and multiple fiber preparations from the ampullary nerves, showed that the neural discharge followed approximately the same time course as that expected for the cupula.

The simple overdamped torsion pendulum model for the semicircular canals, as proposed by Rohrer and amplified by Lowenstein and Sand (1940b) and van Egmond, Groen and Jongkees (1949) is still the one generally accepted today. There have been occasional suggestions that the system is underdamped rather than overdamped, usually in an attempt to explain the phenomenon of secondary post-rotational nystagmus, though it seems more likely that this phenomenon is neural in origin. More recently there have been some more detailed studies of the hydrodynamics of the canals , and more precise models are being developed. Finally there have been suggestions that the endolymph may not behave as a fluid under normal conditions, but rather as a colloidal gel with rather anamalous viscous properties. These matters will be considered below.

3.2 IMPLICATIONS OF THE DAMPED PENDULUM MODEL

The work of Rohrer and Masuda, and of Steinhausen, showed that the dynamic response of the cupula, i.e., the time course of cupula movement in response to head rotation, could be likened to that of an overdamped torsion pendulum, such as for instance an inertial disc suspended in a viscous medium by a wire having rotational elasticity. The behaviour of such a system is well known. Thus if the head were very suddenly to start rotating with constant angular velocity, the cupula would be expected to deflect rapidly (relative to the head) and then return slowly to its resting position. Mathematically this response is described as the difference between two decaying exponentials having respectively a short and a long time constant. In a heavily overdamped system the short time constant is to a close approximation equal to the ratio of the moment of inertia to the coefficient of viscous retardation, while the long time constant is to a similar approximation equal to the ratio of the coefficient of viscous retardation to the elastic coefficient. Peak cupula deflection following such a "step change" in head angular velocity would be proportional to the velocity of head movement, the ratio of peak cupula deflection to head velocity (the sensitivity or "gain") being proportional to the short time constant.

The widely used "turning test" or "stopping stimulus" (van Egmond & Groen, 1955), is based on the fact that, according to the torsion pendulum model, if the head is rotated at constant velocity for a long time so that the cupula returns to its resting position, then when the turntable is suddenly stopped the cupula will swing out in the opposite direction following the same time course as that described above. Ideally, in order to obtain the simple two-exponential time course of response, the onset and offset of rotation should be instantaneous, although in practice such an ideal stimulus is very difficult to approximate. However, the time course of the slow decay of the cupula to zero is affected relatively little by the acceleration profile used to attain a given constant velocity, so that the turning test is quite adequte for determining the long time constant.

It is misleading however to think of canal function exclusively in terms of the response to a turning test, which in fact tends to overemphasize errors in the cupula response. Normal head movements tend to consist of short unidirectional displacements, in which the profile of head velocity may be approximated by short pulses. In such circumstances the cupular elasticity does not have time to produce appreciable response decay, and the resulting canal signal gives a good running indication of head angular velocity, a fact which has been pointed out by a number of authors (Mowrer, 1932; van Egmond et al., 1949; Mayne, 1950; Jones & Milsum, 1965).

Mayne (1950, 1965b) and Jones and Milsum (1965) have emphasized that in normal circumstances the canal seems to function primarily as an angular velocity transducer. Subjective sensations experienced during rotation point to this conclusion, and strong support comes from the steady state response of the canals to sinusoidal oscillation at various frequencies. The frequency response plots, consisting of graphs of the phase shift and amplitude of cupula movement ("gain") relative to the input variable may be obtained directly, or by inference from other data (see below). When gain and phase are measured relative to the angular velocity of head motion in man it is found that in the range of frequencies from about 0.1 to 5.0 cycles per second (Jones & Milsum, 1965), the gain is almost constant and the phase shift almost zero (Fig.3-2). Since most physiologically occurring head movements probably contain frequency components lying almost exclusively within this range, it would seem that in natural life the canal nearly always operates as a velocity transducer.

There is rather striking evidence that velocity transduction by the canals may have considerable significance in natural selection. It appears that the physical dimensions of the semicircular canals in different animals have been nicely adapted so that the frequency range for velocity transduction corresponds to the frequency range of head movement expected from consideration of head size and living habits (Jones & Spells, 1963; Mayne, 1965b; Jones, 1969).

3.3 PHYSICS OF THE SEMICIRCULAR CANAL

3.3.1 Physical Basis of the Torsion Pendulum Model

Theoretical analysis of semicircular canal function from the point of view of its physical structure has been attempted many times in varying detail (Mach, 1875; Gaede, 1922; Rohrer, 1922; Schmaltz, 1925; Rohrer & Masuda, 1926; Steinhausen, 1927; Lowenstein & Sand, 1940b; van Egmond, Groen & Jongkees, 1949; Groen, Lowenstein & Vendrick, 1952; Spells, 1959; Groen, 1956; Mayne, 1965a; Newman, 1966; Steer, 1967). There is little to be gained by going into a complete derivation of the relevant equations. It will be useful however to consider briefly some of the factors which must be taken into account.

Fluid inside a closed circular tube is free to move relative to the tube under the influence of inertial forces, and such motion is opposed by viscous resistance. In the semicircular canal, fluid flow is also opposed by the movable cupula which appears to form a watertight flap in the ampullary region. The cupula may be assumed to contribute elastic and presumably viscous resistance, as well as the effect of its own small inertia. Motion of the endolymph can thus be likened as a first approximation to that of a mass whose motion is constrained by a damped spring. The motion of such a mass relative to its suspension is described by a second order differential equation whose solutions are well known.

After making certain assumptions whose validity will be examined briefly below, a similar equation may be derived for the semicircular canals, describing cupula motion as a function of head motion. Consider the idealized canal shown in Fig. 3-1. The canal is assumed to be circular and of uniform cross section, and filled with a perfect fluid whose flow is laminar. Assuming that viscous and elastic retarding forces are proportional respectively to angular velocity and angular displacement of the fluid relative to the canal, and lumping all inertial components into a single term, we obtain as an expression of Newton's second law of motion,

$$J\frac{d^2\theta_F}{dt^2} = -b\frac{d}{dt}(\theta_F - \theta_H) - k(\theta_F - \theta_H) \text{ ....Eq. 3.1}$$

where

θ_F = angular displacement of fluid relative to space,

θ_H = angular displacement of head relative to space,

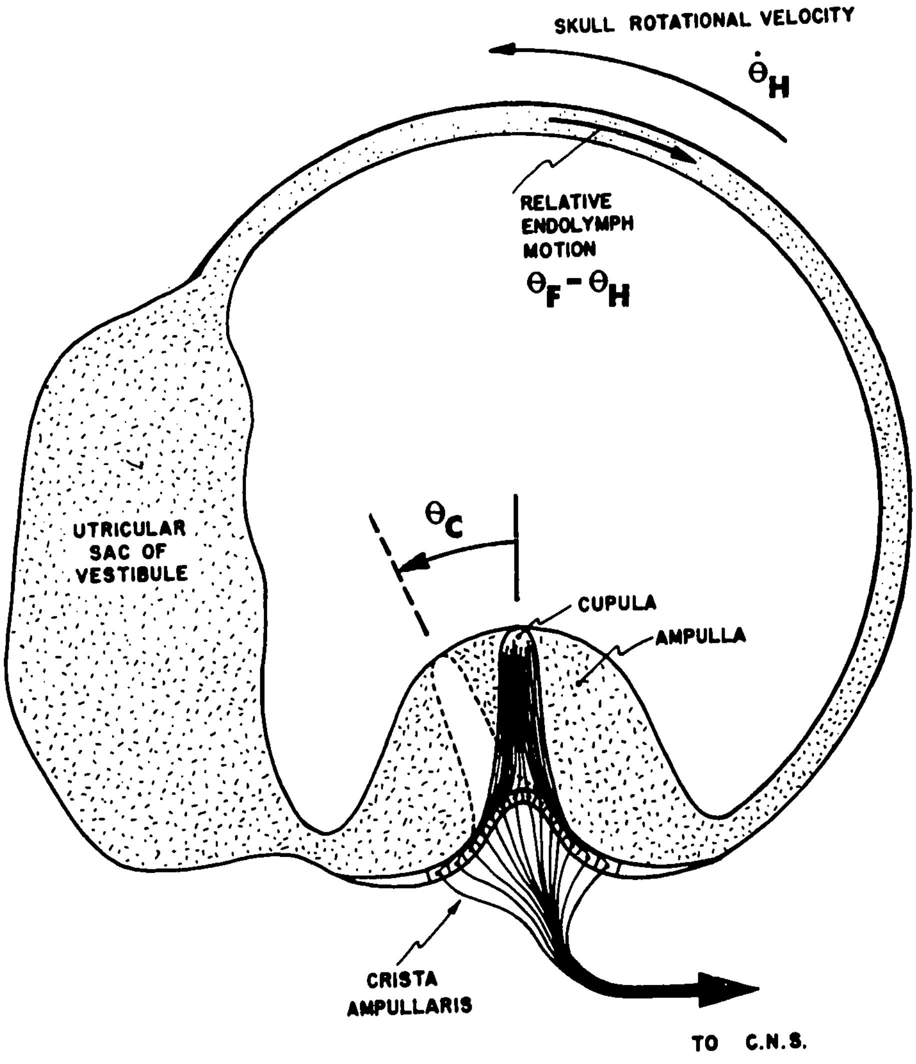


Fig. 3-1 DIAGRAMATIC REPRESENTATION OF AN IDEALIZED SEMICIRCULAR CANAL (modified from Jones and Milsum, 1969)

J = moment of inertia of the fluid ring,

b = moment of viscous retardation per unit relative angular velocity of the fluid,

k = moment of elastic retardation per unit relative angular displacement of the fluid.

Rearranging, using the dot notation for differentiation, yields

$$J(\ddot{\theta}_F - \ddot{\theta}_H) + b(\dot{\theta}_F - \dot{\theta}_H) + k(\theta_F - \theta_H) = -J\ddot{\theta}_H \ldots\ldots\ldots\ldots\ldots \text{Eq.3.2}$$

Assuming that cupula deflection, θ_C, is proportional to relative fluid movement,

$$\theta_C = -\alpha(\theta_F - \theta_H) \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \text{Eq. 3.3}$$

and hence

$$J\ddot{\theta}_C + b\dot{\theta}_C + k\theta_C = J\alpha\ddot{\theta}_H \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \text{Eq. 3.4}$$

It is informative to consider the assumptions and approximations implicit in this expression.

(i) Viscous Forces and Laminar Flow. The cross section of the semicircular canal is very small relative to its circumferential length, and hence viscous forces are large relative to inertial forces (i.e. the Reynold's number is very small). This is true even though the fluid is not very viscous, having probably a viscosity only two or three times that of water (Rossi, 1914; Money et al., 1966; Miery & Young, 1966). Fluid velocity is never great either (Steinhausen, 1927; Dohlman, 1935), and hence flow may be expected to be laminar at all times. When the fluid moves with constant velocity the flow will be parabolic; during accelerating fluid motion non-parabolic flow-profiles will occur and the effective viscous coefficient(b) will vary with time.

Theoretical studies of this latter point have reached conflicting conclusions. Newman (1966) suggests that changes in the velocity profile during accelerating fluid flow may cause significant departure from the simple model especially during certain forms of stimulation. Steer (1967) however has also studied the contribution of viscous drag of the cupula over the ampullary surface and feelsthat this term, which may not be time dependent, may dominate over viscous drag effects in the fluid itself.

(ii) Effect of the Utricle. This large region of increased and non -

uniform cross-sectional area in the closed fluid loop has a number of effects which have not always been assessed correctly. It is clear that because of the greater cross section, viscous retarding forces in this region will be negligible, a fact recognized by van Egmond et al.(1949). Thus in computing the viscous coefficient only the circumferential lengthof the narrow portion of the tube need be considered. In addition, Mayne (1965a) and Newman (1966) have pointed out that the utricular region makes no significant contribution to the effective moment of inertia of the ring, owing to the much reduced velocity in this region. The extra-utricular circumference is thus the important length parameterin calculating both J and b in Eq. 4.1. This length is usually taken as one-half or two-thirds of the circumference, though in some cases, as in the anterior canal of the pigeon, this may be an underestimate.

(iii) Non-uniform Shape of the Canal. The narrow portion of the semicircular canal does not form a uniform circular arc, nor does it always lie in one plane. These factors, as discussed by Groen (1956), affect the evaluation of b and J, and also the directional specificity of the canal. It is easy to show that, provided the non-uniformity does not significantly affect the laminar flow pattern, there will be, for the non-uniform canal, a single axis, rotation around which produces maximum fluid flow, and that the non-uniform canal will behave as a circular canal lying in the same plane.

(iv) Assumptions About the Cupula. There can be little doubt that the cupula exerts a restoring force when displaced from its rest position. Its structure supports this view, and there is direct evidence for it from microscopic observations of the cupula in motion (Steinhausen, 1927; Dohlman, 1935). It is usually assumed that the cupular restoring force is proportional to its displacement, and that the angle of cupula displacement is proportional to the angular deflection of fluid within the membranous canal. The validity of each assumption depends on the actual magnitude of cupula movement. From the observations of Dohlman (1935) in fish, it would appear that the angular excursion of the cupula was about equal to the angular excursion of endolymph within the tubular portion of the membranous canal. Van Egmond et al. (1949) state this as a general rule, and Jones and Spells (1963) came to the same conclusion from calculations based on measurements of preserved specimens and the stereo photographs of Gray (1907). The actual excursion of fluid within the canal during rotational stimulation is not completely clear from the early direct observations. Steinhausen (1933) stated that the excursion was small, and Maier and Lion (1921) observed excursions of "a few degrees" at most. The peak fluid excursion following for example a step change in head angular velocity can be calculated from the torsion pendulum model (see below) if the value of the ratio J/b is known. Using the value calculated by Mayne (1965a) for man, the angular excursion of the fluid, and presumably of the cupula, would appear to be about one degree for a 200°/sec. velocity step. The assumptions stated at the beginning of this paragraph may therefore be accepted without great reservations.

It should be mentioned finally that some recent studies have raised serious doubts about the physical basis of the classical model described above. Dohlman (1968) has suggested that the endolymph, though fluid in vitro, may exist in the membranous canal as a colloidal gel due to the presence of small amounts of mucopolysaccharides. If this is true, the physical model would have to be revised to account for the behaviour of a mesh-like ring of long, interlaced mucopolysaccharide molecules sliding around within the membranous canal. It is not clear that the behaviour of such a system would be compatible with the observed results.

3.3.2 Estimation of Canal Parameters from Physical Dimensions and Properties.

The effective moment of inertia of the endolymph (J), and the coefficient of velocity-dependent retarding torque (b), were calculated for an idealized canal by Gaede (1922), Schmaltz (1925) and van Egmond et al. (1949), assuming laminar parabolic flow. The equations abtained were

$$J = \pi \rho l_J r^2 R^2,$$

$$b = 8\pi\eta R^2 l_b;$$

where

r = internal radius of the endolymphatic canal,
R = mean radius of curvature of the canal,
η = viscosity of the endolymph,
ρ = density of the endolymph,
l_J = effective length of the canal circumference contributing to the inertial term,
l_b = effective length of the canal circumference contributing to the viscous damping term.

The coefficient of position dependent retarding torque (k), and the gain coefficient (a), were calculated by Jones and Spells (1963) to be

$$k = \mu \pi r^2 R,$$

$$a = \pi^2 r^2 R/V,$$

where

μ = pressure exerted by the cupula per unit angular deflection of the endolymph,
V = volume of the ampulla.

The value of a, as discussed above, is probably about one according to the data of Jones and Spells (1963), and this agrees roughly with the estimates of other authors.

The long time constant is shown in the next section to have a value very nearly equal to the ratio b/k. The formula for the spring term (k) contains the coefficient of cupula stiffness (μ) which has never been measured. However from the data of Jones and Spells (1963) it may be inferred that while individual interspecies differences exist, the overall variations in cupula stiffness among different species is not great. Thus one can obtain an estimate, albeit very approximate, of the long time constant in a new species by comparison with species for which the value is known. Alternatively considerations based on animal size and configuration could be used for comparative estimates, as suggested by Mayne (1965b).

More reliable estimates may be obtained for the short time constant, which is approximately equal to the ratio J/b, that is the ratio of inertial to viscous terms. Since both terms involve measurable quantities, it is theoretically possible to obtain an estimate of this time constant for any single semicircular canal. There have been differences of opinion over what values should be used for the effective length terms, l_J and l_b, van Egmond et al. (1949) and Mayne (1965a) coming to slightly different conclusions that Gaede (1922) and Schmaltz (1925), but the difference is only a factor of two. Spells (1959) and Newman (1966) in derivations arising from more basic considerations, reached approximately the same conclusions as van Egmond et al. and Mayne. As mentioned earlier, however, there have been recent studies which throw some doubt on the validity of the simply hydrodynamic model of the canal. Thus Newman (1966) emphasizes the possible significance of changes in the velocity profile of the fluid during acceleration, Steer (1967) raises the question of viscous drag between the apposed sufaces of the cupula and ampulla, and the experimental observations of Dohlman (1968) suggest that the endolymph may not be a simple near-Newtonian fluid but rather a colloidal gel.

In spite of these objections, one can argue against discarding the conclusions of the simple model, especially as they relate to estimation of the short time constant. First, the rather striking observations of Jones and Spells (1963) and Mayne (1965b)are based on these simple equations. Their analyses show a systematic tendency for the dimensions of the semicircular canals in a wide range of animal species to be adjusted to produce dynamic characteristics appropriate to the size (Jones & Spells) and configuration (Mayne) of the animals. Secondly, in the single experimental study in which records have been made of peripheral vestibular neural response during rotational stimulation of sufficient variety to permit a reasonably accurate estimation of the short time constant, the value so obtained was remarkably close to that obtained by calculation from the relevant physical dimensions. It was perhaps a fortunate coincidence that these experiments , described by Groen, Lowenstein and Vendrick in 1952, were performed on the ray, which in common with other fish has rather large canals (Jones &Spells, 1963) so that their short time constant is expected to be somewhat longer than that of other species, and hence easier to measure. However it may still be argued that the data of these authors does not include measurements at frequencies high enough to ensure a good estimate of the short time constant.

In the case of man, the short time constant obtained by calculation from physical dimensions of the canal is considerably shorter than that of the ray, and the same appears to be true for most other mammals. Taking the value of the ratio of viscosity to density of the endolymph (η/ρ) to be 0.01 cm^2/sec (based on the determinations of Money et al.(1966) and Miery and Young (1966)), and using canal dimensions described by Jones and Spells (1963), one obtains for man a value of 0.005 sec. for the short time constant. This must however be regarded as a low estimate, since the specimens used by Jones and Spells were fixed in formalin, which may be expected to have caused some shrinkage.

3.4 SEMICIRCULAR CANAL DYNAMICS: PARAMETER ESTIMATION FROM INPUT-OUTPUT RELATIONS

3.4.1 The Canal Transfer Function.

The differential equation generally accepted as giving a good description of semicircular canal response was given above and is rewritten here for convenience.

$$J\ddot{\theta}_C + b\dot{\theta}_C + k\theta_C = \alpha J\ddot{\theta}_H \quad \text{.........................Eq. 3.4}$$

Taking the Laplace transform with all initial conditions equal to zero, and rearranging, we obtain the transfer function relating cupular deflection to head angular acceleration,

$$\frac{\theta_C(s)}{\ddot{\theta}_H(s)} = \frac{J\alpha}{(Js^2 + bs + k)} \quad \text{...................Eq. 3.5}$$

It appears from the observations of Steinhausen (1927), and from calculations by many authors based on the physical dimensions of the system, that cupularmotion is very heavily damped, probably more than 10 times critically damped. This apparently is largely due to the very low Reynold's number of the system and the presumably small value of the spring coefficient

k. The system therefore will not show spontaneous oscillations or ringing, and the denominator in Eq. 3.5 will have the real roots,

$$s_{1,2} = \frac{-b \pm (b^2 - 4Jk)^{1/2}}{2J}$$

Since b is very large relative to J and k, we can use the first two terms of the binomial expansion to obtain, with very small error, the approximation

$$(b^2 - 4Jk)^{1/2} \approx b - 2Jk/b$$

and hence,

$$s_1 \approx -k/b$$
$$s_2 \approx -b/J$$

Setting $T_1 = -1/s_1 \approx b/k$, and $T_2 = -1/s_2 \approx J/b$, Eq. 3.5 can be rewritten in the time constant form

$$\frac{\theta_C(s)}{\ddot{\theta}_H(s)} = \frac{aT_1T_2}{(T_1s + 1)(T_2s + 1)} \quad \text{..................Eq. 3.6}$$

which has a number of conceptual advantages in discussing system response. Eq. 3.6 has equivalent counterparts relating cupula position to head velocity and to head position respectively, i.e.,

$$\frac{\theta_C(s)}{\dot{\theta}_H(s)} = \frac{aT_1T_2s}{(T_1s + 1)(T_2s + 1)} \quad \text{................Eq. 3.7}$$

$$\frac{\theta_C(s)}{\theta_H(s)} = \frac{aT_1T_2s^2}{(T_1s + 1)(T_2s + 1)} \quad \text{................Eq. 3.8}$$

It will be seen from this and subsequent sections that, assuming the canal does indeed behave in the manner defined by Eq. 3.4, the response to any input waveform can be predicted in detail provided a few response parameters are known. Eqs. 3.6 - 3.8 contain only the three parameters a,

T_1, and T_2, and these three are sufficient for this purpose. The constant a is called a "gain" or scaling parameter, since it affects only the magnitude of the response. The precise form or time course of the response to a given input is independent of a, and is completely defined by the "dynamic response parameters" T_1 and T_2, or equivalent parameters such as the natural frequency and the damping ratio. These may in principle be determined either by calculation from the physical parameters J, b and k, or from a study of input-output relations.

A point of particular interest emerges here, namely that from the point of view of the investigator interested in neuromuscular reflex systems, one of the great advantages of canal-based systems lies in the confidence which may be placed in the computed time course of sensory endorgan response.

3.4.2 Frequency Response.

The frequency response representation is a useful means of summarizing the dynamic characteristics of a given system. In theory any waveform which might act as input to the system of interest, may be expressed as an infinite sum of sinusoids of different frequencies, so that each waveform may be regarded as having a distinctive "frequency content". The steady-state response of a linear system to a sinusoidal input is a sinusoid of the same frequency but having in general a different amplitude and phase than the input sinusoid. The frequency response or Bode plots are graphs of gain (input-output amplitude ratio) and phase shift, as functions of frequency. These plots are particularly useful in the present case, as they emphasize the normal function of the semicircular canal. The assertion, made earlier in this chapter, that the semicircular canal acts as a velocity transducer in a given frequency band, is considerably clarified using this method. In addition the experimentally measured frequency response may be used to estimate the important dynamic response parameters of the canals.

In Fig. 3 - 2, which is adapted from Belanger and Mayne (1965), the frequency response of the semicircular canals is plotted in three different ways.

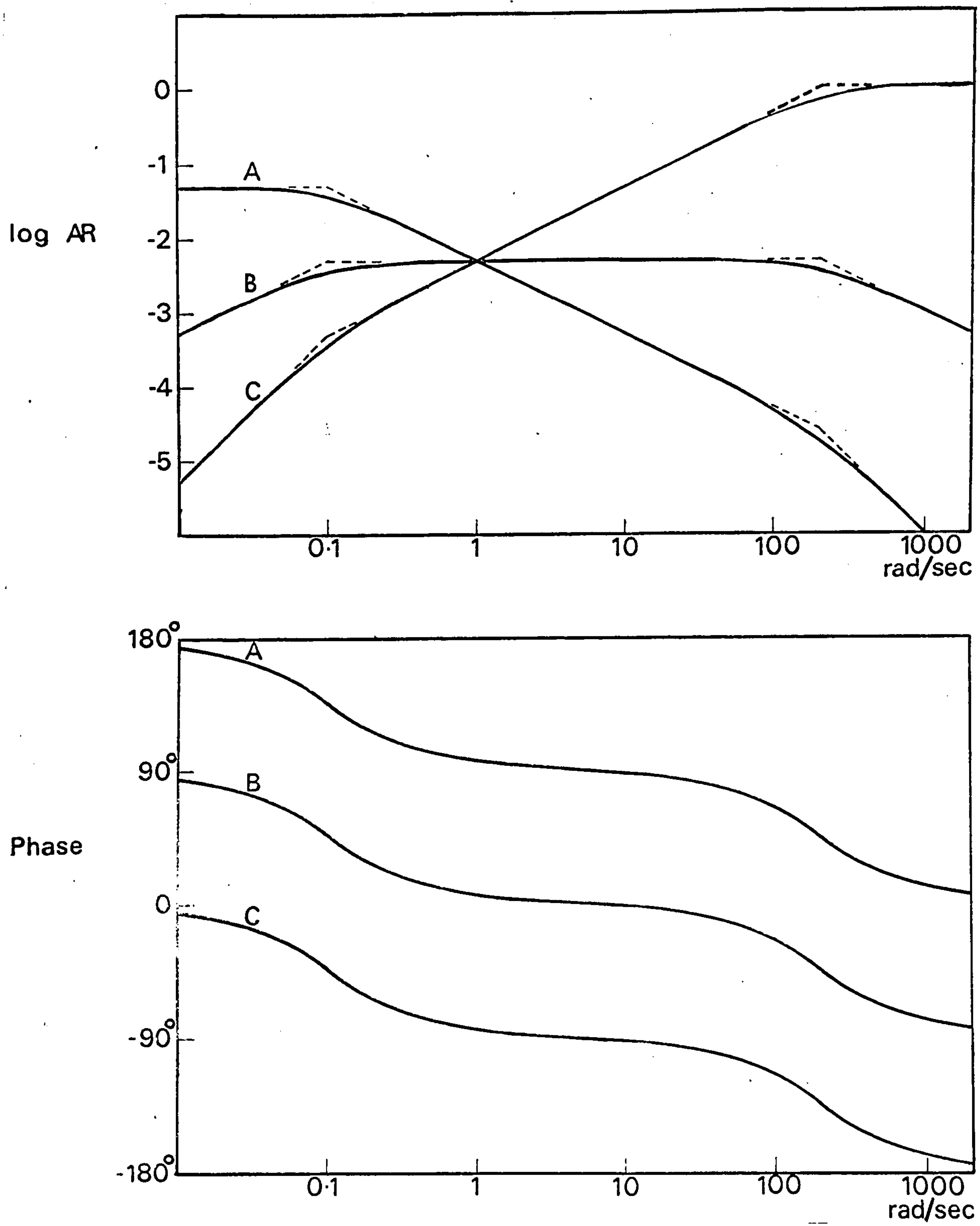


Fig. 3 - 2 FREQUENCY RESPONSE OF THE SEMICIRCULAR CANALS (after Belanger & Mayne, 1965) Amplitude Ratio (AR) and Phase Shift relating Cupula Position to Head Acceleration (A), Head Velocity (B), Head Position (C) Canal parameters: $\alpha = 1.0$; $T_1 = 10.0$ sec.; $T_2 = 0.005$ sec.

Curves A for gain and for phase correspond to Eq. 3.6 relating cupula position to head acceleration, that is with head acceleration taken as the input variable. Curves B correspond to Eq. 3.7, with velocity as input, and curves C correspond to Eq. 3.8, with position as input. All curves are drawn for the time constants $T_1 = 10$ sec., $T_2 = 1/200$ sec., as suggested by Mayne (1965a). The constant α of Eq. 3.3 is taken as unity for convenience. In each case there is a frequency band within which the gain remains almost constant and the phase shift relative to the respective input variable is almost zero. The semicircular canal can thus be regarded as an angular accelerometer at very low frequencies, as an angular velocity transducer at intermediate frequencies, and as an angular position transducer at very high frequencies. Notice that the gains in these three modes are very different, and that the differences are related to the time constants.

The curves relating gain or amplitude ratio to frequency may be characterized by three straight-line asymptotes when plotted on dual logarithmic axes as in Fig. 3-2, where the asymptotes are indicated by dotted lines. The upper and lower "break frequencies" are found at the intersections of the respective asymptotes and are related to the system time constants. Thus the lower break frequency, expressed in radians per second, is found to be

$$\omega_1 = \frac{1}{T_1}$$

and the upper break frequency is

$$\omega_2 = \frac{1}{T_2}$$

In the velocity mode (Fig. 3-2, curves B), the gain at the break frequencies is attenuated by a factor of 0.707 compared to the asymptotic value of the gain at the centre of the velocity transducing range. There is a corresponding phase shift of plus and minus 45° at the lower and upper break frequencies respectively. Thus with break frequencies of 0.10 and 200 radians per second, the frequency range for accurate velocity transduction is somewhat smaller than this, extending from say 0.5 to 50 radians per second or approximately

0.08 to 8.0 cycles per second.

With this view of the semicircular canal as a velocity transducer we shall henceforth take Eq.3.7 as the transfer function of the semicircular canal. For this case the relationships between gain and phase respectively and the frequency of sinusoidal rotation are as follows. The gain or amplitude ratio (AR) is given as

$$AR = \left| G(s) \right|_{s = j\omega}$$

$$= \frac{a\, T_1 T_2 \omega}{[(T_1^2\omega^2 + 1)(T_2^2\omega^2 + 1)]^{1/2}}, \qquad \text{..................Eq. 3.9}$$

where

$$G(s) = \frac{\theta_c(s)}{\dot{\theta}_H(s)}$$

$$= \frac{aT_1T_2 s}{(T_1 s + 1)(T_2 s + 1)},$$

and

$$\phi = \tan^{-1} \left[\frac{\mathrm{Im}\,\{G(s)\}}{\mathrm{Re}\,\{G(s)\}} \right]_{s = j\omega}$$

$$= \frac{\pi}{2} - \tan^{-1}\omega T_1 - \tan^{-1}\omega T_2. \qquad \text{................Eq. 3.10}$$

(Re $\{G(s)\}$ and Im $\{G(s)\}$ are respectively the real and imaginary parts of the complex function $G(s)$, and $|G(s)|$ is its absolute value)

The asymptotic value for the gain in the frequency range of accurate velocity transduction is

$$aT_2 \approx \frac{a\,J}{b}$$

Experimentally determined frequency response plots can be used to estimate dynamic response parameters in a number of ways. The estimates so obtained are of course not independent in an ideal linear system. In practice, however, the several estimates are useful if available since their degree of consistency gives some indication of the linearity of the real system.

Two methods are particularly well suited in the present case for estimating response parameters from the gain-frequency relationships. The three asymptotes may be drawn by eye if the data available cover a sufficient frequency range, and the time constants calculated from the break frequencies so estimated. Alternatively, as has been suggested by Jones & Milsum (1969b), the asymptotic gains in acceleration mode, velocity mode and position mode may be estimated and the time constants obtained by appropriate calculations from these values. Knowing the time constants, the constant a could in principle be calculated from any of the gain values if the relationship between observed output and cupula position were precisely known. More accurate estimates of parameters from gain-frequency relationships in general require detailed curve-fitting methods.

Phase-frequency relationships can yield estimates of all dynamic parameters (time constants) but not of the constant a or other scaling factors. The points of 45^{o} phase shift (in the velocity mode) give crude estimates of the break frequencies, and the point of zero phase shift, difficult to estimate if the time constants are widely separated, yields an estimate of the undamped natural frequency, defined by the expression

$$\begin{aligned} \omega_o^{2} &= \frac{k}{J} \\ &\approx \frac{T_1}{T_2} \end{aligned}$$

Again the best estimates require curve-fitting methods taking all available phase data into account, but asymptotic fitting, as suggested by Groen (1956), can give satisfactory results. The latter is simpler, requiring only that the tangent of the phase angle be plotted first as a function of the period of oscillation and then as a function of the frequency. Since the tangent of the phase angle is directly proportional to the time difference upon which any phase measurement is based, this method results in a considerable reduction of time spent looking up tables of tangents. The method derives from the fact that for the second-order equation relating cupula deflection to head velocity, the phase shift (ϕ) may be defined

$$\tan \phi = (\omega_o^2 - \omega^2) \cdot \frac{J}{b\omega}$$

where ω_o is the undamped natural frequency, defined above. Hence for high frequencies, $\omega >> \omega_o$,

$$\tan \phi \approx -\omega \frac{J}{b} \approx -\omega T_2$$

and for low frequencies, $\omega << \omega_o$,

$$\tan \phi \approx \frac{k}{b\omega} \approx \frac{1}{T_1 \omega}$$

3.4.3 Transient Responses.

Subjective and reflex responses to transient forms of stimulation of the semicircular canals have been widely used in the investigation of vestibular function because of the relative simplicity of this method. Step changes in head angular velocity and acceleration have most commonly been used for this purpose; sudden changes in head position are also of interest but have been considered mainly as they occur in voluntary head movements.

The theoretical responses of the second order model of the canal to unit positive step changes in the angular acceleration, velocity and position of the head are listed in Table 3-I and illustrated in Fig. 3-3. The figure illustrates responses of an analog computer model of the canal, having the time constants $T_1 = 10$ sec. and $T_2 = 1.0$ sec. The short time constant, T_2, has been made rather large for the purpose of illustration, since when it is made much smaller its contribution is very difficult to detect on the scale of this figure, and the ordinate scales have been adjusted for convenience in plotting. The more realistic case with the short time constant being of the order of 0.005 sec. can readily be imagined, bearing in mind that the canal response in each case may be regarded as the sum of two exponential terms.

The initial value of the position step response ("position gain"), the peak

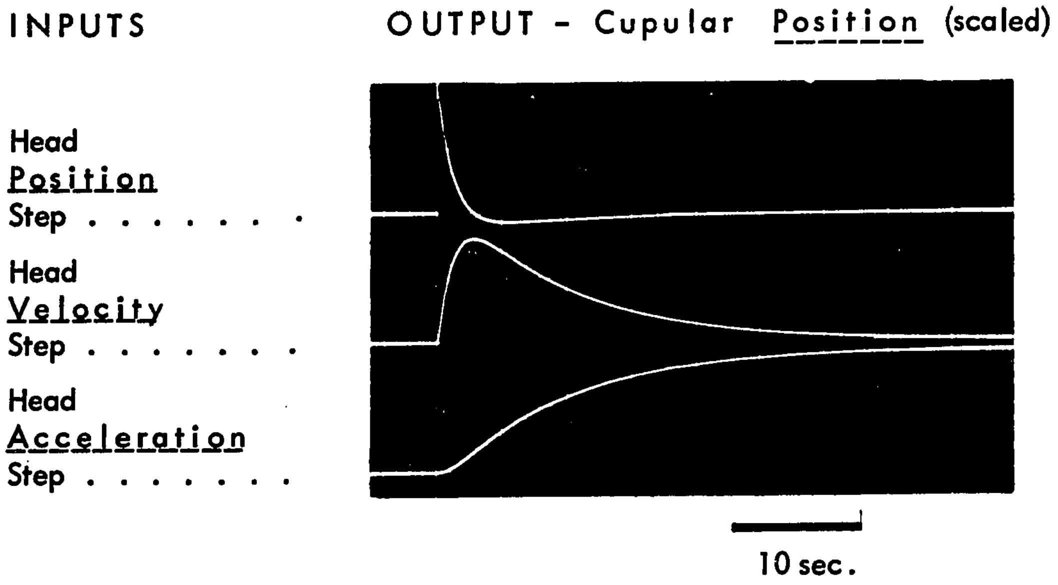


Fig. 3-3 SCALED RESPONSES OF THE CANAL MODEL TO UNIT STEP CHANGES IN HEAD POSITION, HEAD VELOCITY AND HEAD ACCELERATION

Canal model parameters: $T_1 = 10$ sec., $T_2 = 1.0$ sec., $\alpha = 1.0$

NOTE: the acceleration step response is reduced in magnitude by a factor of ten in the figure.

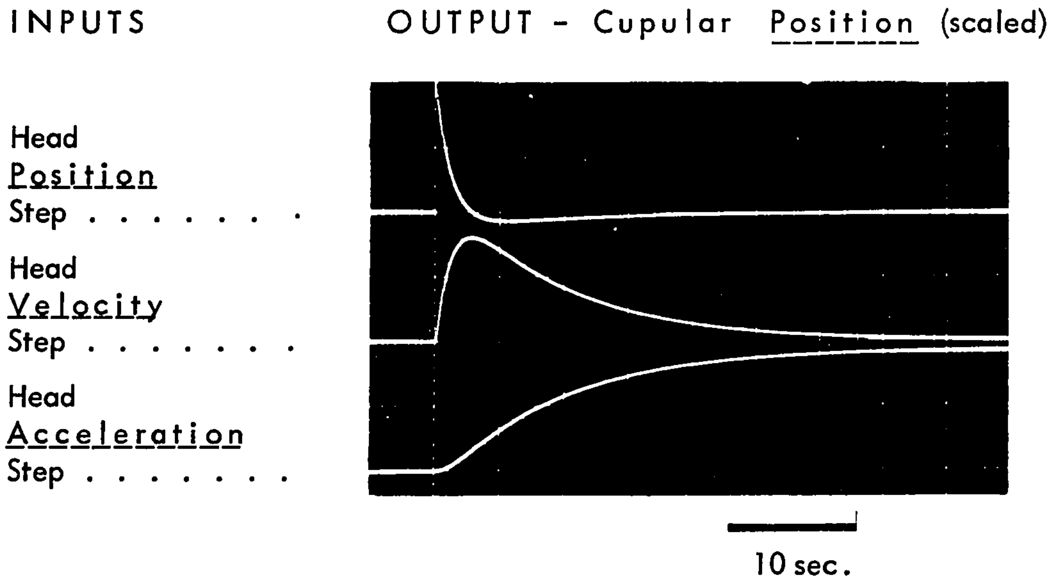


Fig. 3-3 SCALED RESPONSES OF THE CANAL MODEL TO UNIT STEP CHANGES IN HEAD POSITION, HEAD VELOCITY AND HEAD ACCELERATION

Canal model parameters: $T_1 = 10$ sec., $T_2 = 1.0$ sec., $\alpha = 1.0$

NOTE: the acceleration step response is reduced in magnitude by a factor of ten in the figure.

TABLE 3 - 1

TRANSIENT RESPONSES OF THE SEMICIRCULAR CANAL

INPUTS	OUTPUT - Cupular Position
Head Position Step	$\theta_C = \frac{\alpha T_1 T_2}{T_1 - T_2} \left(\frac{1}{T_2} e^{-t/T_2} - \frac{1}{T_1} e^{-t/T_1} \right)$ $\cong \alpha e^{-t/T_2}$
Head Velocity Step	$\theta_C = \frac{\alpha T_1 T_2}{T_1 - T_2} \left(e^{-t/T_1} - e^{-t/T_2} \right)$ $\cong \alpha T_2 e^{-t/T_1}$
Head Acceleration Step	$\theta_C = \frac{\alpha T_1 T_2}{T_1 - T_2} \left(T_1 (1 - e^{-t/T_1}) - T_2 (1 - e^{-t/T_2}) \right)$ $\cong \alpha T_1 T_2 (1 - e^{-t/T_1})$

value of the velocity step response ("velocity gain"), and the final value of the acceleration step response ("acceleration gain") are related in the proportion 1 : J/b : J/k approximately. For the time constants (10 sec. and 1.0 sec) used in Fig. 3.3., these proportions are 1 : 1 : 10 and the approximation is poor as the figure shows. With a more realistic value for T_2, say 0.005 sec., the proportions become 1 : 0.005 : 0.05 and the error in the approximation is small.

Transient response testing has been the basis for most estimates of semicircular canal time constants, the response to a step change in head angular velocity (the classical "stopping stimulus") having been most extensively used. The transient responses each consist of two exponential terms, so that the time constants T_1 and T_2 and the gain α may in principle be obtained by the well known method of graphical decomposition, or by other curve-fitting methods. Because the time constants are separated by at least one order of magnitude, the long time constant T_2 is readily obtained, but the contribution of the short time constant is difficult to isolate with adequate resolution. On the one hand it is difficult to provide a transient stimulus sufficiently abrupt that it can be assumed to change instantaneously as in the ideal case, and on the other hand with velocity ramp and velocity step inputs the contribution of the short time constant term is so small that amplitude resolution is a problem. This could be alleviated somewhat by using stepwise or impulsive changes in head <u>position</u>, since these inputs have the effect of emphasizing the contribution of the short time constant term in the response. However because of physical limitations these forms of input are much more difficult to apply to the canals, and as a result transient response testing has been used mainly to estimate the long time constant. It is probably desirable to use frequency response testing for estimation of the short time constant, since for mechanical reasons it is easier to produce high frequency oscillation of the head than an accurate step change in head velocity or position.

Because of the nature of some variables used as indices of cupula motion, a number of investigators have estimated the long time constant by methods involving measurement of the elapsed time between the application of a transient stimulus and the point when the response reaches a certain magnitude. The classical method of cupulometry as initiated by the Utrecht school (van Egmond et al., 1948) is such a method, using the velocity step as input and the point when sensation or nystagmus dies away as the end-point. Hallpike and Hood (1953a) refined this method somewhat by using a more precisely defined endpoint based on the oculogyral illusion. A similar method using a velocity ramp as input and the time of first detectable response as endpoint was suggested by Mayne (1950) and has been used in modified form by Guedry and Richmond (1957), Meiry (1965) and others.

CHAPTER 4

NEURAL PROCESSING IN VESTIBULAR SENSORY AND REFLEX PATHWAYS

4.1 ANATOMICAL CONSIDERATIONS

The possibility of neural processing of the semicircular canal signal was briefly touched upon in Chapter 2 in connection with the mechanisms of mechano-neural transduction and the question of efferent connections to the sensory epithelium. The actual nature of such neural processing is the theme of the present chapter, which is largely in the form of a running commentary on the principal experimental findings which are relevant.

Inferences about the nature of neural processing may be made on the basis of two groups of experimental findings, namely (a) observations of neural activity within the vestibular sensory system,and (b) observations based on reflex and subjective sensory responses to vestibular stimulation. The discussion is divided along approximately the same lines. There is overlap of course, particularly in the case of "adaptation" phenomena. In this particular case there are very pertinent neurophysiological observations in the periphery, so the question of adaptation is considered with other neurophysiological data, leaving the rather distinctive "habituation" phenomena to a separate section. The final section of this chapter discusses the implications which emerge relevant to the dynamic response of reflex systems based on the semicircular canal signal and to the evaluation of canal parameters from observations at different points in these systems.

The considerations of this chapter point to the need for quantitative theoretical studies of vestibular reflex systems and form the basis for the discussion of original theoretical studies in the vestibulo-ocular system presented in Chapters 5 and 6. However, before proceeding to discuss neurophysiological features of the system, it is necessary to discuss briefly the relevant anatomical connections.

The vestibular portion of the eighth cranial nerve is composed of primary afferent neurones, originating in vestibular end organs, most of which terminate in the vestibular nuclear complex. In addition to the main afferent bundles, there is a relatively small efferent innervation of the end organ (Chapter 2). Also Gernandt (1949) has raised the question of secondary vestibular neurones with cell bodies along the course of the nerve, which would mean that some secondary fibers exist in the proximal portions of the nerve trunk.

The anatomy and connections of the vestibular nuclei have been the subject of a comprehensive monograph by Brodal, Pompeiano and Walberg (1962) and this, together with some more recent publications, forms the basis of the present discussion. The nuclear complex is divided into four main groups by these authors, the superior, lateral, medial and descending vestibular nuclei. There are in addition some smaller groups of cells which are of lesser importance in a brief description. The precise location, anatomy and cyto-architecture of the vestibular nuclei is considered by Brodal et al., but not in the present discussion, which is largely confined to the connections.

Primary afferent vestibular neurones are distributed to all four major nuclei, although none of these nuclei receive primary afferents in all regions (Brodal et al., 1962). The distribution among vestibular nuclei of fibers from specific labyrinthine receptors was studied by Lorente de No (1933), who found afferents from the semicircular canals reaching superior, medial and descending (or "inferior") vestibular nuclei, while macular afferents were distributed to lateral and descending vestibular nuclei. Another group of primary vestibular afferent fibers, whose origin was not ascertained by Lorente de No (1933a) and may have been mixed, entered the lateral vestibular nucleus. Other primary afferent fibers from the vestibular sensory epithelium are distributed homolaterally to the phylogenetically older vestibular portion of the cerebellum (Brodal et al., 1962). These fibers reach the fastigial nucleus and also enter the flocculus and nodulus. Termination of these fibers in synaptic contact with Purkinje cells has been demonstrated in the frog by Llinas, Precht and Kitai (1967). The possibility of primary afferent fibers descending directly into the spinal cord without synapsing in the vestibular nuclei is a moot point, discussed further in a later chapter in connection with the vestibular control of head movement..

The vestibular nuclei have extensive reciprocal connections with the cerebellum, in addition to the reciprocal connections between cerebellum and vestibular sensory epithelia mentioned above. Fibers from medial and descending vestibular nuclei extend to flocculus, nodulus and uvula, and to the fastigial nuclei. There is a complex projection, from both cerebellar cortex and fastigial nuclei, which is distributed to all the major vestibular nuclear groups. Many details of these projections have been worked out by Brodal and his collaborators, and are discussed in the monograph mentioned above.

The precise nature and termination of ascending projections from the vestibular nuclei is not completely known. Brodal et al. (1962) after reviewing the literature conclude that the majority of ascending fibers, which originate from all four vestibular nuclei, travel in the medial longitudinal fasiculus. Both crossed and uncrossed ascending fibers occur, and they are distributed to oculomotor nuclei and to the upper mesencephalon, in particular to the interstitial nucleus of Cajal. There is less conclusive evidence for other sites of termination of ascending fibers, though there appear to be some fibers terminating in the thalamus (Carpenter & Strominger, 1965). Cortical evoked responses have been recorded following vestibular stimulation (e.g., Andersson & Gernandt, 1945) but the vestibulo-cortical pathway is unknown.

Connections from vestibular to oculomotor nuclei have been extensively investigated particularly in connection with horizontal conjugate eye movements. The work of Lorente de No (1933b) and Szentagothai (1950) outlined the details of the basic three-neurone vestibulo-ocular reflex arc, involving crossed and uncrossed fibers in the medial longitudinal fasciculus. Their work however leaves little doubt that other less direct vestibulo-oculo-motor connections exist, which are essential for the normal operation of this system. The question of neural connections involved in nystagmus is very confusing despite a great deal of investigation. The difficulty is to be expected since nystagmus may result from several forms of vestibular stimulation involving linear and angular receptors, as well as from visual stimuli as in optokinetic nystagmus and visual tracking. The subject is discussed by Brodal et al.

(1962) and has recently been reviewed briefly by Monnier (1967).

Descending connections to the vestibular nuclei have not been very extensively investigated. Pompeiano and Walberg (1957) found that most fibers descending from higher levels in the medial longitudinal fasciculus originated in the interstitial nucleus of Cajal, but the connections to this nucleus are not well known. Brodal et al. (1962) are of the opinion that most descending influences on vestibular nuclei are exerted by other routes involving the reticular formation to a large extent. Vestibulo-spinal and spino-vestibular connections have received increased attention recently, but since these are not of great importance for the present chapter, their description will be left to a later section where they will be considered in relation to the vestibular control of head movement.

There is of course a great deal of further anatomical information, particularly in the work of Brodal and Pompeiano and their colleagues, from which one may infer possible locations for certain types of neural processing which are expected to occur. However at present little can be inferred about the nature of the processing from such anatomic studies.

4.2 NEURAL MODIFICATION OF THE SEMICIRCULAR CANAL SIGNAL

4.2.1 Introduction

As outlined above, the object of this section is to examine the existing experimental observations of activity in the vestibular neural pathway with a view to determining, in so far as possible, the nature and location of changes which may occur in the rotational signal as it proceeds from the peripheral endorgan (the semicircular canal) to the central nervous system.

It is difficult to decide how far in an anatomical sense it would be desirable to follow this rotational signal if it were possible to do so. There is reason to believe that the subjectively sensed rotation signal is significantly different from the signal which is involved in various reflex manifestations of vestibular stimulation. Thus it may be reasonable to distinguish for conceptual purposes a subjective rotation signal from a brain stem rotation signal. In practice the latter might be very hard to define uniquely, but there are a number of phenomena, which may be interpreted as due to dynamic neural processing, and which are seen in very similar form in the response of several neural and neuromuscular systems during vestibular stimulation. For this reason it might be advantageous if it were possible to measure, or at least develop as a concept, a single brain stem rotation signal which could be regarded as the unique input to the various sensory and effector systems. These systems would in turn presumably effect dynamic and perhaps other transformations before yielding their respective outputs. The neural activity in primary afferent vestibular neurones is probably not ideally suited to be regarded as this basic rotational signal, since in the intact preparation such activity may be modified by central mechanisms via the vestibular efferent pathway.

Changes which may occur in the rotational signal may be considered as resulting from transformations, the latter being presented here under two headings, static and dynamic. Static transformations are independent of time, or in effect instantaneous, a linear static transformation being equivalent to pure amplification or attenuation. Non-linear static transformations, of greater interest here, include threshold and saturation phenomena. Dynamic transformations may be characterized by their fundamental property which is time dependence. Thus the output of the processor producing a dynamic transformation is dependent not only on the instantaneous value of the input but also on the past history of the input, or equivalently, on the "state" of the processor, which in turn is a function of the past history of the input. Dynamic transformations may also be divided into linear and non-linear varieties, the former being describable by linear differential equations. A necessary and sufficient condition for linearity is the property of "superposition", which requires that the response to a number of inputs applied simultaneously be identical to the algebraic sum of the responses to the same inputs applied individually. No attempt is made here to separate the two types of dynamic transformation except in certain specific cases. It is important to appreciate that dynamic response characteristics cannot be determined from a knowledge of static response alone.

4.2.2 Static Transformations

Trincker (1957) obtained a sigmoid curve relating static cupula deflection to changes in the generator potential in the crista (Fig. 2-3). Similar curves were obtained by Groen, Lowenstein and Vendrick (1952) recording single fiber ampullary nerve activity in the ray, and by Ledoux (1949, 1958) recording the mass discharge of ampullary nerves in the frog. The three curves are shown in Fig. 4-1. However while Trincker used static, artificially-induced cupula deflections, Groen et al. and Ledoux plotted the peak neural activity following a step change in velocity of rotation as a function of the magnitude of the step, arguing from theoretical considerations that peak cupula deflection should be proportional to step magnitude.

Both mechanical and neural mechanisms have been proposed to explain the non-linearity. Trincker (1962) suggested that the curve is sigmoid because the hair cells are sensitive to shearing forces only, as seems to be the case for the otoliths and perhaps the cochlea. The implication is that the magnitude of such forces would be proportional to the sine of the angle of cupular deflection, but this is probably not the only explanation of the nonlinearity. Trincker used enormous cupula deflections, and found the generator potential varied linearly with cupula angle, in one direction at least, for deflections up to 20°. Evidence has been presented in the preceding chapter which suggests that normal cupula deflections are much smaller, perhaps by a factor of ten or more. Thus it seems that the relationship between cupula deflection and generator potential, described by Trincker, only begins to be non-linear for cupula deflections far exceeding the normal range of cupula movement. This suggests that saturation phenomena in the neural encoding mechanism are the major cause of the non-linearity observed by Groen et al. and by Ledoux.

There is additional neurophysiological evidence to support this view. Groen et al. (1952) reported that while most fibers showed a characteristic curve

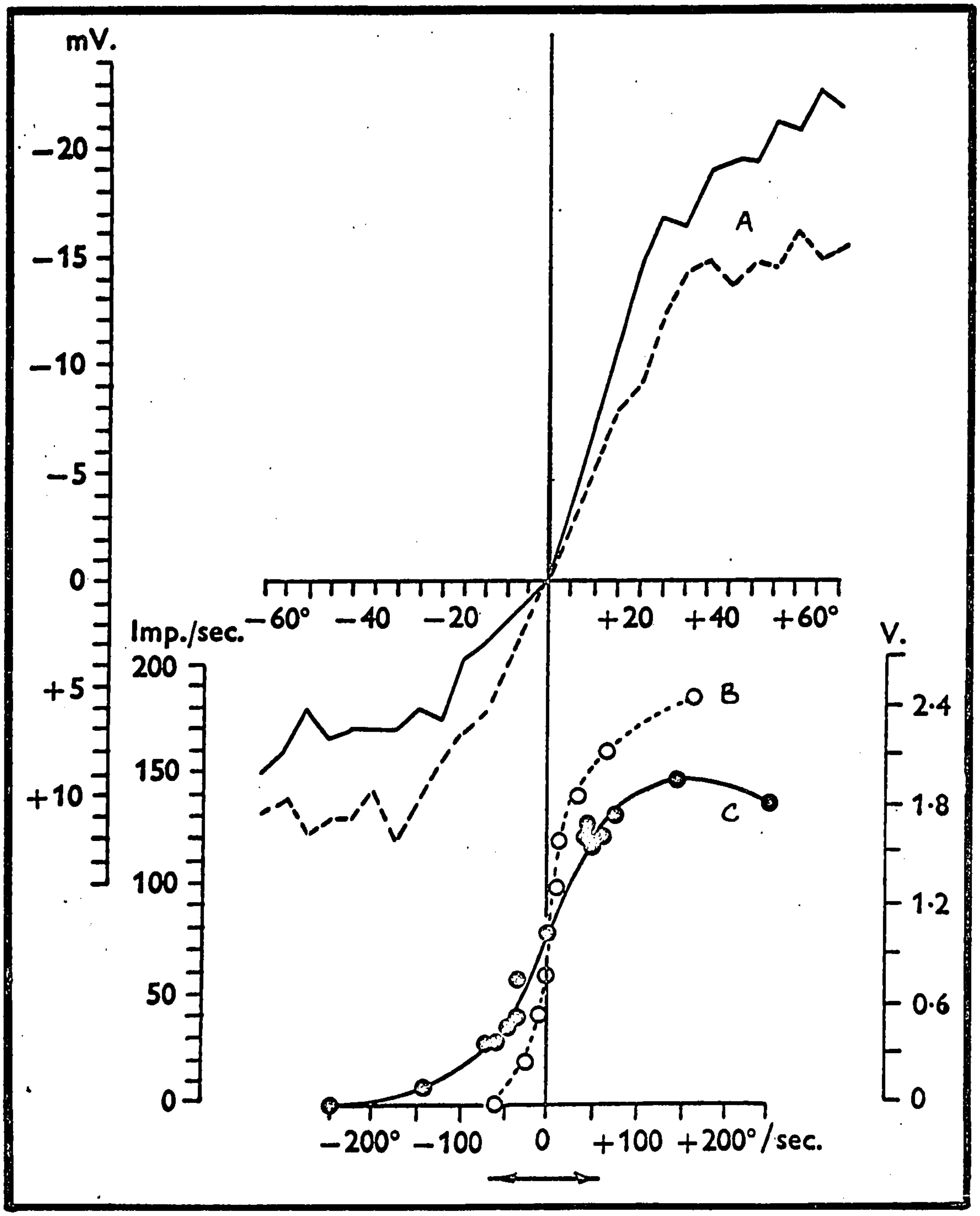
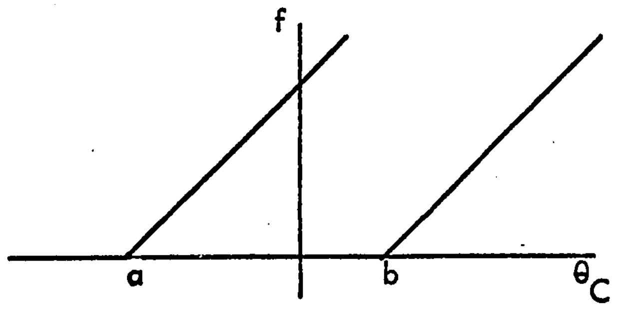


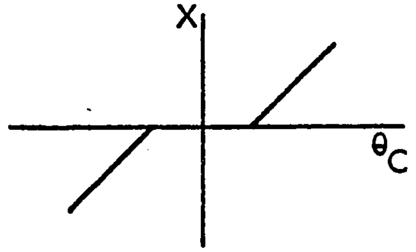
Fig. 4-1 STATIC NON-LINEARITIES IN THE VESTIBULAR AFFERENT PATHWAY (from Trincker, 1962) A - changes in DC potential (mv) in the crista ampullaris due to static cupular deflections(degrees)(Trincker, 1958); B - peak discharge of whole frog ampullary nerve(volts)(Ledoux, 1958), and C - peak pulse frequency of single ampullary nerve fibers in the Ray(Imp./sec.)(Lowenstein & Sand, 1940b) following an angular velocity step vs. the magnitude of the step (°/sec)

which was fairly symmetrical with respect to the resting discharge frequency, the response of other fibers was markedly asymmetrical, some showing no response until stimuli of high intensity were used. Subsequently Lowenstein (1955, 1956), studying the effects of steady polarizing currents on the discharge of ampullary nerve fibers, found that some responded symmetrically to rotation alone, but gave a distinctly asymmetrical response when exposed to combined rotational and electrical stimulation. This would imply a variation of the cell's working point on its characteristic curve as a result of electrical stimulation, and suggests that the non-linearity must be due in part to some property of the sensory cell or primary neurone.

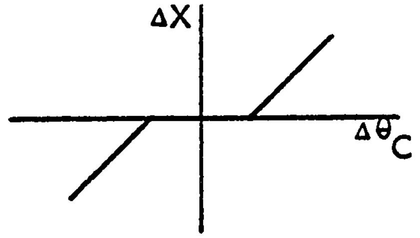
Threshold phenomena form another class of static non-linearities; however confusion arises here because of terminology. A neurone whose output is taken to be action potential frequency can always be regarded as showing a threshold since negative frequencies do not exist. For example, a primary vestibular neurone which has a spontaneous discharge at zero cupula deflection has as its threshold stimulus a negative cupula angle (see Fig. 4-2a). The existence of a threshold effect or "dead zone" (Fig. 4-2b) in the vicinity of zero cupula deflection is an additional possibility. Though such a dead zone is often postulated (e.g., van Egmond et al., 1949; Miery, 1965), it is not clear why it should be centered around the resting position of the cupula. Neural mechanisms are unlikely to cause such a phenomenon, since, as pointed out by Groen et al. (1952), the majority of primary vestibular neurones have a spontaneous discharge. The concept of a "threshold" cupula deflection has arisen because in the many experiments on subjective and reflex response to small step changes in angular acceleration (reviewed by Clark, 1967), there always appears to be a lower limit to the magnitude of the step change which can be detected. By analogy with other sensory threshold phenomena, it may presumably be assumed that it is immaterial whether or not the initial acceleration is zero when the acceleration step is administered. This implies a moveable "dead zone" (Fig. 4-2c) which comes into play whenever the cupula is stationary in one position for a



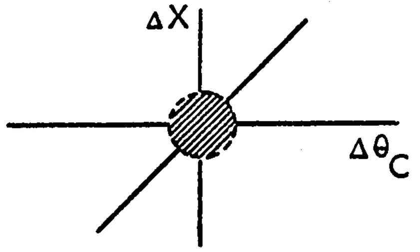
A. Idealized characteristic curves for neurones with negative (a) and positive (b) thresholds. f = neural pulse frequency; θ_C = cupula position.



B. Dead-zone non-linearity centered about zero cupula deflection
X = perceptual or reflex response.



C. "Moveable" Dead Zone
X = small change in perceptual or reflex response, θ_C = small change in cupular angle.



D. Graphical representation of a Resolution Uncertainty

Fig. 4-2 THRESHOLD, DEAD ZONE AND RESOLUTION UNCERTAINTY
For explanation see text.

sufficiently long time. Such an effect might occur as a result of static friction ("stiction") between the cupula and the ampulla, though this would imply a relationship between the shape of the dead zone characteristic and the acceleration waveform. Cupula restoring force might in addition make this characteristic asymmetrical except at zero cupula angle.

However there is evidence which indicates that the minimum perceptible acceleration step varies in size depending on the amount of extraneous stimulation or "noise" which occurs in the experimental setup (Ek, Jongkees & Klijn, 1959). This implies, as these authors point out, that the phenomenon is a problem of resolution and not a true dead zone or threshold manifestation. Malcolm and Jones (1969) have made a similar observation. A more suitable graphical representation might be that given in Fig. 4-2d. The very wide range of observed angular acceleration "thresholds" in man (Clark, 1967) tends to support this view.

In existing studies of the discharge of canal dependent second order neurones in the vestibular nucleus, discussed in more detail below, there has been no specific investigation of further static transformations occurring at this higher level. Response patterns in these cells vary however, some being silent in the absence of stimulation and showing a threshold, and others having a resting discharge and showing in effect a negative threshold, as in Fig. 4-2c. It is not clear to what extent this threshold depends on properties of respectively the first or the second order neurone.

4.2.3 Dynamic Transformations

At the endorgan level, it is clear from basic principles that electrochemical phenomena, whether in the hair cell and generator potential mechanisms in the neural encoder, or in the primary afferent neurones, could contribute to dynamic signal modification in addition to the static transformations mentioned above. Ross (1936) and Adrian (1943) recorded respectively from single first order neurones and from vestibular nuclear cells, during rotatory stimulation. They concluded that vestibular receptors must be of the "slowly adapting" type, since the slow decay of neural activity following a step change in stimulus angular velocity could be adequately explained on the basis of semicircular canal mechanics. Lowenstein and Sand (1940b), using more precisely controlled rotational stimuli and recording from single VIIIth nerve fibers in the isolated labyrinth of the ray, reached similar conclusions.

More recent evidence is not contradictory but emphasizes the possible significance of such slow adaptation, and suggests its time course may involve a time constant somewhat longer than the long time constant attributed to semicircular canal mechanics.

Lowenstein (1955, 1956) studied the effects of DC polarization on the discharge of single ampullary nerve fibers, and found that the sudden onset of an ascending current or sudden offset of a descending current produced a sudden increase in discharge frequency followed by a decline which was at first rapid and then continued at a slower rate towards the resting level. In the case for which he gives detailed data, the rapid decline was over in about two seconds and accounted for about 40% of the initial increase in firing rate; the subsequent slow decline would appear to have required several minutes to return to the resting level.

Ledoux (1958, 1961) made extensive studies on the mass discharge of whole ampullary nerves in the frog during prolonged rotational stimuli with periods of both constant velocity and constant acceleration. His principal findings are summarized in Fig. 4-3, which is taken from his 1961 publication. Figs. 4-3a and 4-3b show the responses to prolonged constant velocity and acceleration respectively, and these are clearly different from the expected responses of the cupula (dotted line) to the same stimuli. The neural discharge shows an overshoot in response to the velocity step input and a late decline in response to the acceleration step. In Fig. 4-3c is shown the response to a complex velocity waveform of mixed steps and ramps. Here the difference

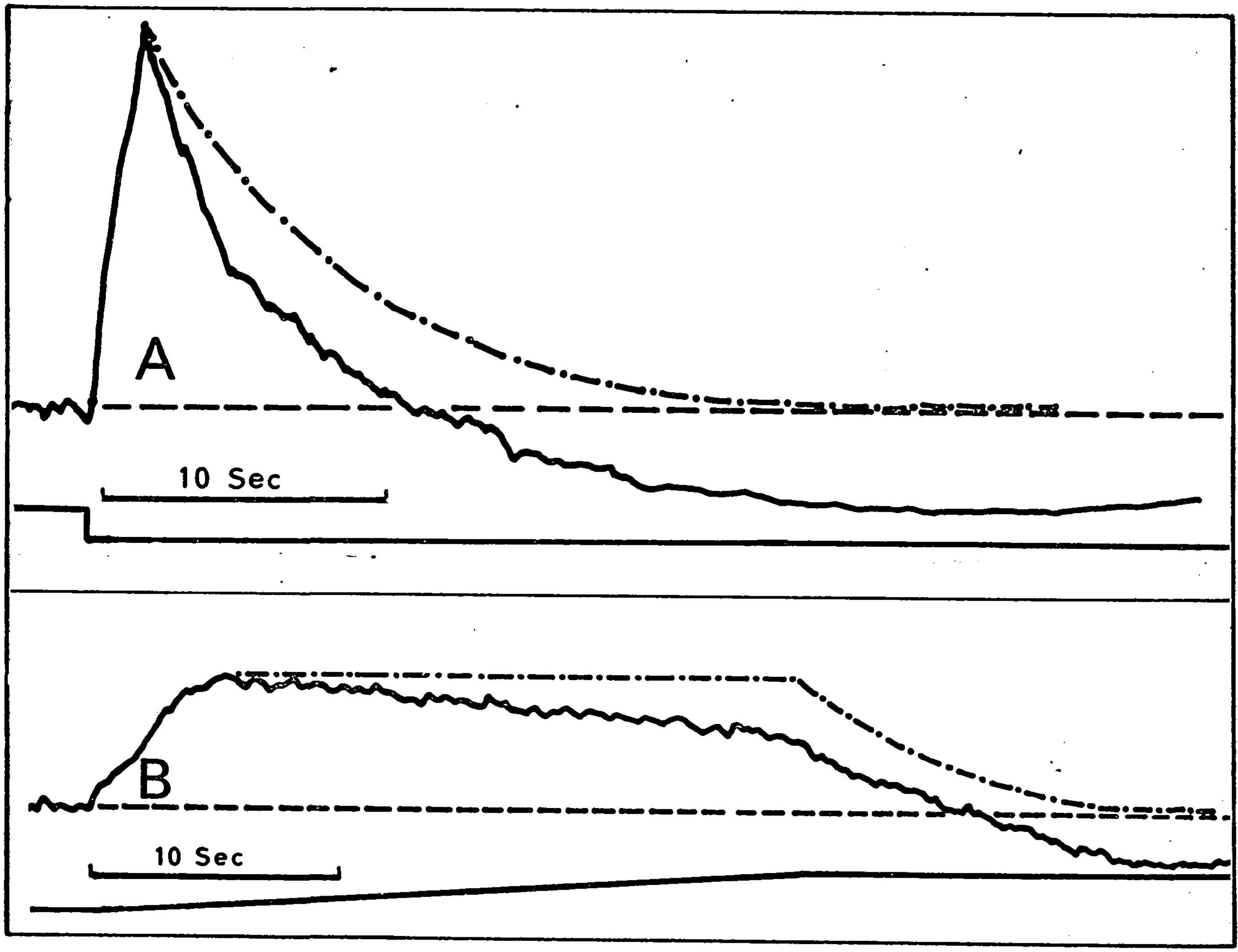


Fig. 4-3 A, B ELECTRICAL RECORDINGS OF MASS DISCHARGE IN FROG AMPULLARY NERVE (irregular lines) DURING STEP (A), AND RAMP (B) CHANGES IN HEAD ANGULAR VELOCITY (lower solid line in each record) Dash-dotted lines indicate expected cupular response. (From Ledoux, 1961).

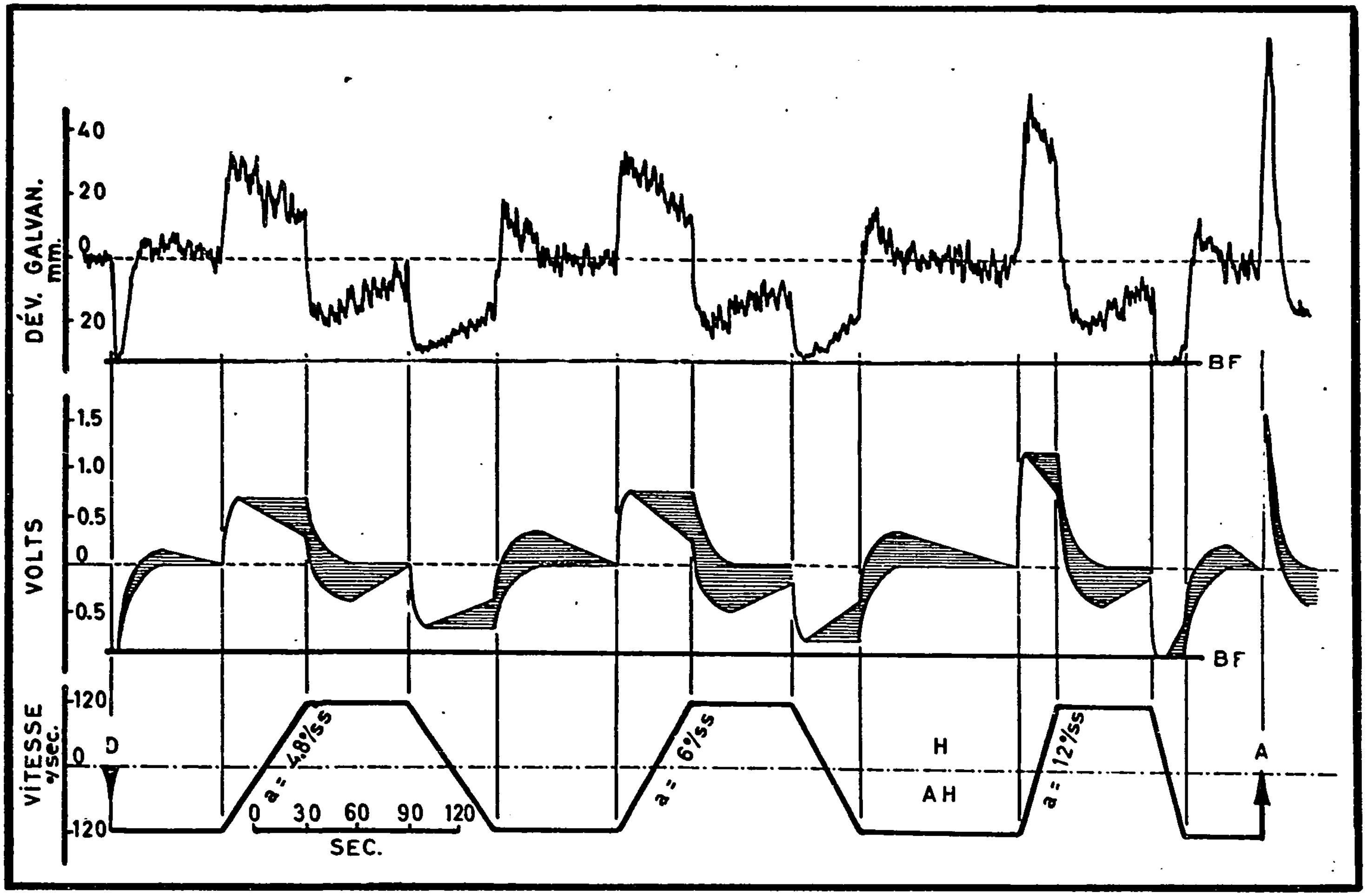


Fig. 4-3 C RECORDING FROM FROG AMPULLARY NERVE DURING ROTATION (Ledoux, 1961)

Input is a sequence of angular velocity steps and ramps (lower trace). Upper trace - mass discharge of ampullary nerve; center trace - shaded areas indicate departure of recorded potential from expected time course of cupular motion.

between observed and expected response, indicated by shading, is very striking. Ledoux studied the velocity step response overshoot in detail and found considerable variation from one animal to another, though in any given preparation the magnitude of the overshoot was consistently related to stimulus magnitude. In ageing preparations the overshoot disappeared long before the resting discharge or the response to rotation, a fact which might implicate efferent mechanisms. However he states that he often cut the ampullary nerves for convenience in recording.

The discharge of canal dependent cells in the vestibular nuclei has been studied recently by several investigators during controlled rotational stimulation of various forms. Constant velocity rotation was used by Duensing and Schaeffer (1958, 1959) and constant angular accelerations by Crampton (1965, 1966) and by Shimazu and Precht (1965). Jones and Milsum, in a series of reports, have described the response to both these forms of stimulation and also to sinusoidal rotational oscillation at various frequencies (Jones, 1967; Milsum & Jones, 1966, 1969). Similar experiments were performed by Gernandt (1949) and by Eckel (1954) using less well defined stimuli. The general outcome of these investigations is that some vestibular neurones show responses similar to those expected on the basis of canal mechanics. However a number of variations from the expected responses were observed in some cells, and these will be described briefly.

First, Jones and Milsum (1967) found some cells responding to a step change in angular acceleration with a firing frequency which increased steadily, in proportion to head angular velocity, for periods of several minutes. Crampton (1966) found cells, normally silent, which were "switched on" by a brief acceleration and fired steadily for some minutes. Jones and Milsum have made a similar observation. Secondly, Jones and Milsum (1967) and Milsum and Jones (1969) noted that cells exhibiting a threshold tended to respond asymmetrically during sinusoidal oscillation. During the portion of the sinusoidal cycle when they were active, the firing frequency of these cells increased more rapidly than it decreased, producing a skewed response in the leading direction. A detailed study of this effect has been made by Milsum and Jones (1969), but its origin remains uncertain, although it was suggested that a form of adaptation attributable to the train of action potentials themselves may be a major factor. These authors suggest that functionally it may be significant in providing temporal "sharpening" of the signal. Third, Shimazu and Precht (1965) using acceleration steps as input, found that the firing frequency of high threshold units reached a steady value more rapidly than was the case for spontaneously discharging cells. The latter authors estimated the time constant for each cell by fitting the response to the curve of expected canal response, and found shorter time constants for spontaneously silent units. It is not clear whether such curve fitting is valid; the apparently reduced time constant of spontaneously silent units may have been due to the same phenomenon as that causing the skewness described by Milsum and Jones (1969).

A forth group of variations from the expected canal response deserves special mention. Crampton (1966), Shimazu and Precht (1965), and Jones and Milsum (1967) found that some cells showed a late decline in firing frequency in response to step changes in angular acceleration. Jones and Milsum (1967) also observed overshoots in some cells in the response to step velocity inputs. These responses are very similar to those observed by Ledoux and described above. Moreover they are very reminiscent of the well known phenomena of "adaptation" to constant acceleration, and secondary per- and post-rotational effects, observed in more remote responses to vestibular stimulation. Secondary ocular nystagmus and sensation following step changes in head angular velocity were well known to early workers (e.g., Baranay, 1907; Buys, 1924) and have recently been extensively studied. The subject has been reviewed by Guedry (1965).

These two phenomena, overshoot in the velocity step response and late decline in the acceleration step response, thus reappear at several points in vestibular sensory and reflex paths. This suggests that they may be the result of fundamental processing of the rotational signal, which in view of Ledoux's findings, probably involves peripheral neural mechanisms to some extent. Recently there have been attempts to relate both phenomena in a single quantitative hypothesis, with results which lead to significant conclusions relating to dynamic considerations of vestibular systems. The topic is deferred to the next section, which considers these and other quantitative hypotheses relating to signal processing in the vestibular sensory pathway.

It is perhaps superfluous to comment on the great potential for processing in the brain stem which exists owing to the multiple interconnections between vestibular nuclei and other structures, in particular the reticular formation and cerebellum. There are also complex interconnections among the vestibular nuclei themselves as shown by anatomical (Brodal et al., 1962) and physiological studies (Precht & Shimazu, 1965; Shimazu & Precht, 1965, 1966). Some findings of the latter authors suggest a quantitative hypothesis as to the mechanism of possible attenuation of high frequency components in the rotational signal and this is presented in the next section. In general however quantitative understanding of central processing mechanisms is lacking.

4.3 MATHEMATICAL MODELLING OF OBSERVED DYNAMIC CHANGES IN THE ROTATIONAL SIGNAL

4.3.1 General

Quantitative explanation of dynamic changes in the neural rotation signal is still in its early stages, but is of considerable interest nevertheless, since the details of such transformations will clearly be of great importance in quantitative studies of reflex mechanisms. In addition they may be of considerable significance for the estimation of semicircular canal parameters from input-output relationships when the time course of cupula motion is inferred vestibular sensory and reflex paths. This suggests that they may be the result of fundamental processing of the rotational signal, which in view of Ledoux's findings, probably involves peripheral neural mechanisms to some extent. Recently there have been attempts to relate both phenomena in a single quantitative hypothesis, with results which lead to significant conclusions relating to dynamic considerations of vestibular systems. The topic is deferred to the next section, which considers these and other quantitative hypotheses relating to signal processing in the vestibular sensory pathway.

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Two forms of dynamic processing are considered here. First the question of "adaptation" phenomena in the response to step and ramp changes in head angular velocity is discussed. It seems possible these may both be explained by a single process, effectively a form of high-pass filter affecting low frequency components of the rotation signal predominantly. Second, tentative suggestions are made as to the location and mechanism of a possible low-pass filter affecting high frequency information in the canal signal.

4.3.2 Adaptation Effects

There have been recurring suggestions since the time of Rohrer (1922) that overshoots and adaptation effects in responses to step changes in head angular velocity and acceleration occur because the hydromechanical system of the canal is really underdamped. This view however is untenable in view of the evidence from experimental studies using the frequency response mode of analysis. The results of Groen, Lowenstein and Vendrick (1952) and of Jones and Milsum (1967) are particularly convincing on this point.

Young (1968) has attempted to explain these adaptation phenomena in terms of a hypothetical neural mechanism which acts as a high-pass filter with a time constant of about 30 seconds. His arguments in support of such a mechanism are based in part on the assumption that adaptation occurs only in the subjective sensory response. Nevertheless, the model illustrates clearly the possible effects of changes in low frequency components of the rotation signal. The model is shown in block diagram form in Fig. 4-4a, and consists of a time delay element, included by Young for other reasons, and a high-pass filter. The time delay may be ignored since its effect would be small at low frequencies. The filter is such as to respond to a step change in cupula position with a simple decaying exponential having a time constant of 30 seconds. In Fig. 4-4b, taken from Young (1968), the response of this model (dotted line)

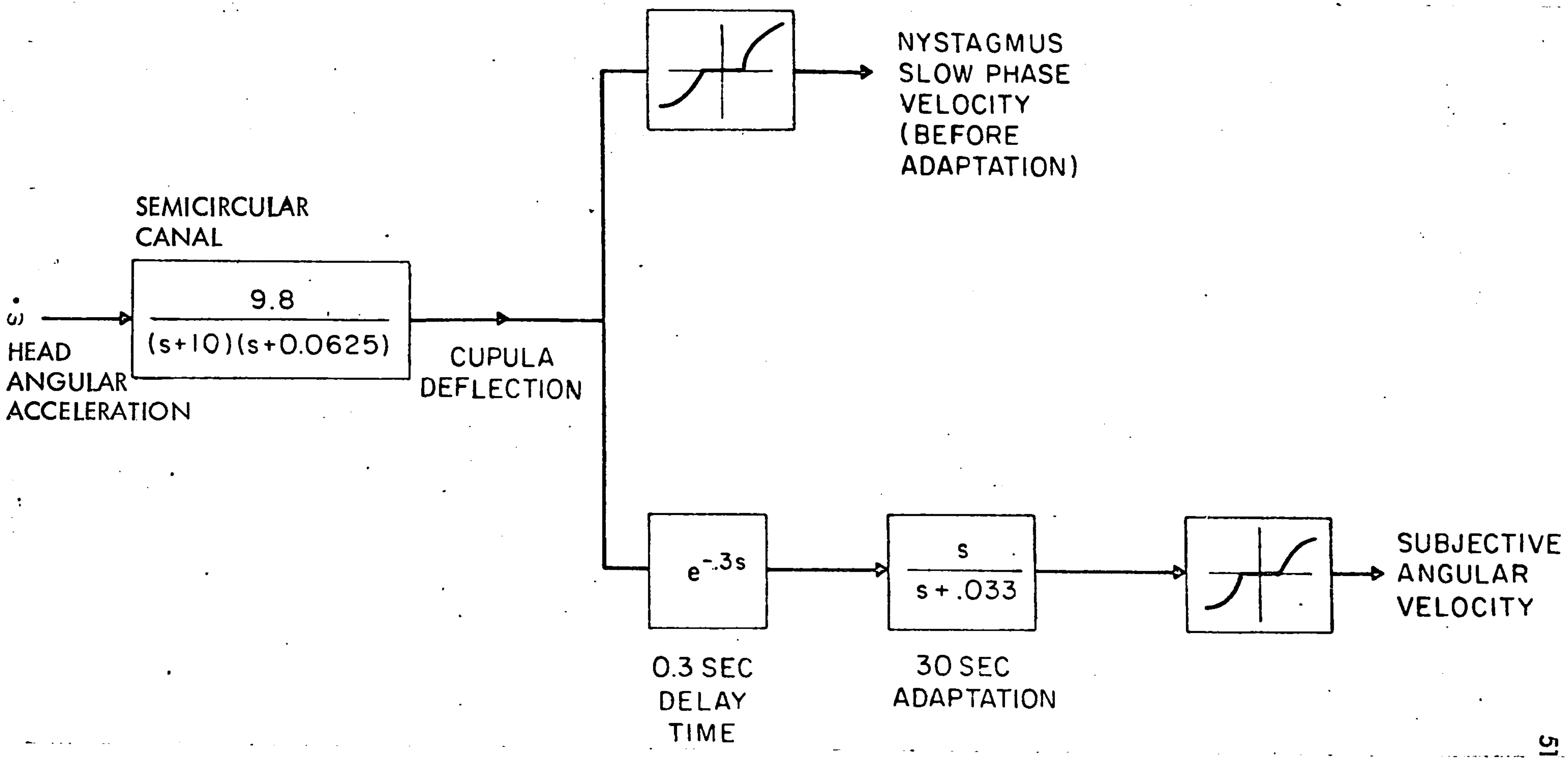

Fig. 4-4(a) MODEL FOR "ADAPTATION" EFFECTS IN THE VESTIBULAR SENSORY SYSTEM (from Young, 1968) To explain adaptation phenomena in the subjective response to canal stimulation Young proposes a high-pass filter with a time constant of 30 sec.

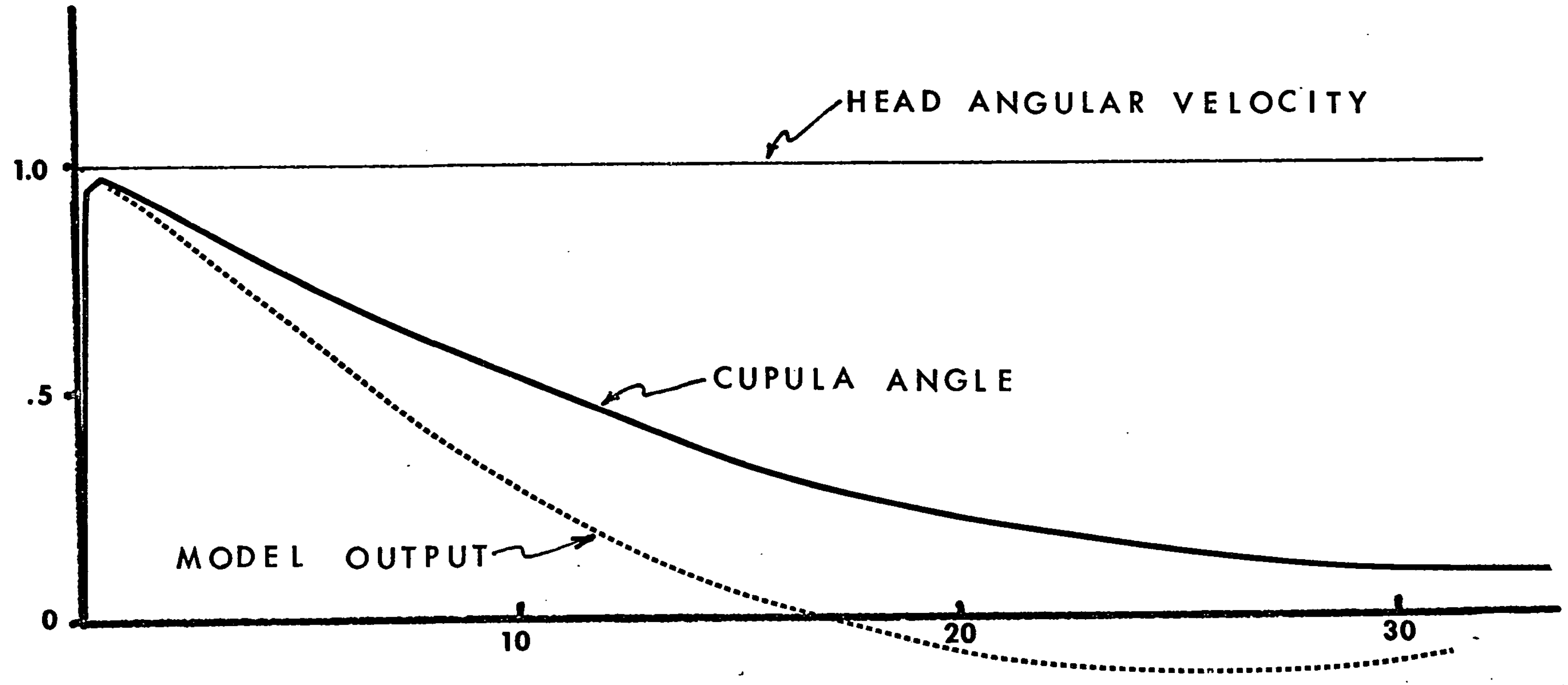

Fig. 4-4(b) COMPARISON OF RESPONSES OF YOUNG'S "ADAPTATION" MODEL AND OF THE CONVENTIONAL CANAL MODEL TO A STEP CHANGE IN HEAD ANGULAR VELOCITY.

to a step change in head velocity is compared with the corresponding theoretical time course of cupula position (solid line). Cupular response is assumed to correspond to the over-damped torsion pendulum model, and decays with a time constant which Young takes to be 16 seconds, a value obtained by fitting his model to experimental step-response data. Young shows that if the same data (e.g., the dotted line in Fig. 4-4b) were fitted to a second-order model in the conventional manner, a considerably lower value would be obtained for the long time constant. This is illustrated in Fig. 4-4c, in which the model output, θ_o, is plotted semilogarithmically against time. Provided the plot stops before the response magnitude becomes zero, then a reasonably straight line is obtained, with a slope corresponding to a time constant of 10 seconds. Thus a serious error in estimation of the "canal" parameter results if an over-simplified model is used. If one takes into account the overshoot which occurs later in the response then it is clear that the second order model is totally inadequate. Fitting the entire response to a third order model would make it possible to extract the correct "canal" time constant. Current work by Malcolm and Jones (1969) in this laboratory is concerned with evaluation of a similar but slightly more complex model of adaptation effects. Preliminary indications are that a more consistent fit to responses to several forms of rotational input may be possible with this model than is the case for that of Young.

Little is known as to the sources of these low frequency effects. Guedry (1965) has reviewed the evidence, relating to the effects of arousal and other factors, which point to a contribution by central neural mechanisms. The fact that some second-order vestibular neurones do not seem to show adaptation (Crampton, 1965, 1966; Shimazu & Precht, 1965; Jones & Milsum, 1967) seems to confirm this view. However the studies of Ledoux (1958, 1961) indicate that elements in the periphery are probably involved. Unfortunately it is not clear from the publications of Ledoux whether or not the neural connection to

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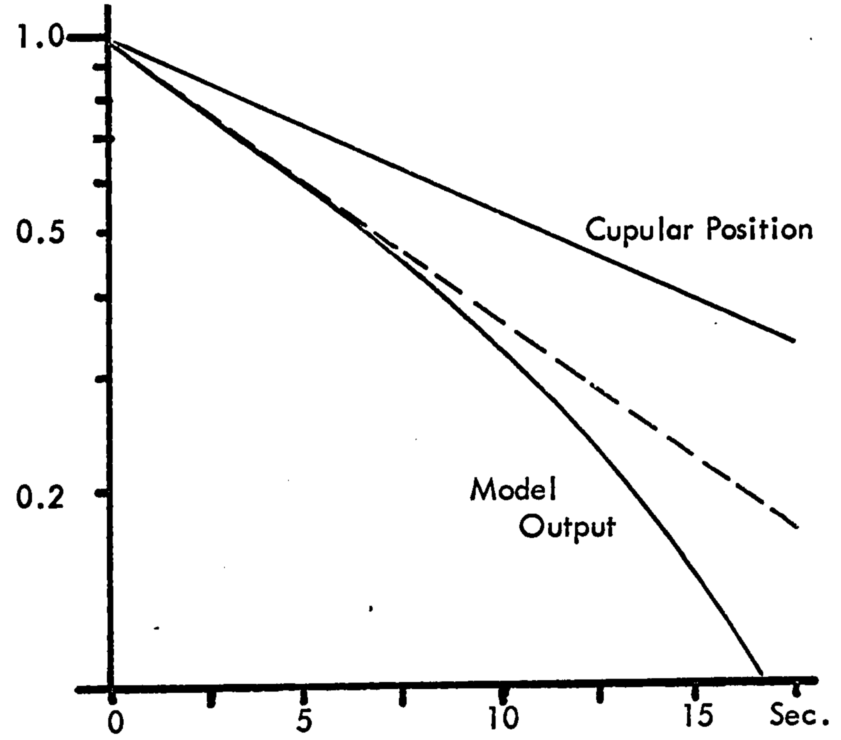

Fig. 4-4(c) SEMI-LOGARITHMIC PLOT TO ILLUSTRATE THE EFFECT OF POSTULATED "ADAPTATION" DYNAMICS ON ESTIMATION OF THE SEMICIRCULAR CANAL TIME CONSTANT.
Cupular position, decaying with a time constant of 16 seconds, yields the upper straight line when plotted vs. time in this way, whereas the output of Young's model yields a curved line owing to the presence of the adaptation term. The dashed straight line, such as might be fitted erroneously to the early part of the model output, has a slope corresponding to a time constant of 10 seconds.

the brain stem was severed in preparations showing adaptation, so that the role of vestibular efferent fibers cannot be assessed. There are of course electrochemical phenomena, common to all neurones, which might contribute to adaptation effects at any or all of several levels in the vestibular sensory pathway.

Those familar with the literature on adaptation may be tempted to ask why no mention has been made of phenomena, similar to the overshoot and response decline discussed above, which are observed in nystagmoid head response of pigeons (e.g., Mowrer, 1935). The answer lies in the much greater complexity of the "vestibulo-coilic" system controlling head movements (see Part III). The phenomena may be related, but there are strong arguments against jumping to such conclusions before the nature of vestibular control of head movement is clarified.

4.3.3 Proposal for a Neural Mechanism for High Frequency Filtering in the Vestibular Nuclei

It is pointed out in Chapter 3 that calculations based on semicircular canal dimensions yield a value of 0.005 sec. for the short time constant of the canals in man. In contrast, experimental studies have yielded much larger estimates. Van Egmond, Groen and Jongkees (1949) using the torsion swing, and Niven and Hixson (1961) and Hixson and Niven (1961) from human vestibulo-ocular response obtained average values of 0.1 sec. Miery (1965) fitted the simple second-order model to data from human vestibulo-ocular response and obtained a value of 0.04 sec. as the short time constant. However he was careful not to imply that this value necessarily characterized the canal response.

It might be argued that the discrepancy between theoretical and experimental estimates is due to technical difficulties. Theoretical estimates from canal dimensions may be too small owing to shrinkage during fixation of the specimens on which measurements were made (Jones & Spells, 1963). On the other hand, the experimental estimates, all of which are based on responses to oscillatory stimuli, may have been inaccurate because an inadequate range of stimulus frequencies was used. However there are more fundamental arguments against assuming that the short time constant determined from such experiments really characterizes the high frequency response of the semicircular canal. In the case of sensation, reaction time delay alone would be expected to cause pronounced phase lag at high frequencies and obscure canal characteristics, as Mayne (1965a) has pointed out, and in the case of reflex vestibulo-ocular response there is evidence, now to be discussed, for filtering of high frequency components in the rotation signal.

Recent work by Sugie and Jones (1966), discussed in detail in Chapter 5, suggests that there exists in the vestibulo-ocular reflex mechanism a low-pass filter with a time constant of one second, which leads to attenuation of high frequency components in the rotation signal. The effect may be due to mechanical and neuromuscular dynamics in the orbit, as discussed in the next chapter. However the possibility of neural filtering in the vestibular nuclei themselves becomes attractive in view of recent work by Shimazu and Precht (1966).

The latter authors found two groups of cells, designated Types I and and II, which were sensitive to horizontal angular acceleration, and located mainly in the superior and medial vestibular nuclei. Type I cells were monosynaptically excited by ipsilateral primary vestibular neurones. Type II cells, probably inhibitory to Type I cells, were excited bisynaptically or trisynaptically by contralateral primary afferents. Thus there appear to be relatively fast crossed and uncrossed pathways exerting respectively inhibitory and excitatory effects on Type I neurones. A shallow midline section between vestibular nuclear regions abolished the crossed inhibition, and uncovered a much slower crossed excitatory effect, presumed to be mediated by reticular connections. Thresholds for the two crossed pathways were found to be of the same order of magnitude.

The time course of the slow crossed excitatory effect on Type I neurones is of great interest. Shimazu and Precht (1966) give one example of this in a record of the firing frequency of a Type I cell, after section of the fast commissural pathway, in response to repetitive stimulation of the contralateral VIIIth nerve (Fig. 5 in Shimazu & Precht, 1966). The data from this record have been converted into a plot of firing frequency versus time in Fig. 4-5 (upper solid line). The lower solid line indicates the duration of nerve stimulation. The firing frequency is seen to rise slowly and then fall slightly during the period of stimulation, following which it declines slowly back to the resting level. The time course of the firing frequency can be approximated roughly by the dotted curve in the figure, which represents the response of a simple low-pass filter with a time constant of 0.25 sec. to a stimulus pulse having the same duration as the VIIIth nerve stimulation. There is an experimentally defined possibility for high frequency low-pass filtering in the vestibular nuclei themselves.

4.4 HABITUATION OF COMPLEX RESPONSES TO VESTIBULAR STIMULATION

Decline in the response to vestibular stimulation following repeated application of the stimulus is commonly known as vestibular habituation. It has been studied almost exclusively through examination of reflex or higher neural systems such as the subjective sensory system, and is generally believed to be due largely to central rather than peripheral mechanisms. The term "habituation" has been used in a specific sense by psychologists (Thorpe, 1950) to refer to a response decline attributable to repeated elicitation, and is supposed to be characterized by three features: "acquisition", "retention", and "transfer". Application of the term so defined to a response which is a complex function of time is difficult and requires a high degree of rigor and consistency in its use.

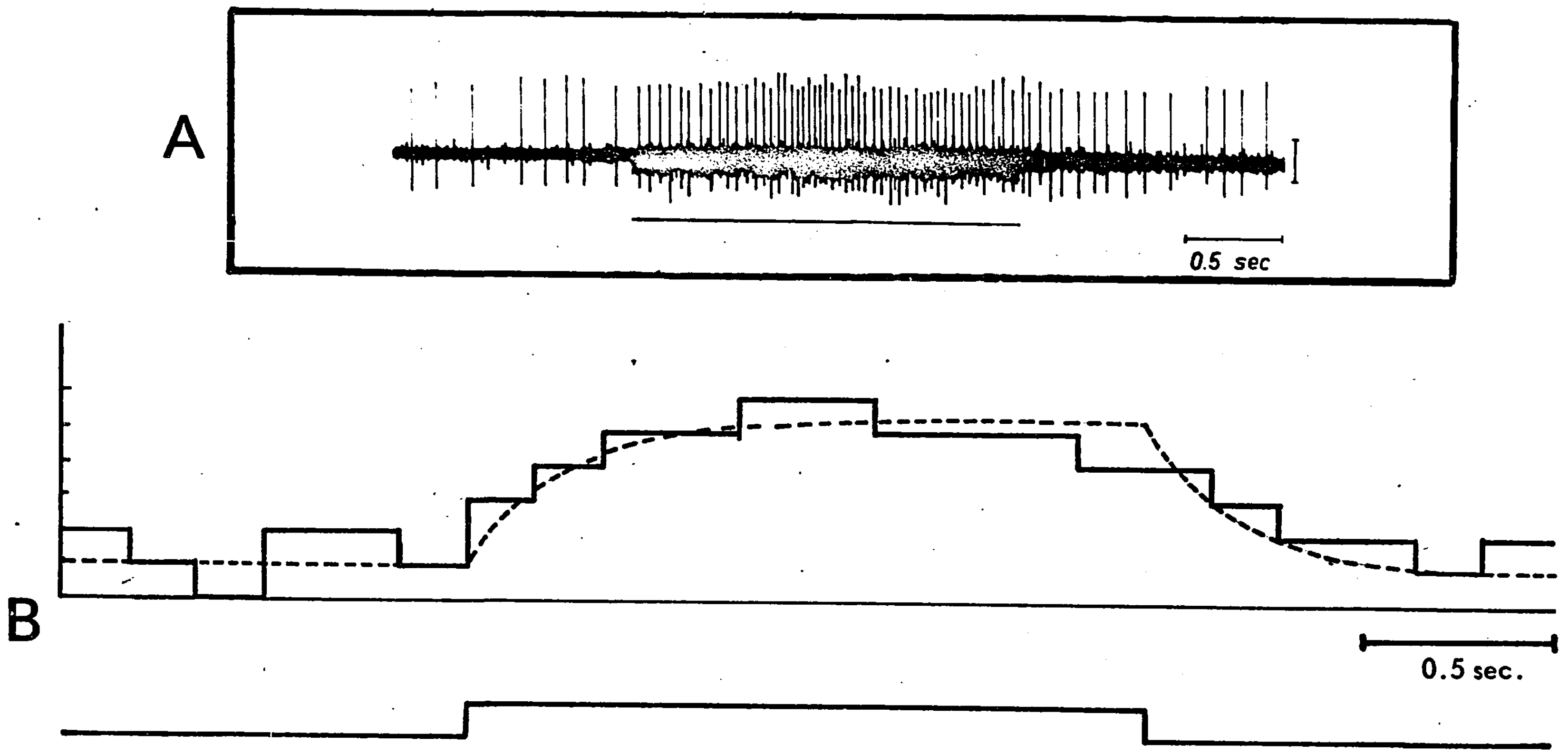

Fig. 4-5 EFFECT OF CONTRALATERAL VESTIBULAR NERVE STIMULATION ON TYPE I NEURONE OF SHIMAZU AND PRECHT, AFTER DORSAL MIDLINE BRAINSTEM INCISION

A – original record, reproduced from Shimazu & Precht, 1966 (their Fig. 5B). B – upper solid line = neural pulse frequency calculated from A; lower solid line = duration of vestibular nerve stimulation; dotted line= response of first order low pass filter with a time constant of 0.25 sec. to the same input. NOTE : time scales in A and B are different.

This definition carries the strong implication that the response-decline comes about by some auto-adaptive of learning process, the requirement for "transfer" being particularly emphatic in this respect. It must be emphasized however that any transformation, occurring within a system and having its dynamic effects at very low frequencies, might manifest itself as a slow, apparent change in the nature of the system's response, and might be interpreted as a change in the supposed parameters of the system if such parameters were defined in terms of an oversimplified model. Very low frequency effects are to be expected in neural systems owing to the complex physico-chemical phenomena which occur, and in the cupula response, as a result of slow mechanical "creep" which presumably occurs under stress. Similar slow dynamic effects might also occur as a result of processing in relatively "fixed" neural networks.

It is not the author's intention to make a case for one or other of these non-learning mechanisms as an explanation of habituation-type phenomena, nor should these comments be construed as an argument against the possible role of auto-adaptive or learning processes in so-called vestibular suppression. Rather the two possibilities must be considered together, and it seems unreasonable to become committed, even if only in terminology, to the more complex of two possible sets of hypotheses without first excluding the simpler one.

With these introductory comments a very brief review of the effects of repeated vestibular stimulation is presented.

Increased tolerance to the disconcerting effects of rotation has been observed frequently in persons occupationally exposed to frequent rotations (Dunlap, 1919; Mowrer, 1934c; de Wit, 1953; Krijger, 1954; Aschan, 1954; McCabe, 1960; Collins, 1965). De Wit (1953) in seamen, Krijger (1954) and Aschan (1954) in pilots and Collins (1965) in skaters found consistently low values for the decay time constant of sensory or reflex response to brief angular accelerations (velocity steps). Both Krijger and Aschan found that fighter pilots who had flat cupulograms (i.e., relatively low values for the long time constant) when flying regularly, frequently developed longer time constants during periods away from flying. Groen and Jongkees (1948) and de Wit (1953) describe reduced time constants (flattened cupulograms) in normal subjects exposed to large or repeated brief accelerations. Cawthorne, Dix, Hallpike and Hood (1956), recording the time course of slow phase eye velocity estimated by the oculogyral illusion, found a change in gain (i.e., in the magnitude of the best-fit exponential) but not in the time constant. They argued that the decline of response gain during the repeated stimulation required for the cupulogram would lead erroneously to a reduction in its slope. However this would only be true if the velocity steps were administered in order of increasing magnitude, a routine which the Utrecht school avoided (van Egmond, Groen & Jongkees, 1948), so that this argument is not valid. The time constant of the single exponential which yields the best fit to the recorded decline of slow phase eye velocity following a stopping stimulus has been shown to change dramatically with changes in head position (Benson & Bodin, 1966) so there seems little doubt that apparent changes in time constant can occur.

Gain changes and time constant changes therefore seem to be possible results of repeated simple stimuli. Unfortunately in the many other studies of "response decline" quantitative estimates of such specific changes have not been made (e.g., Abels, 1906; Bentley & Dunlap, 1918; Mowrer, 1934c; Hood & Pfaltz, 1954; Suzuki & Totsuka, 1960; Fernandez & Schmidt, 1963). In many cases the duration of nystagmus, or the number of saccades has been recorded; each of these could be affected by changes in the gain or in the time constant. Response decline also occurs following repeated caloric stimulation (Henriksson, Kohut & Fernandez, 1961; Fluur & Mendel, 1962; Fernandez & Schmidt, 1963).

Such studies are more difficult to relate to quantitative theories, though mathematical modelling of events involved in caloric nystagmus (Steer, 1967) may make this more feasible.

"Response decline" has also been studied in situations where conflicting sensations may be expected from linear and angular acceleration receptors as well as proprioceptive and other sensors. These studies have recently been reviewed by Guedry (1965), and they provide considerable food for thought, though few consistent relationships have emerged as yet.

Studies on the "retention" of vestibular habituation have yielded very variable results. De Wit (1953) reported almost complete recovery of the cupulogram slope in human subjects two hours after the end of a series of repeated stopping stimuli. Groen and Jongkees (1948a) in man noted suppression lasting several days. Fernandez and Schmidt (1963) found suppression in cats lasted days or weeks depending on the number of stimuli and the degree of suppression. Griffith (1924) reported that in man the effects lasted for years.

Factors governing the rate of "acquisition" of the suppression are not clear. According to Hood and Pfaltz (1954) the decline in rabbits depends largely on the number of stimuli, the interval between them having little effect. In their study the interval between stimuli was varied from one minute to one week. This indicated a very slow recovery rate in these animals. Other detailed studies on the interplay between suppression and recovery appear to be lacking, though an exhaustive literature search has not been made by this writer. The question is a significant one for any quantitative description of the phenomenon.

Habituation is often related to the learning process (Groen, 1961; Guedry, 1965; Howard and Templeton, 1966) and there can be little doubt that such phenomena are involved to some extent. This implies that the suppression should be specific to the stimulus, or more properly to stimuli having certain salient properties in common. The carry-over of suppression from the response to the original stimulus to the response of a different stimulus would be called "transfer" and is a manifestation of the extrapolative nature of the learning process. As such one would expect it to be less striking in lower animals but this aspect has not apparently been investigated.

In recent studies of "transfer" using simple stimuli, Crampton (1962) found no transfer using rotations in opposite directions. Correspondingly Fernandez and Schmidt (1963) and Henriksson et al. (1961) found that repeated caloric stimulation with hot water in one ear resulted in reduced response to ipsilateral hot and contralateral cold stimulation, but normal response to ipsilateral cold and contralateral hot stimulation. Hood and Pfaltz (1954) obtained no suppression with repeated caloric testing, and no transfer from rotational to caloric modes of stimulation. Guedry (1965) has reviewed transfer experiments using various complex forms of stimuli; the results are complex also and no useful generalizations seem to emerge as yet.

A possible factor in vestibular suppression is the predictive ability of the human subject. This phenomenon has been extensively studied in man-machine applications (Wilde & Westcott, 1963; Morgan et al., 1963) and in the visual tracking system (Young, 1962; Michael & Jones, 1966). The implication is that the subject, perhaps unconsciously, identifies the nature of a repetitive stimulus and is thus able to predict what will happen next and so improve the tracking response. In visual tracking it is found for example that when an oscillatory target motion is suddenly stopped the eye continues for some seconds along the path the target would normally have followed. Travis and Dodge (1928) and von Bekesy (1955) observed a similar phenomenon in the vestibular system, subjects reporting that the sensation of oscillatory rotation continued up to 20 seconds after actual oscillation of the turntable had ceased. However, in this case prolonged exposure to the oscillatory motion was necessary. This finding may be related to findings of Cramer, Dowd and Helms (1963) who studied in cats the effect of prolonged daily rotational oscillation at a given frequency. Though poorly defined in the preliminary study, there is clearly a change in phase shift of the vestibulo-ocular response to stimulation at the test frequency and neighbouring frequencies. These phenomena in the vestibular system are different from the manifestations of "prediction" demonstrated by Young (1962) and others in the visual tracking system. It would be interesting to study the response of vestibular systems such as the vestibulo-ocular reflex using unpredictable inputs in the manner of Young. It might be possible in this way to study slow dynamic phenomena without interference from the usual learning or predictive mechanisms.

Before leaving the topic, mention should be made of some of the confusing factors which plague studies of vestibular suppression. The concept of habituation as learning implies learning to weight non-vestibular inputs in favour of "undesirable" vestibular sensations. Non-learning contributions to vestibular suppression are difficult to evaluate since it is difficult if not impossible to suppress all non-vestibular sensory input. On the other hand, it is difficult to ensure reproducible results from the learning mechanism, because arousal plays so important a role in this process. Arousal variations contribute in other ways also. Nystagmus under any circumstances is very sensitive to change in arousal, and may disappear completely in drowsy subjects. The corneo-retinal potential, commonly used as the basis for recordings of eye movement, is also reduced in drowsy subjects (Kris, 1960). Finally, this potential also varies dramatically during changes in retinal dark adaptation (Kris, 1958; Gonshor & Malcolm, 1968).

4.5 CONCLUSION - PART I

This section brings to an end the first portion of this thesis, which reviews current understanding of the vestibular sensory pathway, particularly those aspects which are relevant to the investigation of reflex phenomena resulting from semicircular canal stimulation. The considerable length of this portion of the thesis results from an emphasis on the possibilities for processing of the rotation signal at different stages in the sensory pathway.

Basic anatomical and physiological knowledge of the labyrinthine receptors has been presented, and the classic hydrodynamic theory of semicircular canal function has been reviewed. Dynamic response characteristics of the canals have been discussed in detail with emphasis on methods, both experimental and theoretical, for estimating the parameters which characterize canal response.

In the present chapter current anatomical and experimental understanding of the vestibular sensory pathway has been reviewed. Special consideration has been given to experimental observations from which useful quantitative hypotheses can be made as to the nature of the neural processing which occurs. In one case, that of high frequency filtering of the rotation signal in the vestibular nuclei, a new quantitative hypothesis has been put forward. The importance of giving careful attention to the possibility of dynamic processing or filtering of the rotation signal by neural mechanisms after its first appearance as a cupula deflection, emerges as a major point of emphasis.

The subject of habituation of complex responses to vestibular stimulation and related phenomena has been given fairly extensive consideration in this chapter. While not central to the theme of this thesis, these phenomena are of interest since they presumably reflect in some degree the vast adaptive and optimizing capability of the central nervous system. Studies of optimization in the vestibulo-ocular system, described in Chapter 6, are related in a broad sense.

Parts II and III of this thesis deal with original theoretical and experimental investigations of reflex responses to the rotation signal. Part II, which is entirely theoretical, carries on the theme of dynamic processing, elaborated in this chapter, to a detailed consideration of a simple mathematical model of the vestibulo-ocular system. The same theme underlies the approach to experimental investigations described in Part III.

PART II

THEORETICAL STUDIES OF THE VESTIBULO-OCULAR SYSTEM

CHAPTER 5

THEORETICAL ANALYSIS OF A MATHEMATICAL MODEL OF THE VESTIBULO-OCULAR REFLEX SYSTEM.

5.1 INTRODUCTION

Buys (1922) was one of the first investigators to suggest using the velocity of compensatory or "slow-phase" eye movement, measured under appropriate conditions, as an index of cupula motion. Support for this view increased with the discovery that in response to the classic stopping stimulus (step change in head angular velocity), slow-phase eye velocity consistently decayed along an approximately exponential time course with a time constant of the same order as that expected of the canal itself. The demonstration by Lorente de No (1933), Szentagothai (1950) and others, of the rather simple three-neurone structure of the basic vestibulo-ocular reflex arc also suggested a close connection between cupula signal and the eye velocity compensating for it.

On the basis of this and other more tenuous evidence, it has become customary to assume or imply that slow-phase eye velocity in the vestibulo-ocular response is directly proportional to cupular angle. The very real possibility of dynamic processing by neural and oculomotor mechanisms thus tends to be glossed over. Recent studies by Sugie and Jones (1965, 1966) clearly indicate the existence of such processing, and suggest specifically the functional nature of one of the mechanisms involved. A major finding by these authors is that in different experimental situations, quantitatively significant variations occur in the dynamic relationship between cupula signal and compensatory eye velocity. In the present chapter, detailed analysis of a mathematical model proposed by Sugie and Jones is undertaken in an attempt to clarify further the nature of some of these variations.

It has been customary to assume that the quick saccadic flicks of eye position, so characteristic of the vestibulo-ocular response, do not affect the velocity of the eye during the ensuing slow-phase movement. This implies that each saccadic flick results from the super-position of an approximate step change of eye position upon the on-going compensatory eye movement. Miery (1967) explicitly makes this assumption in computing "cumulative eye position", this being a running estimate of the eye position which would supposedly have occurred if saccades had been absent. Miery has obtained fairly consistent results by this method in the analysis of records of human eye movement during sinusoidal head motion. The utility of this method is not seriously prejudiced by the ensuing discussion, but there is evidence that this explanation of the observed eye movement is inadequate.

It has been known for some time that saccadic activity in the vestibulo-ocular system may be differentially suppressed at certain stages of ether anaesthesia and in some other situations, and that with complete suppression of all saccadic flicks a form of continuous, smooth, tracking eye movement persists. Sugie and Jones (1966), in experiments on cats, have studied the consequences of different degrees of saccadic suppression using varying levels of ether anaesthesia, and note that the occurence of a saccade has a clearly defined effect on eye velocity during the ensuing slow-phase interval. The magnitude of the effect, which is to increase slow-phase eye velocity, is dependent on the magnitude of the saccadic flick, and repeated saccades have a cumulative effect.

These authors have developed a mathematical model for the vestibulo-ocular system which appears to explain their findings, and this is illustrated in Fig. 5-1. The basic feature of the model is the hypothesis that there is a mechanism, which when unforced always tends to drive the eye towards its resting or central position at a rate proportional to its instantaneous displacement from that position. Such a mechanism, if assumed to have an input $x(t)$ and an output $y(t)$, may be characterised by the differential equation

$$T_3 \frac{dy(t)}{dt} + y(t) = T_3\, x(t),$$

or by the Laplace transfer function

$$\frac{y(s)}{x(s)} = \frac{T_3}{T_3 s + 1} \quad .$$

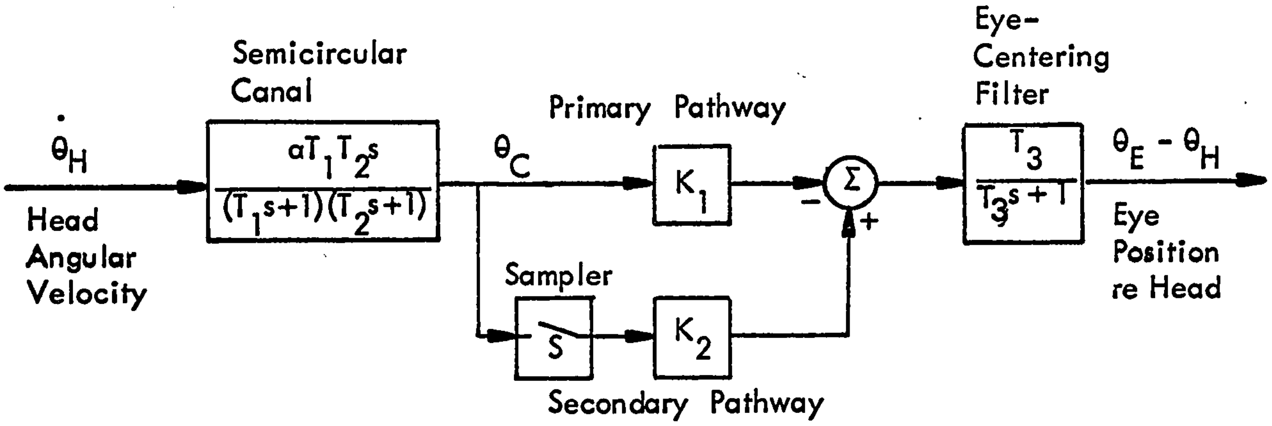

Fig. 5-1 SUGIE-JONES MODEL FOR THE VESTIBULO-OCULAR SYSTEM (from Sugie and Jones, 1965, 1966)

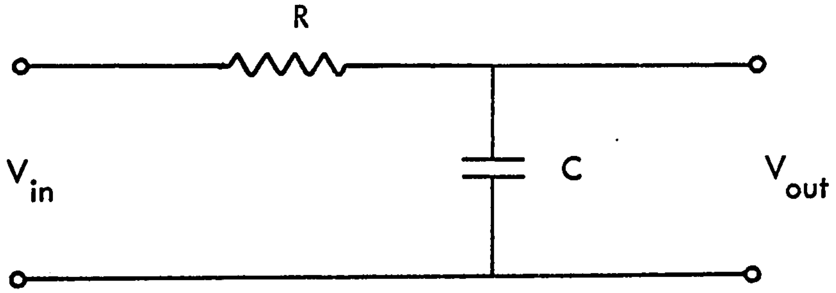

Fig. 5-2 A LOW-PASS R-C FILTER, OR APPROXIMATE INTEGRATOR This circuit has the transfer function 1/(RCs+1), and may be used as an analog of the eye-centering filter of the Sugie-Jones model

This is a simple low-pass filter with a time constant T_3, which Sugie and Jones estimated to be about one second in the cat.

A first-order low-pass filter is equivalent to the electronic R-C filter shown in Fig. 5-2, sometimes called an "integrator with leak". It integrates high frequency components in the input, but passes low frequency components without change.

In the model proposed by Sugie and Jones, the filter has two inputs. One is a continuous signal, directly proportional to cupula deflection, which is carried by the "primary pathway" (Fig. 5-1). A "secondary pathway", responsible for the saccades, carries a "sampled" signal consisting of a train of pulses whose effects are described below. It should be emphasized that the semicircular canal signal (i.e. cupula deflection) is assumed to be a velocity signal, as discussed in Chapter 3.

When saccades are completely suppressed, then according to the model the only input to the filter would be the continuous signal from the canals. Input components at high sinusoidal frequencies (above about 1.6 cps.) would be accurately integrated, providing an output, eye position, appropriate to compensate for the velocity signal from the canals. At such frequencies one would expect smooth, non-saccadic tracking to be adequate, at least in so far as phase relationships are concerned.

At frequencies near and below the break frequency of the filter, the model leads one to expect serious errors to occur in non-saccadic vestibulo-ocular response, eye position becoming progressively phase advanced and attenuated until it is more closely related to head velocity than to head position. Sugie and Jones have shown that this does indeed occur, and that under these conditions in which integration by the continuous pathway is poor, the occurrence of saccades effectively acts to improve the quality of integration, producing an increase in the velocity of the eye during the slow phase and causing the points of zero eye velocity to occur later in the sinusoidal cycle than is the case in the non-saccadic response. At these frequencies therefore the occurrence of saccades results in compensation for head velocity, which though it is intermittent, is much more precise than in the non-saccadic case.

Sugie and Jones explain the saccade as the result of a pulse acting on the same filter mechanism as that providing approximate integration of the continuous canal signal, and propose a sampled or saccadic pathway in the vestibulo-ocular system, carrying a train of pulses, one pulse corresponding to each saccade. The pulses are not of course to be thought of as single action potentials, but presumably as narrow bursts of action potentials, such as are commonly seen in association with saccades in recordings from the oculomotor nuclei (Jones & Sugie, 1965 Schaeffer, 1965).

In the preliminary version of the Sugie-Jones model illustrated in Fig. 5-1, the saccadic pulse train is considered to have a fixed frequency of about five per second, with the pulse-amplitude modulated by the cupula signal. These assumptions of fixed frequency and amplitude modulation are admittedly approximations, though in simulation studies they provide results which quite closely resemble experimental records. In actual fact there appears to be some form of frequency modulation of the saccadic pulse train, perhaps also by the canal signal, and there is some inconsistency with the assumption of amplitude modulation. Further experimental studies on these points are thus required before definitive statements can be made.

Before continuing to examine some implications of the model, it is interesting to consider the possible nature and site of the filter mechanism. One possibility, that of a neural filter in the vestibular nuclei, has been considered in Section 4.3.3. There is another possibility however, and the two are not mutually exclusive. Robinson (1964, 1965) has made a detailed study of the dynamics of human eye movement, and has proposed a mathematical model relating eye movement to the active-state tension exerted by the extra-ocular muscles. The eye was found to be very heavily damped, and orbital dynamics, which are assumed to include the effects of neural control loops involving the extra-ocular muscles, are represented by two visco-elastic "Voigt" elements in series. The model is described by a fourth-order differential equation, and its frequency response

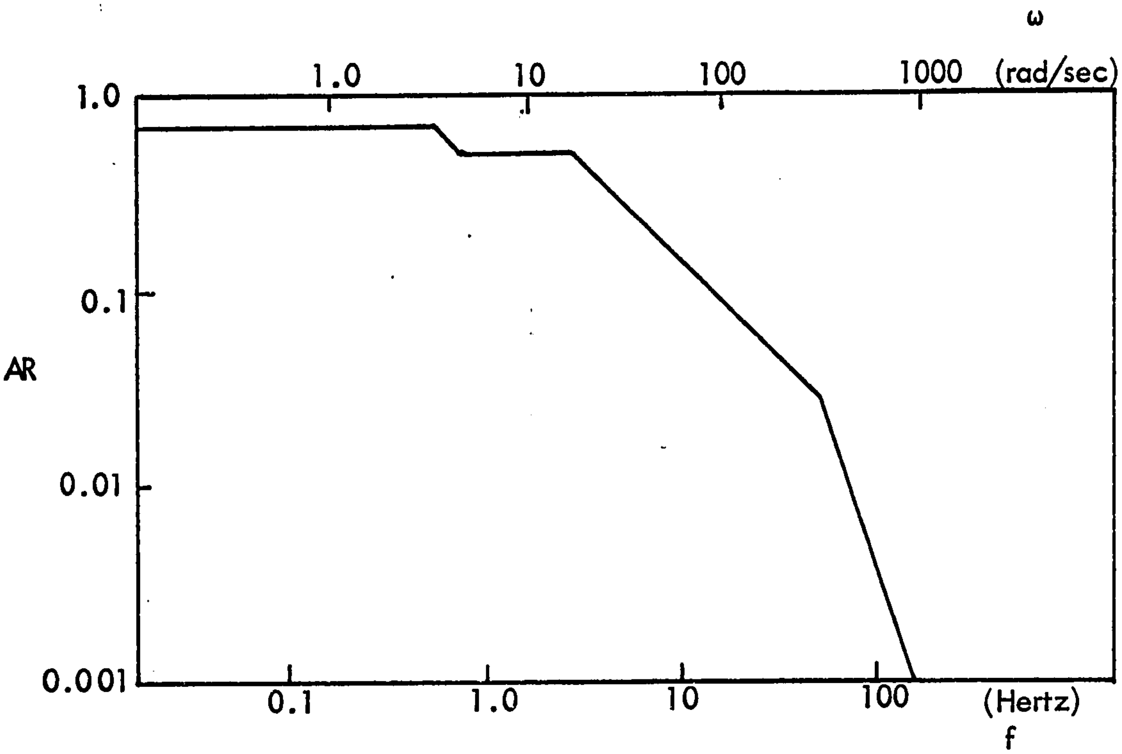

Fig. 5-3 FREQUENCY RESPONSE (AMPLITUDE RATIO) OF ROBINSON'S MODEL (1968) OF HUMAN ORBITAL DYNAMICS.
(Model input is Active State Tension of muscle, output is Eye Position)

(Robinson, 1968) shows a first break down at a frequency corresponding approximately to the time constant of the slowest "Voigt" element, which is 0.3 seconds (Fig. 5-3). In other words active-state tension, which presumably is closely related to action potential frequency in the muscle nerve, would produce a proportionate eye movement at low frequencies, with attenuation and phase lag at high frequencies. In a suitably restricted frequency range this is very similar to the effect of the simple low-pass filter or leaky integrator proposed by Sugi and Jones, and the time constants correspond fairly well. The filter required to explain vestibulo-ocular responses may thus be entirely due to orbital dynamics. Current studies (Tarlo & Jones, 1968) are aimed at elucidating this point but as yet it is impossible to be certain whether central or orbital mechanisms are more significant.

5.2 MATHEMATICAL ANALYSIS

5.2.1 General

In this section the Sugie-Jones model for the vestibulo-ocular system is analysed in detail. The initial portion of the analysis, including the content of Sections 5.2.2 and 5.2.3 has been reported by Sugie and Jones (1966). Most of the remaining two sections is original; analytical results obtained by Sugie and Jones are so indicated as they occur. The entire analysis is presented together for the sake of continuity.

It is convenient for the purpose of analysis to redraw the block diagram of the model as in Fig.5-4 to show two distinct pathways, one continuous and one discontinuous or sampled. The cupula signal θ_C divides to form the input to the continuous and sampled pathways, and their outputs, y_1 and y_2 respectively, are combined algebraically to yield the final output $\theta_E - \theta_H$, the resulting position of eye in skull. The transfer function G(s) and the corresponding impulse response[1] g(t), are assumed to be the same for both pathways, so that the block diagram is functionally

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[1] The impulse response of a dynamic system is the response of the resting system to a unit impulse funtion, and is the time domain equivalent of the Laplace transform. The unit impulse function or 'delta function' of Dirac, may be regarded for conceptual purposes as a pulse of unit area and infinitesimally short duration. In the present case the impulse response is the response which would be obtained if, with no input to the system, the eye were passively deflected through a unit angle and then suddenly released.

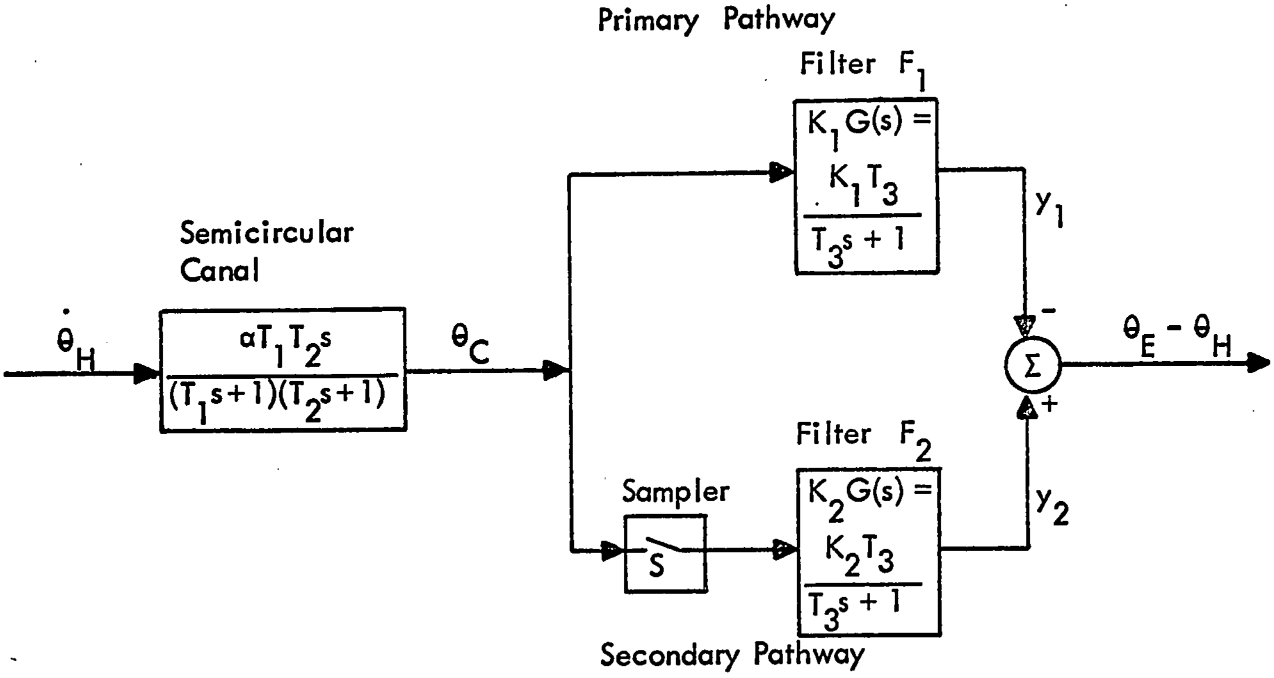


Fig. 5-4 SUGIE-JONES MODEL FOR THE VESTIBULO-OCULAR SYSTEM
(Redrawn from Fig. 5-1 to emphasize the two pathways)

identical to that of Fig. 5-1.

The continuous pathway consists of a simple first-order lag with the Laplace transfer function

$$\frac{Y_1(s)}{\theta_C(s)} = K_1 G(s)$$

$$= \frac{K_1 T_3}{T_3 s+1}$$

and impulse response

$$h_1(t) = K_1 g(t) = K_1 e^{-t/T_3} \quad \text{(for } t>0)$$

$$= K_1 e^{-at} U_{-1}(t)$$

where

$$a = 1/T_3$$

The symbol $U_{-1}(t)$ is used to denote a unit step function occurring at $t=0$.

The sampled pathway involves a similar transformation, but it is preceded by a sampler indicated by the switch S which closes momentarily every T seconds. To simplify analysis it will be assumed that the sampler is ideal, closing for an infinitesimally short time every T seconds to produce a train of impulses, the area of each impulse being proportional to the instantaneous cupular deflection. In a real model, in which idealimpulses are approximated by rectangular pulses, an adjustment must be made to the gain of the sampled pathway, but there is little other effect except at very high frequencies, provided the actual pulses are short compared to the duration of the sampling interval T.

It is assumed throughout that inputs are applied at time $t=0$, and that the sampler S closes for the first time T seconds after the application of an input. The latter assumption is made because of the fact that experimentally observed transient responses in the vestibulo-ocular system nearly always begin with a compensatory ("slow phase") movement, while saccades are in the anti-compensatory direction.

The output of the sampler is a train of impulses, amplitude modulated by the cupula signal, and represented

$$\theta_C^*(t) = \theta_C(t) \sum_{k=1}^{\infty} U_0(t-kT)$$

where $U_0(t-kT)$ represents a unit impulse function occurring at time $t=kT$. The output of the filter F_2 will thus be the weighted sum of a series of delayed impulse responses

$$y_2(t) = K_2 \sum_{k=1}^{\infty} \theta_C(kT)\, e^{-a(t-kT)}\, U_{-1}(t-kT) \qquad \text{............Eq. 5.1}$$

Note that the magnitude of the $(k)^{th}$ impulse response is $K_2\theta_C(kT)$, and that the $(k)^{th}$ "saccadic" jump is of the same magnitude.

At the $(n)^{th}$ sampling instant, $t=nT$, and

$$y_2(nT) = K_2 \sum_{k=1}^{n} \theta_C(kT)\, e^{-a(nT-kT)} \qquad \text{......................Eq. 5.2}$$

During the $(n)^{th}$ sampling interval, $t= nT + (t-nT)$, and hence

$$y_2(t) = e^{-a(t-nT)}\, K_2 \sum_{k=1}^{n} \theta_C(kT)\, e^{-a(nT-kT)}, \quad nT \leqslant t < (nT+T)$$

$$= e^{-a(t-nT)}\, y_2(nT), \quad nT \leqslant t < (nT + T) \qquad \text{.............. Eq. 5.3}$$

Thus during each sampling interval the saccadic pathway output decays exponentially from its value immediately after the preceding saccadic jump. The decay has a time constant of $a = 1/T_3$, and is always the same regardless of the form of the input θ_C.

The velocity $\dot{y}_2$ due to the saccadic pathway is obtained by differentiating Eq. 5.1, i.e.,

$$\dot{y}_2(t) = -a\, K_2 \sum_{k=1}^{\infty} \theta_C(kT)\, e^{-a(t-kT)}\, U_{-1}(t-kT)$$

$$+ K_2 \sum_{k=1}^{\infty} \theta_C(kT)\, e^{-a(t-kT)}\, U_0(t-kT)$$

$$= -a\, y_2(t) + K_2 \sum_{k=1}^{\infty} \theta_C(kT)\, U_0(t-kT) \qquad \text{..............Eq. 5.4}$$

The second term in this expression represents a series of impulse functions which occur on differentiation owing to the jump discontinuities ("saccades") which exist in the position output at the sampling instants. The impulses thus correspond to "quick-phase" velocity. The functionally important slow-phase velocity due to the saccadic pathway will be denoted

$$\dot{y}_{2,s}(t) \; = \; -a \, y_2(t) \; \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \; \text{Eq. 5.5.}$$

Thus it emerges that the waveform of slow-phase saccadic pathway velocity is, except for a scale factor and polarity reversal, identical in every respect to the waveform of saccadic pathway position . This is a general result and is of some importance. In contrast, the relationship between position and velocity in the continuous pathway is of course frequency dependent.

5.2.2 Response to a Step Change in Cupula Position

This response, described by Sugie and Jones (1966), is useful to consider as it illustrates in a simple way the characteristic features of the basic filter mechanism with its sampled and continuous inputs. It must be emphasised however that the response considered here is the response to a step change of cupula position and not of head position or head velocity. Such an input is unnatural, but has the analytical advantage that it demonstrates the effect of continuous and saccadic pathways without the confusion of a continuously varying cupula signal.

If the cupula signal, θ_C, is a unit step function occurring at time $t=0$, then the output of the continuous pathway will be

$$y_1(t) = \frac{K_1}{a}\left(1 - e^{-at}\right),$$

$$\dot{y}_1(t) = K_1 e^{-at}.$$

To obtain the output of the sampled pathway note that the output of the sampler, θ_C^*, will be a train of unit impulse functions, that is

$$\theta_C^*(kT) = 1, \quad k = 1, 2, 3, \ldots..$$

Substitution in Eq. 5.2 yields

$$y_2(nT) = K_2 \sum_{k=1}^{n} e^{-a(nT-kT)}.$$

This can be summed as the partial sum of a geometric series, yielding

$$y_2(nT) = K_2 \frac{1 - e^{-anT}}{1 - e^{-aT}}.$$

Hence by Eq. 5.3 and Eq. 5.5 ,

$$y_2(t) = K_2 e^{-a(t-nT)} \frac{1 - e^{-anT}}{1 - e^{-aT}} \quad , nT \leq t < (nT+T)$$

$$\dot{y}_{2,s}(t) = -aK_2 e^{-a(t-nT)} \frac{1 - e^{-anT}}{1 - e^{-aT}} \quad , nT \leq t < (nT+T).$$

The responses of continuous and saccadic pathways are displayed individually in Fig. 5-5, position outputs being shown in Fig. 5-5(a) and velocity outputs in Fig. 5-5(b). The curves were obtained from an analog computer model using the parameter values $a = 1.0 \text{ sec}^{-1}$, and $T = 0.2$ sec, as suggested by Sugie and Jones (1966), and with $K_1 = K_2 = 1.0$. As noted earlier the velocity output of the saccadic pathway is seen to be identical to its position, except for the reversal of sign and the presence of impulses in the velocity output at the sampling instants. The impulses are not seen in Fig. 5-5(b).

It must be emphasized that the jagged curves of Fig. 5-5 represent the contribution of the saccadic pathway only, and not the final eye movement, which is considered below.

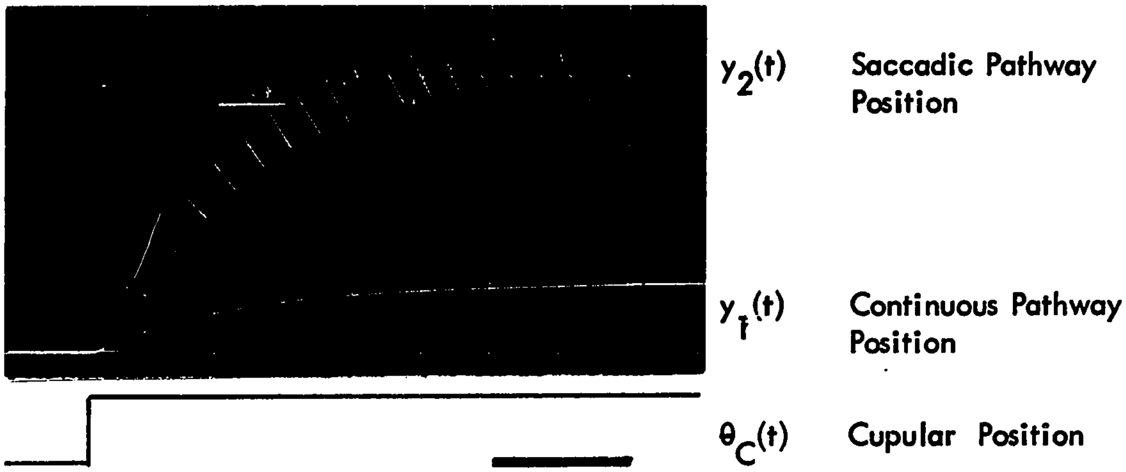
Position output of the sampled pathway at the sampling instants follows the same time course as the output of the continuous pathway, but has a greater magnitude (Fig. 5.5 (a)). For the parameter values stated, the output $y_2(nT)$ reaches an asymptote which is greater than the asymptotic value of $y_1(t)$ by the factor,

$$F = \frac{a}{1 - e^{-aT}}$$

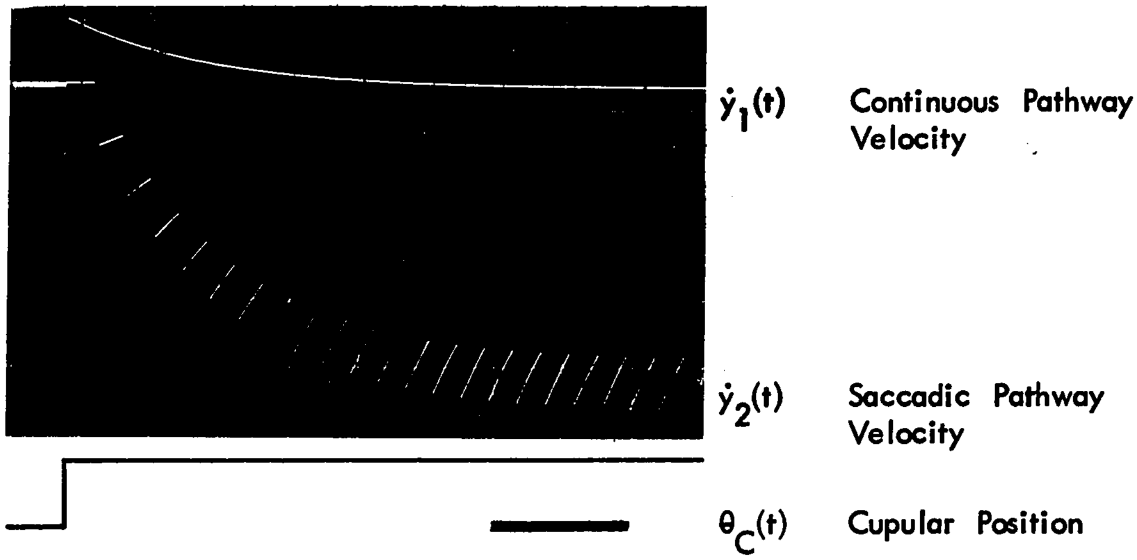
Using the well known series expansion for the exponential, and truncating after the second term yields the approximation

$$F \approx 1/T.$$

Thus in the present case the final asymptotic value of the saccadic pathway position



(a) POSITION OUTPUTS



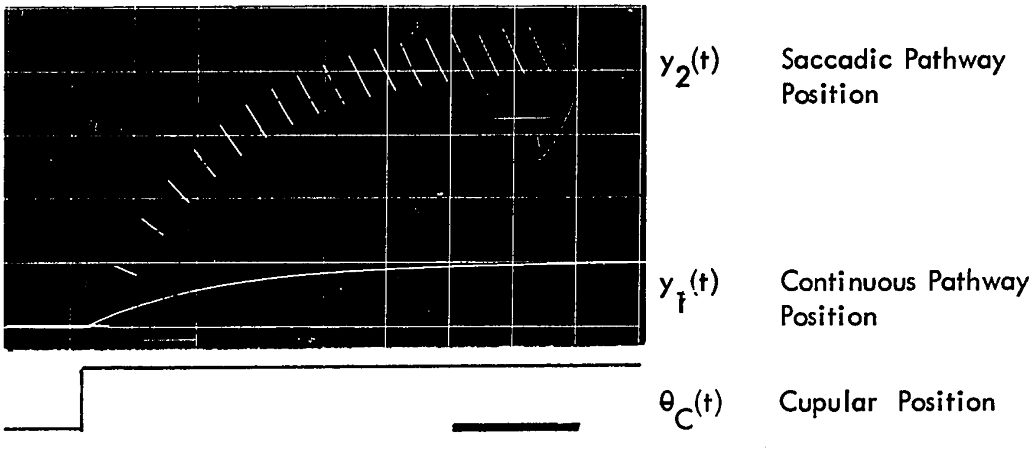
(b) VELOCITY OUTPUTS

Fig. 5-5 RESPONSES OF THE CONTINUOUS AND SACCADIC PATHWAYS OF THE SUGIE-JONES MODEL TO STEP CHANGES IN CUPULAR POSITION

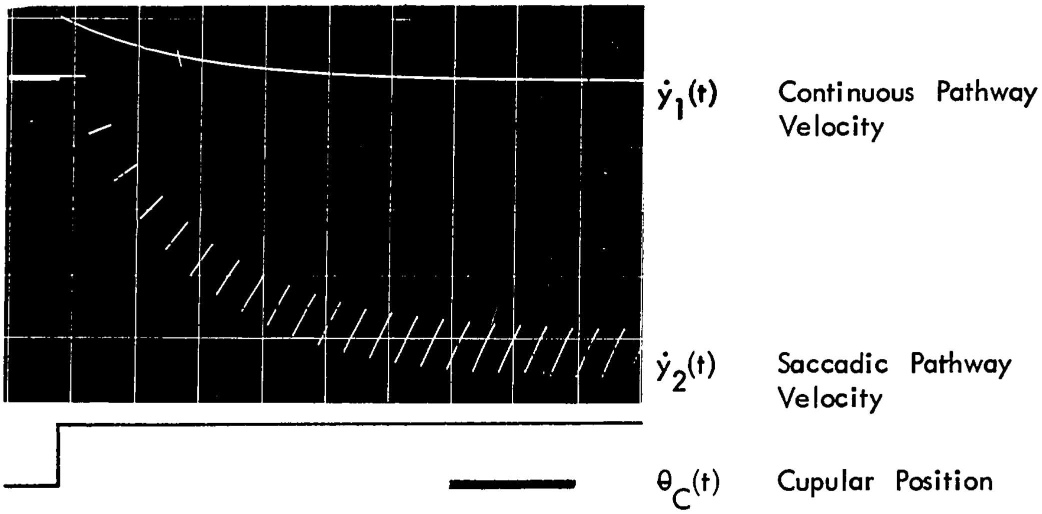
Model parameters: $K_1 = K_2 = 1.0$; $T = 0.2$ sec.; $T_3 = 1.0$ sec.

(Note that the impulses which theoretically occur in the saccadic pathway velocity output are omitted for the sake of clarity.)

Horizontal bars = 1 second.



(a) POSITION OUTPUTS



(b) VELOCITY OUTPUTS

Fig. 5-5 RESPONSES OF THE CONTINUOUS AND SACCADIC PATHWAYS OF THE SUGIE-JONES MODEL TO STEP CHANGES IN CUPULAR POSITION

Model parameters: $K_1 = K_2 = 1.0$; $T = 0.2$ sec.; $T_3 = 1.0$ sec.

(Note that the impulses which theoretically occur in the saccadic pathway velocity output are omitted for the sake of clarity.)

Horizontal bars = 1 second.

output at the sampling instants is approximately five times the final value of the continuous pathway postion output. However if the gain K_2 of the saccadic pathway is set equal to $1/F$, or approximately equal to the magnitude of T, the sampling interval, then the final eye position output,$(\theta_E - \theta_H) = y_2 - y_1$, becomes that shown in Fig. 5-6(a). The corresponding slow-phase eye velocity, $(\dot{\theta}_{E,s} - \dot{\theta}_{H})$, is shown in Fig. 5-6(b). It will be seen that in these circumstances the nystagmoid eye movement which occurs is centered very near the zero position. However the time course of successive slow-phase eye movements is identical, and all have the same mean slope. Thus the combined action of the two pathways at this particular value of the relative gain $(K_1/K_2 = 1/T)$ results in a response showing two major advantages. On the one hand the overall eye deviation is small, and on the other hand the time course of mean slow-phase eye velocity is essentially the same as the time course of cupula position but in the opposite (i.e., compensatory) direction.

Sugie and Jones (1966) have shown that this appears to be a general result, which holds for all the usual types of test input. That is, provided the gain ratio (K_1/K_2) remains approximately equal to $1/T$, the time course of mean slow-phase eye velocity will be very nearly the same as the time course of cupula position. This appears to validate the time-honoured assumption that slow-phase eye velocity is proportional to cupula deflection. However it must be emphasized that the model only substantiates this assumption for a certain specific value of the gain ratio. When the gain ratio differs from this value the model predicts that the time course of mean slow-phase eye velocity will deviate considerably from that of cupula position. An evaluation of the effect of variation in the gain ratio on the response of the model is one of the significant features of the analysis described in the next two sections.

A brief note concerning the actual value of the critical gain ratio is in order. In the ideal case considered here, in which the saccadic pathway carries a train of ideal impulses, the value $K_1/K_2 \cong 1/T$ yields slow-phase eye velocity very nearly proportional to cupula deflection. However in a real system in which finite-width pulses occur, the unattenuated saccadic pathway output would be

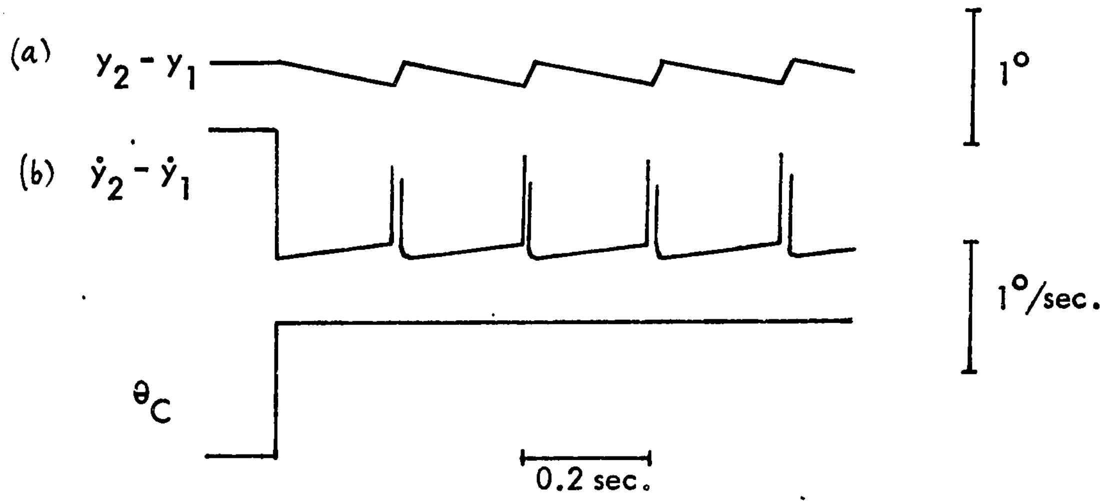


Fig. 5-6 MODEL RESPONSE TO STEP CHANGE IN CUPULA POSITION (Tracing of analog computer output)

Impulses in the velocity trace are not shown in their entirety, but their location and direction are indicated.

Model parameters: $K_1 = K_2 = 1.0$; $T = 0.2$ sec.; $T_3 = 1.0$ sec.

relatively smaller. Hence the critical gain ratio would be smaller also, although still proportional to 1/T.

5.2.3 Response to a Step Change in Head Velocity

The model response to this input, the classic stopping stimulus, was considered by Sugie and Jones (1966) but these authors investigated the saccadic response by analog computer simulation only. An analytic expression describing the response is derived here, and results in better understanding of the nature of the response and its variations. In particular it will be shown below that variations in the gain ratio K_1/K_2 may be the cause of certain experimentally observed deviations from the single exponential decay of slow-phase eye velocity which has come to be expected.

To simplify analysis it is assumed that the short time constant of the semicircular canal is so short as to have a negligible effect. Thus the variation in cupula position following application of the step velocity input may be approximated by

$$\theta_C(t) = e^{-t/T_1}$$

$$= e^{-ct}$$

where $T_1 = 1/c$ is the long time constant of the canals. It then emerges that the output of the continuous pathway is

$$y_1(t) = \frac{K_1}{a - c}(e^{-ct} - e^{-at}), \text{ ....Eq. 5.6}$$

$$\dot{y}_1(t) = \frac{K_1}{a - c}(ae^{-at} - ce^{-ct}) \text{ ....Eq. 5.7}$$

The output of the saccadic pathway is obtained in the same way as in the preceding section and is found to be

$$y_2(t) = \frac{K_2 e^{aT}}{e^{aT} - e^{cT}} e^{-a(t-nT)}(e^{-cnT} - e^{-anT}) \text{ ....Eq. 5.8}$$

$$\dot{y}_{2,s}(t) = \frac{-a K_2 e^{aT}}{e^{aT} - e^{cT}} \; e^{-a(t-nT)}(e^{-cnT} - e^{-anT}) \; \ldots\ldots \text{Eq. } 5.9$$

The position outputs y_1 and y_2 obtained by analog computer simulation, are shown in Fig. 5-7 for the parameter values $K_1 = K_2 = 1.0$, $c = 1/T_1 = 0.1 \text{ sec}^{-1}$, $a = 1/T_3 = 1.0 \text{ sec}^{-1}$, $T = 0.2$ sec. This figure corresponds, for the head velocity step input, to Fig. 5-5 for the cupula position step input. It is clear from the figure, and from Equations 5.6 and 5.8, that the overall time course of saccadic pathway position output and the time course of continuous pathway position output are both described by the scaled algebraic sum of the same two decaying exponentials. The time constants are of course $T_1 = 1/c$, and $T_3 = 1/a$.

The two position waveforms parallel each other, since the amplitudes of the two pertinent exponentials have the same ratio. Thus it may immediately be predicted that at some critical value of the gain ratio K_1/K_2, the combined position output $(\theta_E - \theta_H) = y_2 - y_1$ will not show any appreciable overall deviation, but will consist of a nystagmoid motion about a steady position which is near zero.

The velocity outputs of continuous and saccadic pathways are also described by the same two exponentials, T_1 and T_3. However, in this case the exponential terms have a different magnitude ratio in the expression for $\dot{y}_1$ (Eq. 5.7) than in the expression for $\dot{y}_{2,s}$ (Eq. 5.9). It is therefore readily apparent that, depending on the gain ratio K_1/K_2, the relative dominance of one or other exponential term may vary widely.

In Fig. 5.8 the effect of varying the gain ratio K_1/K_2 on the predicted eye velocity (combined output) is illustrated. Here the velocity outputs, $\dot{y}_1$ and $\dot{y}_{2,s}$ of continuous and saccadic pathways respectively, and the final predicted slow-phase eye velocity $(\dot{\theta}_{E,s} - \dot{\theta}_H)$ are shown for three different values of the gain ratio, namely 1/T, 2/T, and 1/2T. When the gain ratio is 1/T (Fig. 5-8(a)) peak slow-phase eye velocity (combined output) follows a time

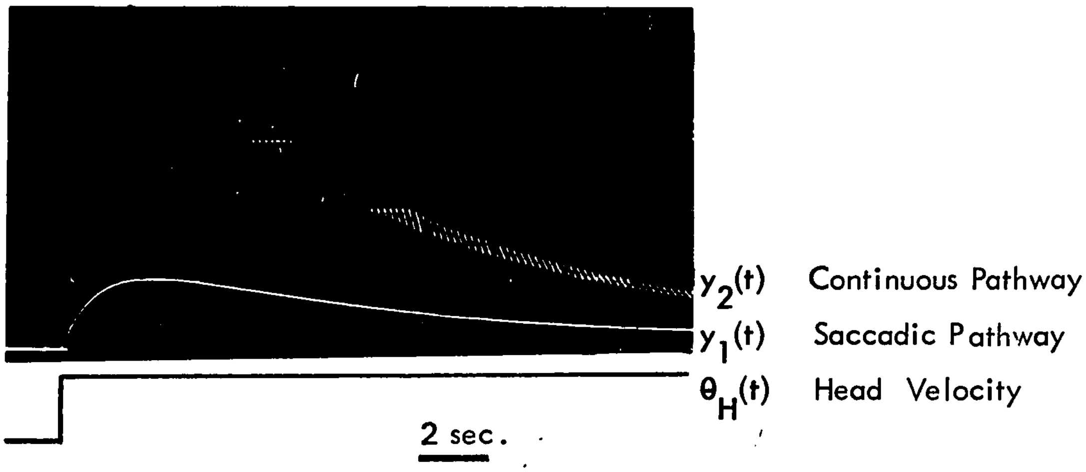


Fig. 5-7 RESPONSES OF CONTINUOUS AND SACCADIC PATHWAYS OF THE SUGIE-JONES MODEL TO A STEP CHANGE IN HEAD VELOCITY

Model parameters: $K_1 = K_2 = 1.0$; $T = 0.2$ sec.; $T_3 = 1.0$ sec.

Canal parameters: $T_1 = 10.0$ sec.; $T_2 = 0$; $\alpha = T_1$.

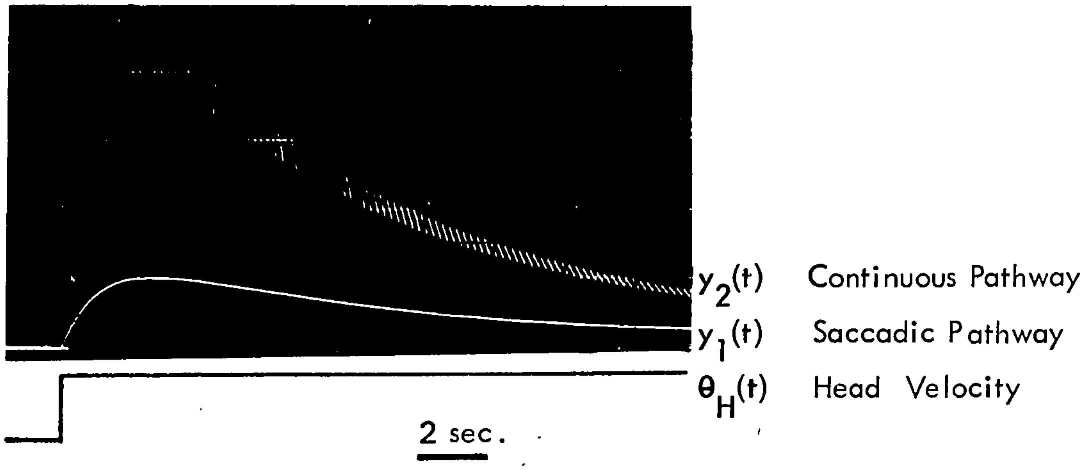
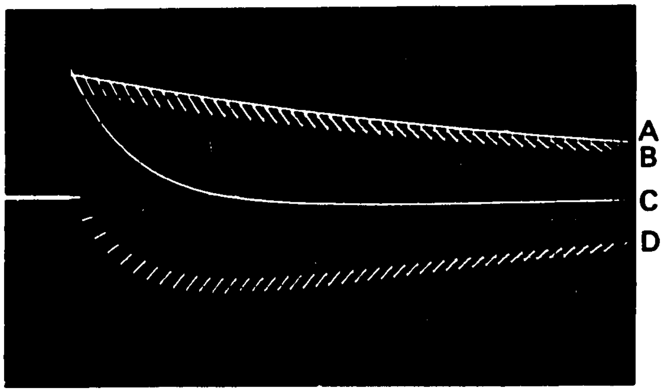


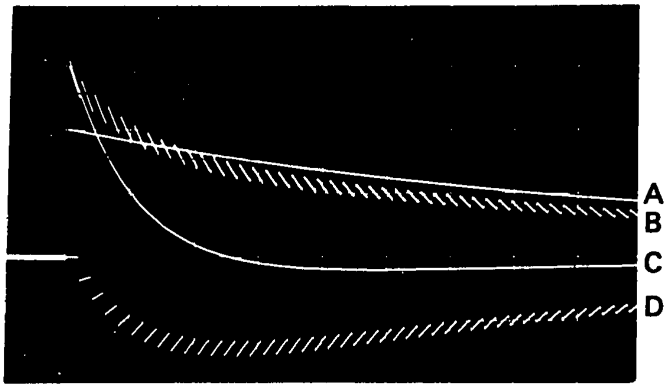
Fig. 5-7 RESPONSES OF CONTINUOUS AND SACCADIC PATHWAYS OF THE SUGIE-JONES MODEL TO A STEP CHANGE IN HEAD VELOCITY

Model parameters: $K_1 = K_2 = 1.0$; $T = 0.2$ sec.; $T_3 = 1.0$ sec.

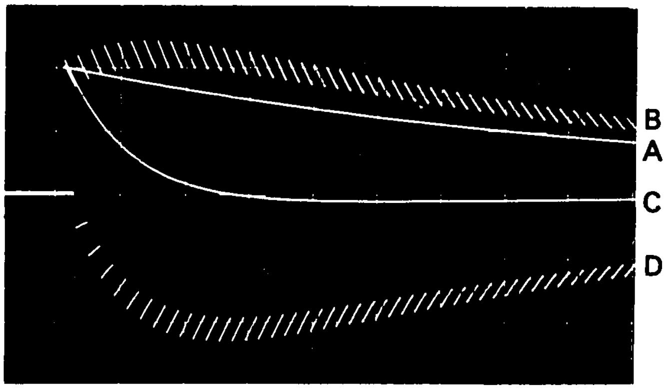
Canal parameters: $T_1 = 10.0$ sec.; $T_2 = 0$; $\alpha = T_1$.



(a) $K_1/K_2 = 1/T$



(b) $K_1/K_2 = 2/T$



(c) $K_1/K_2 = 1/2T$

A - Cupular Position (θ_C)

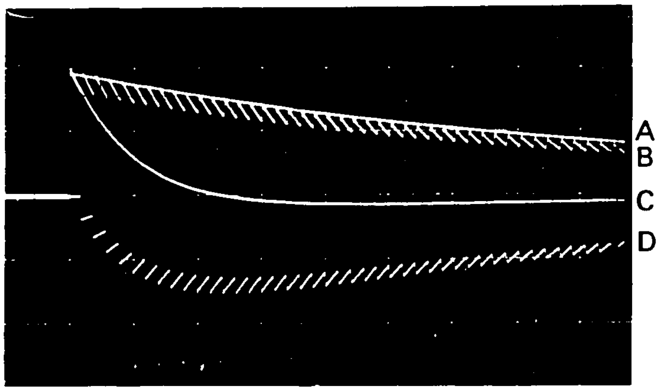
B - Eye Velocity re Head ($\dot{y}_2 - \dot{y}_1$)

C - Continuous Pathway Velocity ($\dot{y}_1$)

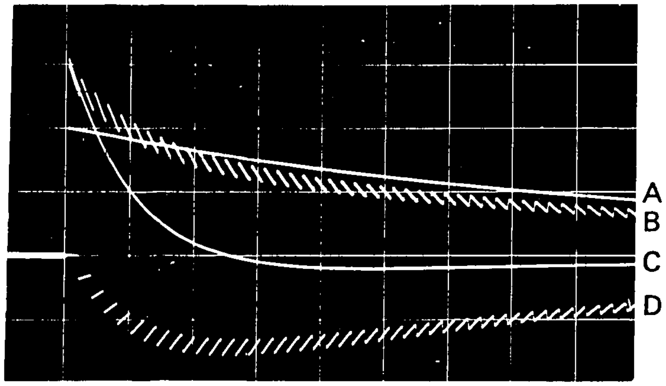
D - Saccadic Pthway Velocity ($\dot{y}_2$)

(Horizontal bars = 1 second)

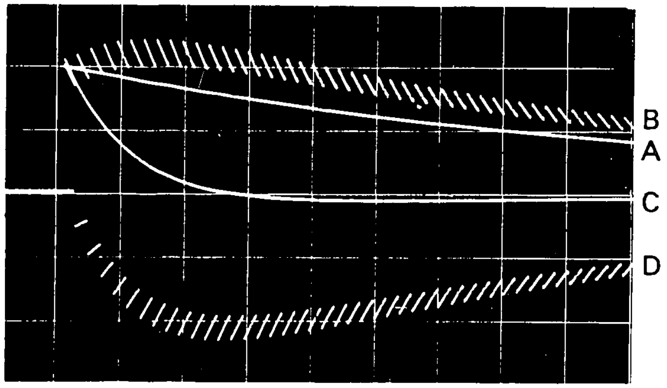
Fig. 5-8 MODEL RESPONSES TO STEP CHANGE IN HEAD VELOCITY FOR VARIOUS VALUES OF THE RELATIVE GAIN (K_1/K_2).
Model parameters: $T = 0.2$ sec.; $T_3 = 1.0$ sec.
Canal parameters: $T_1 = 10$ sec.; $T_2 = 0$; $\alpha = T_1$
(Saccadic velocity pulses are omitted for clarity)



(a) $K_1/K_2 = 1/T$



(b) $K_1/K_2 = 2/T$



(c) $K_1/K_2 = 1/2T$

A - Cupular Position (θ_C)

B - Eye Velocity re Head ($\dot{y}_2 - \dot{y}_1$)

C - Continuous Pathway Velocity ($\dot{y}_1$)

D - Saccadic Pthway Velocity ($\dot{y}_2$)

(Horizontal bars = 1 second)

Fig. 5-8 MODEL RESPONSES TO STEP CHANGE IN HEAD VELOCITY FOR VARIOUS VALUES OF THE RELATIVE GAIN (K_1/K_2).
Model parameters: $T = 0.2$ sec.; $T_3 = 1.0$ sec.
Canal parameters: $T_1 = 10$ sec.; $T_2 = 0$; $\alpha = T_1$
(Saccadic velocity pulses are omitted for clarity)

course which is very nearly that of a single exponential with a time constant of $1/b = T_1$. Mean slow-phase eye velocity clearly must have a similar time course. In Fig. 5-8(b) the gain ratio is made greater than 1/T by increasing the continuous pathway gain (K_1). As a result the time course of slow-phase eye velocity $(\dot{\theta}_{E,s} - \dot{\theta}_H)$ shows a rapid initial decline but later declines more slowly, at the same rate as the cupula decline. Reducing the gain ratio (Fig. 5-8(c)) has essentially the opposite effect ; slow-phase eye velocity, the combined output, shows an initial rise before a final slow decay which again parallells cupula decay.

Any one of these three forms of response to the classic stopping stimulus or head velocity step input may be observed experimentally in the vestibulo-ocular system. The model attributes these response variations to variations in the overall amplitude of saccadic flicks, though variations in saccade frequency may be expected to have similar effects. It is of course well known that such variations in saccadic activity do occur in different states of arousal and from other causes (Guedry, 1965).

5.2.4 Response to Sinusoidal Inputs

Sugie and Jones (1966) have considered the response of the model to sinusoidal inputs at various frequencies, and have shown analytically that for a particular value of the gain ratio K_1/K_2, the smoothed waveform of mean slow-phase eye velocity has amplitude and phase characteristics similar to those of the cupula response except at high input frequencies. The critical value of the gain ratio is again $1/T$.

The method of analysis used here is slightly different, and emphasis is placed on conditions in which the frequency characteristics of smoothed slow-phase eye velocity differ from those of the canal signal. In addition the effect of input frequency on the nature of the smoothed waveform of eye position has been examined.

Consider first the response of the saccadic pathway to a sinusoidal input. If the canal signal is

$$\theta_C(t) = \sin(\omega t)$$

then from Equation 5.2

$$y_2(nT) = K_2 \sum_{k=1}^{n} e^{-a(nT-kT)} \sin(k\omega T).$$

This expression can be summed as before if the sine function is first expressed in terms of imaginary exponentials, and yields

$$y_2(nT) = K_2 \frac{\sin(n\omega T) - e^{-aT}\sin(\omega T+nT) + e^{-a(nT+T)}\sin(\omega T)}{1 - 2e^{-aT}\cos(\omega T) + e^{-2aT}}.$$

Ignoring the final transient term in the numerator, the steady-state response is found to be

$$y_2(nT)_{ss} = \frac{K_2}{(1 - 2e^{-aT}\cos(\omega T) + e^{-2aT})^{1/2}} \sin(n\omega T+\alpha), \ldots\ldots \text{Eq. } 5.10$$

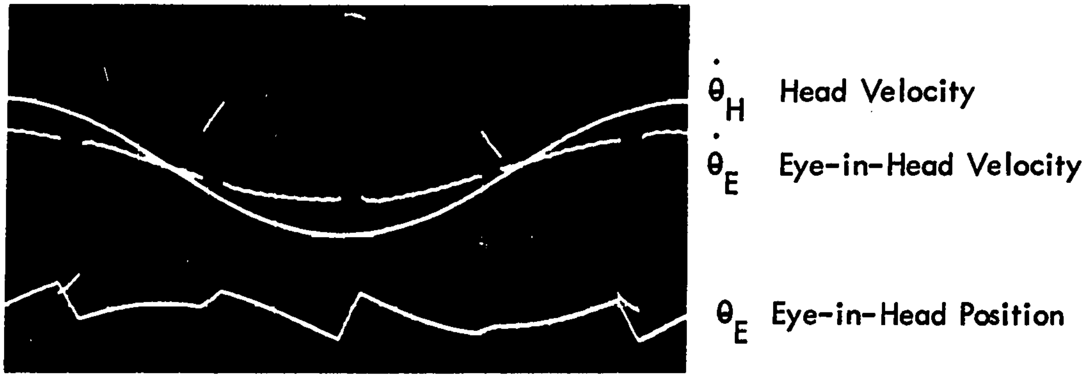
where

$$\alpha = \tan^{-1} \frac{\sin(\omega T)}{\cos(\omega T) - e^{aT}}$$

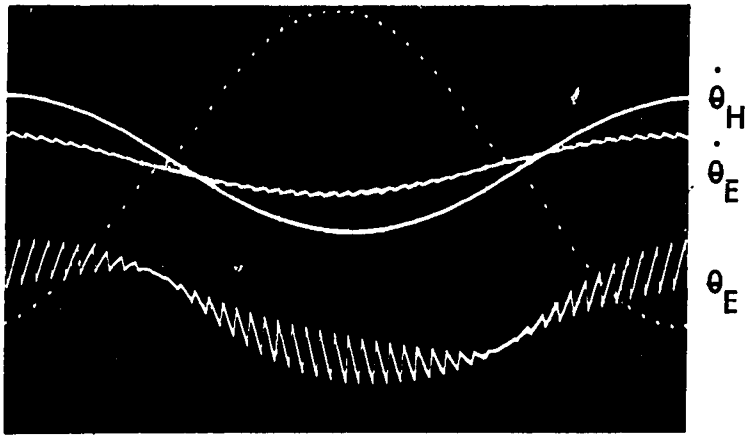
From this expression the position and slow-phase velocity during the $(n)^{th}$ sampling interval are obtained from Equations 5.2 and 5.5.

Typical steady state responses of the model, obtained on an analog computer, are shown in Fig. 5-9(a) and 5-9(b). In each case the upper two curves represent head velocity and predicted eye velocity, while the lower curve represents predicted eye position. The gain ratio K_1/K_2 is equal to $1/T$ in each case. Since the curves were obtained on an analog computer, it was necessary to use pulses of finite width, instead of impulses, in the sampler output. The necessary adjustment of the gain of the saccadic pathway, to make its output magnitude equal to the magnitude predicted for the ideal case of impulse sampling, was made before adjusting the gain ratio K_1/K_2. The succession of dots or line segments seen in each velocity record are the tops of pulses which result from the differentiation.

It is desired now to construct a frequency response plot relating steady-state amplitude and phase of eye position and eye velocity to head velocity for sinusoidal inputs. This is not straightforward, since the output of the saccadic pathway is not sinusoidal. It is possible in principle to expand the output in



(a) 1.0 Hz.



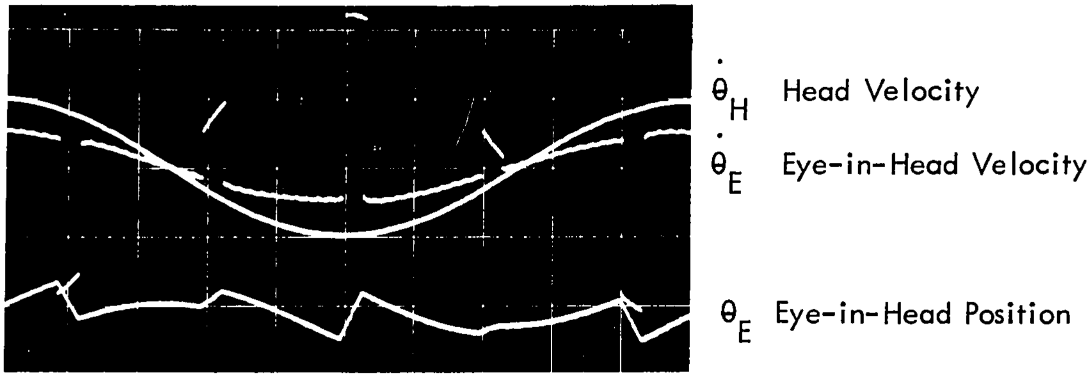
(b) 0.1 Hz.

Fig. 5-9 MODEL RESPONSES TO SINUSOIDAL CHANGES IN HEAD VELOCITY

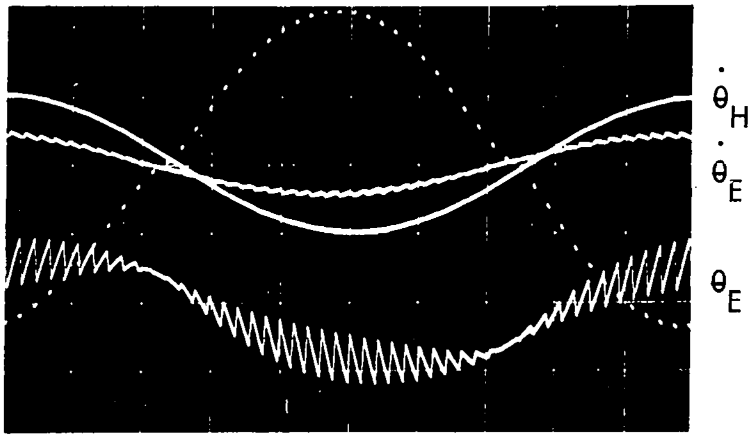
Model parameters: $T = 0.2$ sec; $T_3 = 1.0$ sec.; $K_1/K_2 = 1/T$.

Canal parameters: $T_1 = 10$ sec.; $T_2 = 0$; $\alpha = 1/T_1$

Saccadic velocity pulses, of finite width, appear in this analog computer simulation. The effect of finite pulse width was taken into account in calculating the effective gain ratio.



(a) 1.0 Hz.



(b) 0.1 Hz.

Fig. 5-9 MODEL RESPONSES TO SINUSOIDAL CHANGES IN HEAD VELOCITY

Model parameters: $T = 0.2$ sec; $T_3 = 1.0$ sec.; $K_1/K_2 = 1/T$.

Canal parameters: $T_1 = 10$ sec.; $T_2 = 0$; $\alpha = 1/T_1$

Saccadic velocity pulses, of finite width, appear in this analog computer simulation. The effect of finite pulse width was taken into account in calculating the effective gain ratio.

a Fourier series with a period equal to the exciting sinusoid, and take the fundamental component of this series as representing the best fit to the output in a least squares sense. However in the general case the input frequency and the sampling frequency are not commensurable, so that a general expression for the fundamental Fourier component cannot be obtained in closed form. In this analysis therefore, an approximate method is used to obtain continuous sinusoids which are representative of changes in eye position and slow-phase eye velocity due to the saccadic pathway during a sinusoidal input cycle.

Consider the steady state position output of the saccadic pathway in response to a sinusoidally varying cupula angle

$$y_2(t)_{ss} = y_2(nT)_{ss} e^{-a(t-nT)}, \quad nT \leq t < (nT+T), \quad n = 1, 2, 3 \ldots\ldots$$

The mean value of the output during the $(n)^{th}$ sampling interval is

$$\bar{y}_2(nT)_{ss} = \frac{1}{T} y_2(nT)_{ss} \int_{nT}^{nT+T} e^{-a(t-nT)}\, dt$$

$$= \frac{1 - e^{-at}}{aT} \quad y_2(nT)_{ss} \quad \ldots\ldots\ldots\ldots\ldots \text{Eq. 5.11}$$

The output $y_2(t)_{ss}$ has this value at time $t = nT + t_m$, where

$$t_m = -\frac{1}{a} \log_e\left(\frac{1 - e^{-aT}}{aT}\right)$$

Clearly in successive intervals the mean value is proportional to the output immediately after the preceding sampling instant, and occurs at a fixed time after that instant. Thus a continuous sinusoid can be constructed which passes through the points in successive intervals at which $y_2(t)_{ss}$ is equal to the corresponding mean value. Such a sinusoid, to be called $x_2(t)$, would have an amplitude given by Equation 5.11, but would be delayed by t_m seconds. Thus

$$x_2(t) = \frac{K_2 (1 - e^{-aT})}{aT (1 - 2e^{-aT} \cos(\omega T) + e^{-2aT})^{1/2}} \sin(\omega t + \beta), \ldots\ldots\ldots \text{Eq. 5.12}$$

where

$$\beta = \tan^{-1}\left(\frac{\sin(\omega T)}{\cos(\omega T) - e^{aT}}\right) - \omega t_m .$$

This function appears to be a good approximation to the sinusoid which is the best fit, in a least-squares sense, to the eye position output $y_2(t)$. It will be taken as an approximate expression of the effective frequency characteristics of the position output of the saccadic pathway.

A similar expression can be derived to represent, in the same sense, the slow- phase velocity output of the saccadic pathway. This function will be called $v_2(t)$, and is found to be

$$v_2(t) = -a\, x_2(t).$$

Using these expressions, the effective eye position output and slow-phase velocity output of the combined continuous and saccadic pathways can be found. These are called $x_E(t)$ and $v_E(t)$ respectively, and their frequency-domain relationships to the head motion input are obtained as follows. Since the expression for $x_2(t)$ in Eq. 5.12 is obtained by assuming that the cupula angle is a unit sine function,

$$\theta_C(t) = \sin\omega t,$$

it is evident that the amplitude and phase in Eq. 5.12 describe the frequency-domain relationship between $x_2(t)$ and $\theta_C(t)$. The relationship may be expressed in the form of a transfer function

$$\begin{aligned} \frac{x_2}{\theta_C}(j\omega) &= F(j\omega) \\ &= B(\omega)\ \exp\left[j\beta(\omega)\right] \end{aligned}$$

where $B(\omega)$ and $\beta(\omega)$ are respectively the amplitude and phase of $x_2(t)$ in Eq. 5.12. The relationship between smoothed eye position x_E and head position θ_H may now be expressed

$$\frac{x_E}{\theta_H}(j\omega) = j\omega H_C(j\omega)\left[F(j\omega) - K_1 . G(j\omega)\right]$$

$$= A_x(\omega)\exp\left[j\phi_x(\omega)\right]$$

where

$$H_C(j\omega) = \frac{\theta_C}{\dot{\theta}_H}(j\omega)$$

is the transfer function of the semicircular canals, and $K_1 . G(jw)$ is the transfer function of the filter F_2 in the continuous pathway (Fig. 5-4). Similarly the relationship between effective slow-phase eye velocity and head velocity is found to be

$$\frac{v_E}{\dot{\theta}_H}(j\omega) = H_C(j\omega)\left[-a . F(j\omega) - K_1 . j\omega . G(j\omega)\right]$$

$$= A_v(\omega)\exp\left[j\phi_v(\omega)\right]$$

The amplitude ratio A_v and phase ϕ_v describing the steady state relationships between mean slow-phase eye velocity and sinusoidal head velocity are plotted in Fig. 5.10 (a,b) for several values of the gain K_2 of the saccadic pathway. Gain of the continuous pathway, K_1, is kept at unity throughout. Other model parameters are $a = 1/T_3 = 1.0 \text{ sec}^{-1}$, $T = 0.2$ sec. The long time constant of the canal is taken to be 10 seconds, and the short time constant 0.005 sec, the effects of the latter being negligible in the frequency range illustrated. It should be noted that for convenience the gain of the semicircular canals in the velocity transducing mode was made equal to one. The curves shown were plotted on the basis of values calculated on a digital computer (IBM 360/50) from the equations described above.

It will be noted from Fig. 5.10 that when the saccadic pathway is inactive ($K_2 = 0$), slow-phase velocity response shows marked attenuation and phase advance at low frequencies. A small contribution by the saccadic pathway ($K_2 = 0.01$) results in major differences in phase and amplitude at the lowest frequencies shown. As K_2 increases there is a further increase in amplitude and decrease in phase advance at low frequencies, until when K_2 becomes equal to

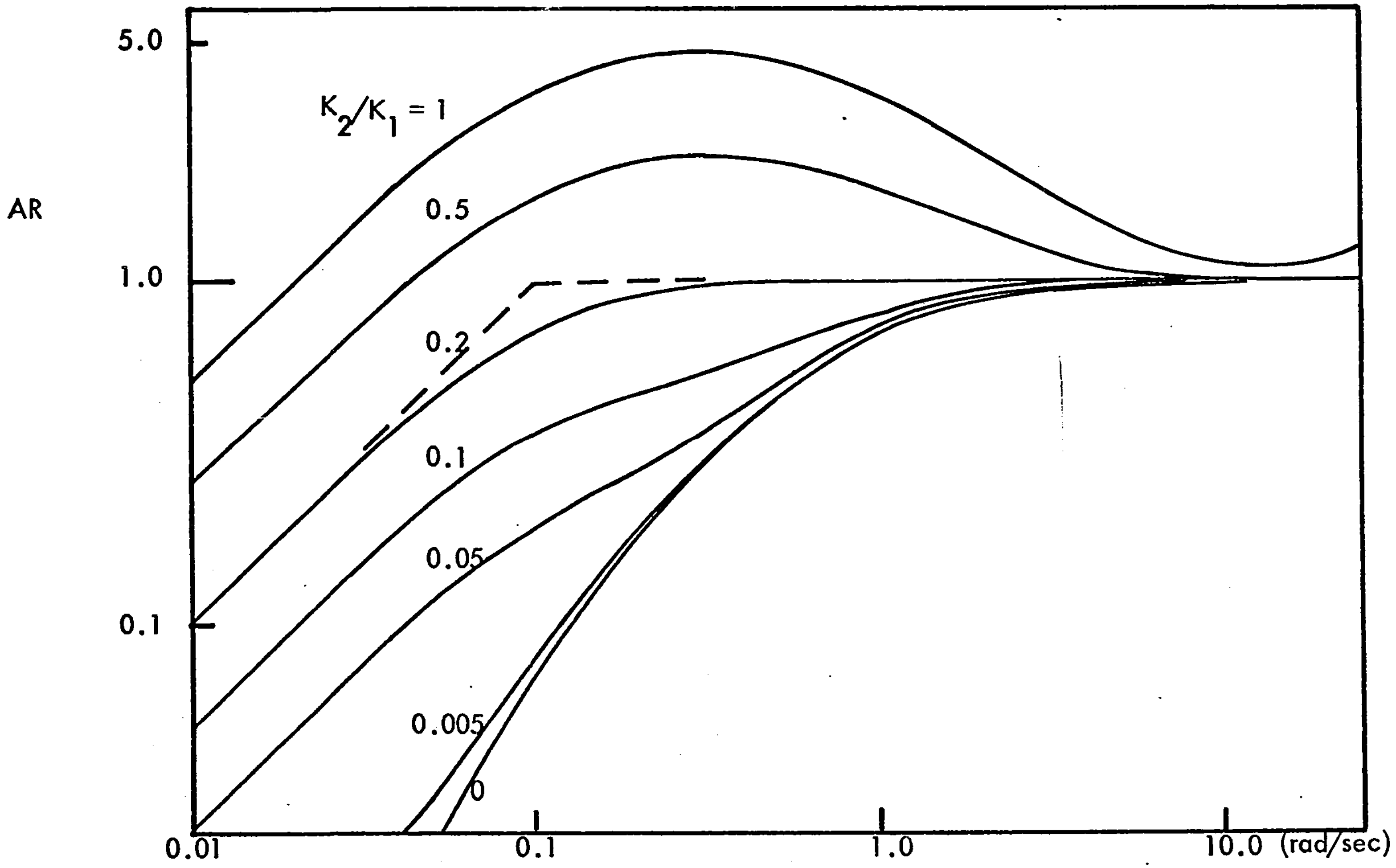


Fig. 5-10 (a) MODEL FREQUENCY RESPONSE: VELOCITY GAIN vs. FREQUENCY, K_2 VARIED

AR = the amplitude ratio of the sinusoid describing slow-phase eye velocity and the sinusoid of head velocity. Model parameters: $T = 0.2$ sec.; $T_1 = 10$ sec.; $T_2 = 0.005$ sec.; $T_3 = 1.0$ sec.; $\alpha = T_1$; $K_1 = 1.0$

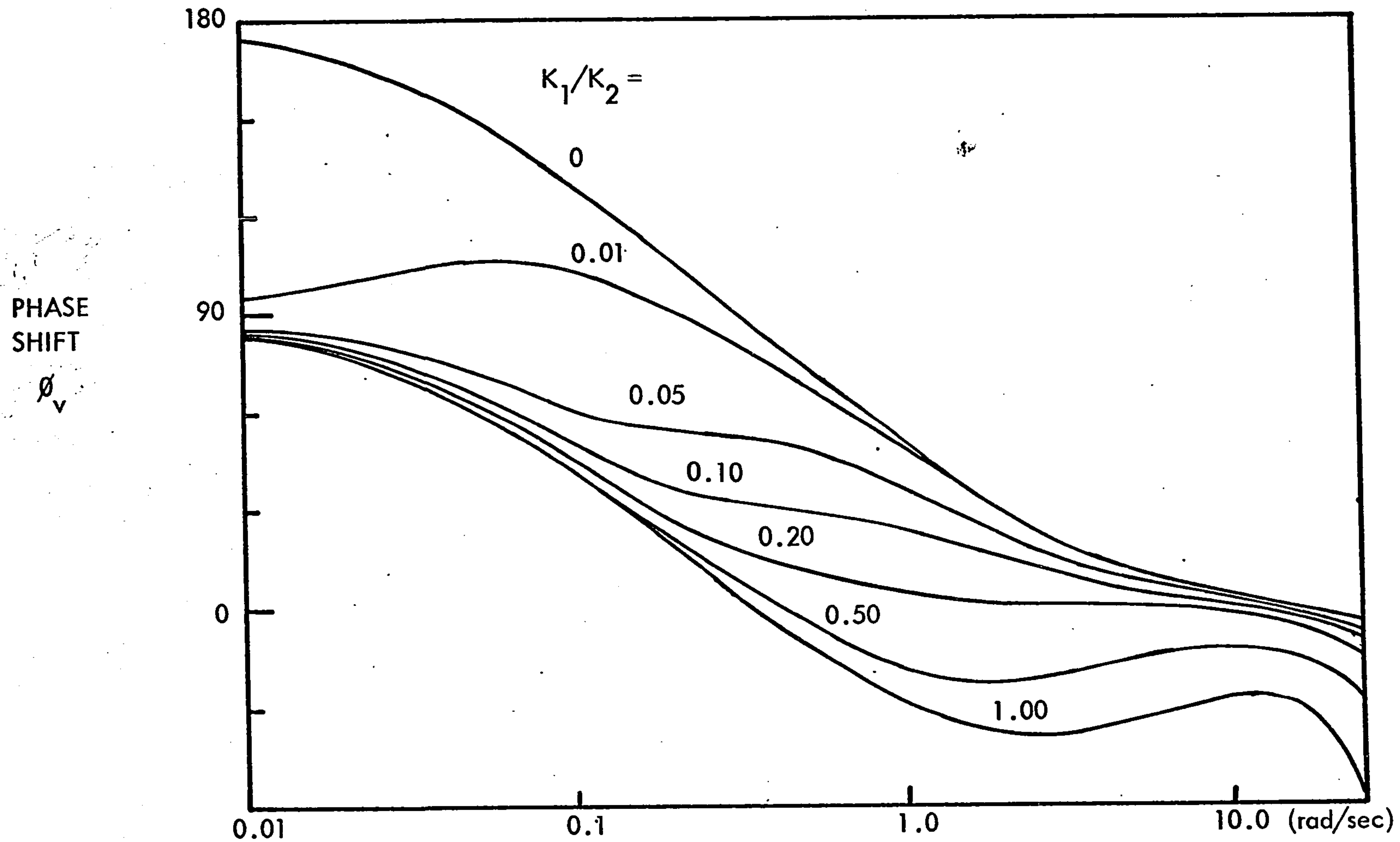


Fig. 5-10(b) MODEL FREQUENCY RESPONSE: PHASE vs. FREQUENCY, K_2 VARIED.

ϕ_v = phase shift of the sinusoid describing slow-phase eye velocity relative to the sinusoid of head velocity. Model parameters: $T = 0.2$ sec.; $T_1 = 10$ sec.; $T_2 = 0.005$ sec.; $T_3 = 1.0$ sec.; $\alpha = T_1$; $K_1 = 1.0$.

the magnitude of the sampling interval, i.e. about 0.2 sec., the variation of amplitude and phase with frequency are very similar to the variations appearing in the semicircular canal response. The asymptotes of the canal amplitude-frequency response are shown as dotted straight lines for comparison. Finally when K_2 exceeds 0.2, response amplitude in the intermediate frequency range rises above the amplitude of the cupula signal, while phase lag appears at the higher frequencies.

In Fig. 5-11 the amplitude ratio A_x and the phase $\emptyset_x$ relating effective eye position to head position for sinusoidal inputs are plotted as functions of the input frequency. These curves were obtained in the same way as those of Fig. 5-10 and with the same model parameters. Again the effects of variation of the relative gain (through manipulation of K_2) are very striking. In this case the shape of the amplitude-ratio and phase curves changes very rapidly when the magnitude of K_2 is in the neighbourhood of T. When $K_2 = T$ there is very pronounced attenuation at low frequencies and marked phase advance at all frequencies considered. As K_2 is increased or decreased, the amplitude-ratio curves change very rapidly and become in each case similar to the curves expected from an overdamped second-order linear system, at least at the lower frequencies. Phase-frequency curves tend towards a corresponding sigmoid shape.

The response of the model to high frequency sinusoidal inputs is somewhat anomalous. At frequencies greater than about half the sampling frequency, the saccadic pathway output shows the effect of beats between the sampling frequency and the sinusoidal excitation frequency. Such beats occur at all frequencies, but their amplitude is inconsiderable at lower input frequencies. In the high frequency range the contribution of the lower beat frequency is particularly striking in analog computer studies (Fig. 5-12). It has a frequency equal to the difference between excitation frequency and sampling frequency, and produces slow response variations which may be of large amplitude.

It is not clear to what extent this type of response occurs in the experimental situation. There appear to have been few studies of vestibulo-ocular

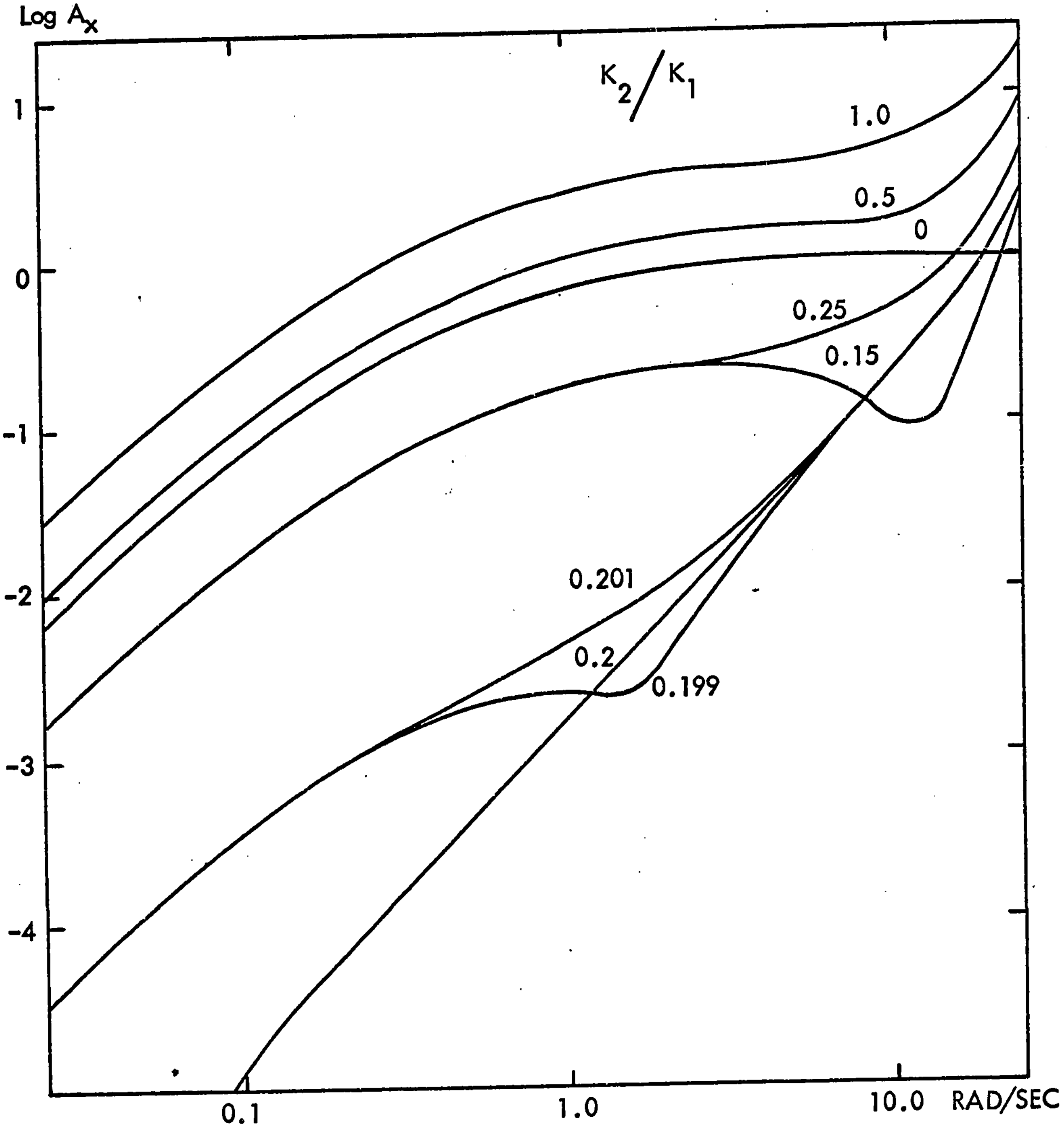


Fig. 5-11(a) MODEL FREQUENCY RESPONSE; POSITION GAIN vs. FREQUENCY

A_x = the amplitude ratio of the sinusoid describing overall ("smoothed") eye position and the sinusoid of head position. Model parameters; $T = 0.2$ sec.; $T_1 = 10$ sec.; $T_2 = 0.005$ sec.; $T_3 = 1.0$ sec.; $\alpha = T_1$; $K_1 = 1.0$, K_2 varied.

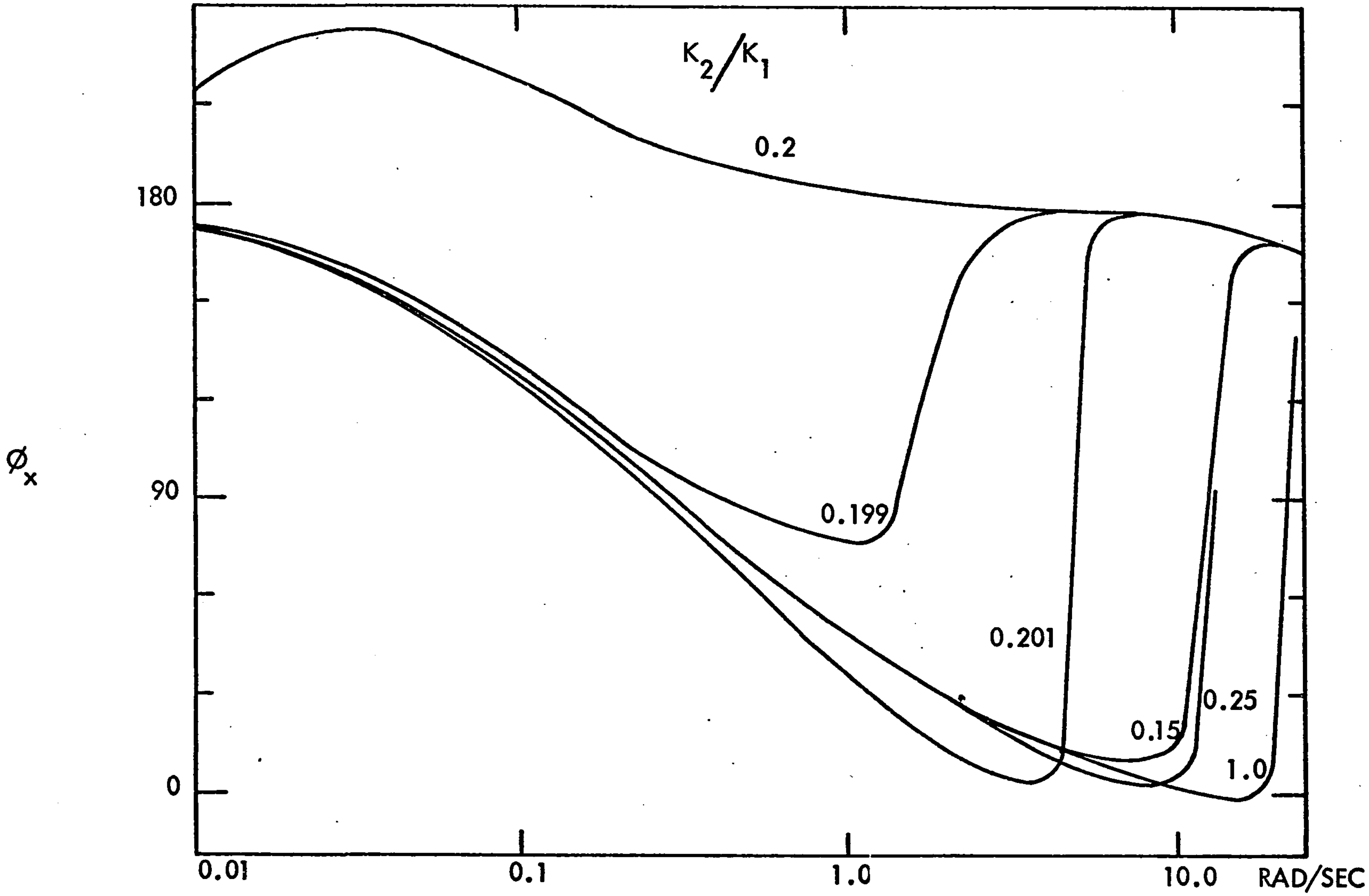


Fig. 5-11(b) MODEL FREQUENCY RESPONSE: PHASE vs. FREQUENCY, K_2 VARIED.

ϕ_x = phase shift of the sinusoid describing overall eye position relative to the sinusoid of head position.

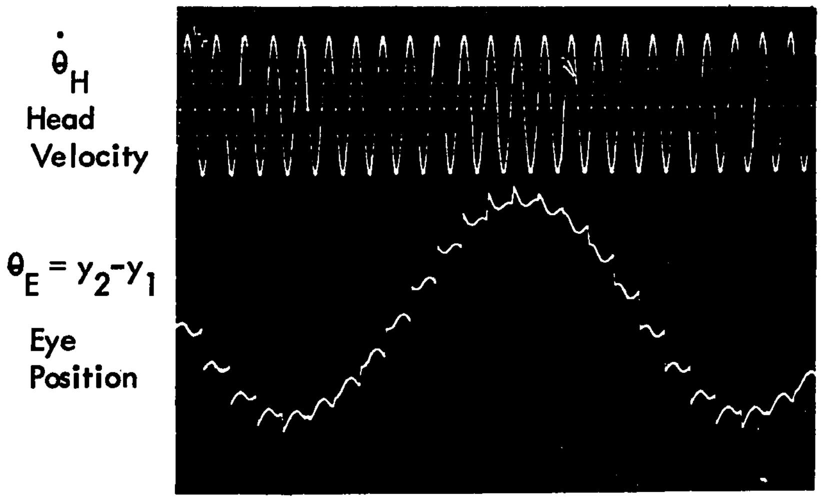


Fig. 5-12 "ANOMALOUS" RESPONSE OF THE MODEL TO HIGH FREQUENCY SINUSOIDAL INPUT.

Input frequency in this case is slightly less than the sampling frequency, resulting in high-amplitude beat.

Model parameters: $T = 0.2$ sec., $T_3 = 0.1$ sec., $K_1/K_2 = 1/T$.

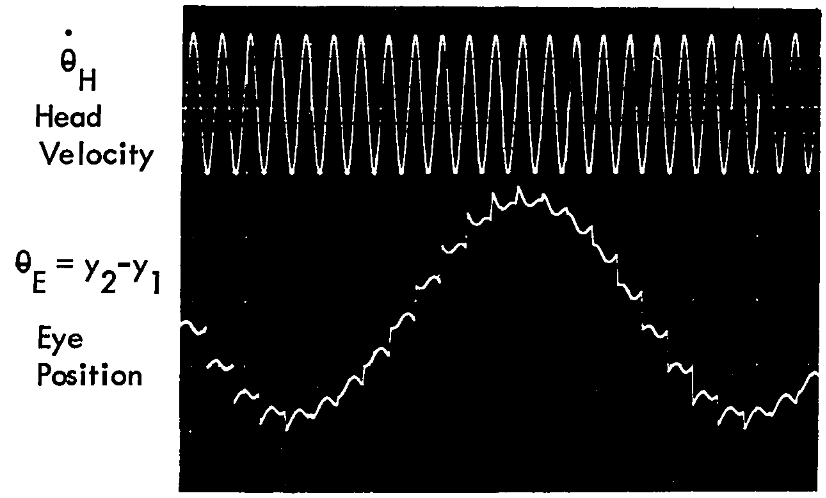


Fig. 5-12 "ANOMALOUS" RESPONSE OF THE MODEL TO HIGH FREQUENCY SINUSOIDAL INPUT.

Input frequency in this case is slightly less than the sampling frequency, resulting in high-amplitude beat.

Model parameters: $T_1 = 0.2$ sec., $T_3 = 0.1$ sec., $K_1/K_2 = 1/T$.

response at such high frequencies, and perhaps the investigator would in any case tend to reject records showing such wandering eye movements, attributing them to drift in the recording apparatus or to some extraneous input to the system. However, in the pigeon vestibulo-ocular responses observed by the author (see Section 12.3.2) there seems to be a tendency for the frequency of saccades to drop far below the usual level when the excitation frequency reaches this range. From a functional point of view such behaviour is more appropriate, since (1) performance of the continuous pathway by itself is quite adequate at these frequencies, and (2) the required variation in eye position at these frequencies is usally small, so that eye-centering saccades are unnecessary. However such reduction in saccade frequency under particular input conditions clearly indicates the existence of a rather flexible saccade-generation mechanism, perhaps involving some threshold device as a trigger.

5.3 DISCUSSION

The work of Sugie and Jones led to the hypothesis that there exists in the vestibulo-ocular system a low-pass filter mechanism receiving both a continuous input, closely related to the canal signal, and also a discontinuous input (pulse train) responsible for saccades. The validity of this primary hypothesis and the general nature of the filter mechanism, are well established by the work of these authors, and are further confirmed by studies of the pigeon vestibulo-ocular response described below in Chapter 12.

Sugie and Jones made a secondary preliminary hypothesis that the saccade-generation mechanism producing the postulated pulse input to the filter could be approximated by an ideal, fixed-frequency sampling device operating upon the cupula signal. As these authors point out, there are reasons for questioning the adequacy of this latter hypothesis, since it fails to explain some fairly consistent tendencies for variation in the intersaccadic interval. Nevertheless it seems likely that in many cases it provides a reasonably good approximation to the real situation in a general sense. Moreover, as demonstrated by the results of this chapter, analysis of the model system incorporating this regular-sampling hypothesis of saccade-generation yields considerable insight into the significance of the basic dual-pathway model.

A major functional conclusion which derives directly from experimental findings of Sugie and Jones and which is intimately related to the primary hypothesis, is that each saccade has a significant effect on the velocity during subsequent slow-phase intervals. Thus the occurrence of saccades is important in determining the accuracy of slow-phase compensation, and is not simply a re-positioning mechanism,as has so often been assumed. The potential magnitude of the contribution made by the saccadic pathway to slow-phase velocity compensation is powerfully emphasized when the secondary, saccade-generation hypothesis is incorporated and the system response is examined. It is evident from the analysis of Sugie and Jones and the further analysis of this chapter that under specified conditions, i.e. $K_1/K_2 = 1/T$, the time course of slow-phase eye velocity can be made to follow the cupula signal very closely indeed, for a wide variety of input waveforms. This means that the poor quality of integration resulting from the low-pass filter mechanism when the continuous pathway alone is operating can be made, effectively, almost perfect through simultaneous operation of the saccadic pathway. The fact that overall eye deviation is simultaneously made very small is obviously also a good result physiologically.

This good result however only obtains when the input frequency is appreciably less than the sampling frequency. If the latter were increased while other system parameters remained the same, it is clear that good performance in the sense considered here would extend to higher stimulus frequencies. Nature however has not taken this course, perhaps because of the energy cost of making more frequent saccades, or because perception fails if the slow-phase interval is too short. An alternative solution appears to have been chosen, namely to utilize a more flexible saccade generation mechanism which adjusts inter-saccadic intervals to suit the input. Thus it is experimentally observed that frequency decreases during sinusoidal inputs at frequencies above about one cycle per second, as noted above.

From the biological point of view there is another flaw associated with the regular sampling scheme, and this comes to light as a result of analysis of the variation in overall eye deviation such as that of the curves $\dot{y}_2 - \dot{y}_1$ in Fig. 5-8. The ratio of overall eye deviation amplitude to head position amplitude is very small when $K_1/K_2 = 1/T$, and this is clearly desireable. However over most of the frequency range considered, the smoothed eye position magnitude increases rapidly when the gain ratio (K_1/K_2) is varied slightly. This feature is emphasized in Fig. 5-13 in which for several input frequencies the amplitude ratio $A_x(\omega)$ is plotted as a function of K_2, K_1 being kept constant. Such a steep approach to the optimal condition is unlikely to be satisfactory in the usual biological system since minor parameter variations due to extraneous influences could then seriously disrupt system performance. In this system, variations in the velocity amplitude ratio $A_v(\omega)$ with changes in the gain ratio are also significant, though not quite as pronounced. It is reasonable to speculate that this steep approach to what is apparently the optimal operating condition for the regular-sampling model is in part the reason why nature has not made use of this simple and elegant mechanism.

An important unanswered question remaining is whether or not the regular sampling model may be useful as an approximation to the real system at frequencies below say 2 radians per second. Further experimental study is required before this point can be clarified,but there is some evidence to suggest that the answer may be in the affirmative. Experimental records of vestibulo-ocular response to low frequency sinusoidal inputs show amplitude and frequency modulation of the saccades, with the same period as the input and usually in phase with each other. Frequency variation is often most noticable during the portion of the cycle when saccade amplitude is minimal, the latter tending to saturate if the input amplitude is sufficiently great. Corresponding observations may be made in most recorded responses to step changes in head velocity. Since the response of a low-pass filter to a frequency-modulated or amplitude-modulated pulse input is somewhat similar if there are many pulses per cycle, it would not be surprising to find the regular-sampling, amplitude-modulation model was

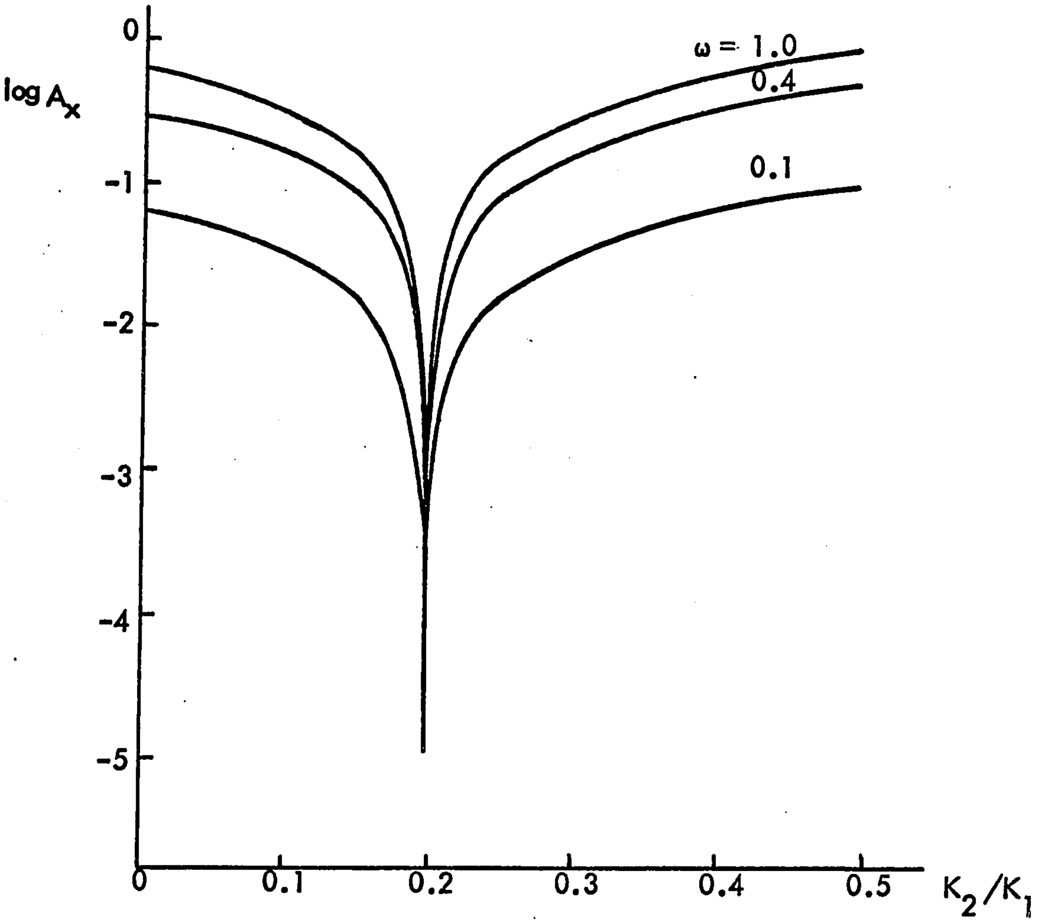


Fig. 5-13 RATIO OF OVERALL EYE DEVIATION AMPLITUDE TO HEAD POSITION AMPLITUDE (SINUSOIDAL) vs. THE GAIN RATIO K_2/K_1, FOR DIFFERENT INPUT FREQUENCIES(ω)

adequate in relatively undemanding applications.

Assuming the argument to be valid, two additional results of the present analysis become of considerable interest, namely the predicted responses to step changes in head velocity, and the frequency response of slow-phase eye velocity for large values of the saccadic-pathway gain. Model responses to head velocity steps for different values of the relative gain K_1/K_2 are shown in Fig. 5-8. Three different types of slow-phase velocity responses occur, corresponding to relative gains equal to, greater than or less than 1/T. As noted earlier, responses generally similar to each of these are observed, experimentally. A response of the third type (Fig. 5-8(c)) is especially interesting since it might easily be misinterpreted, after smoothing, as having a basic time course of the form

$$V_T = A(e^{-t/T_L} - e^{-t/T_S})$$

It will be apparent this equation has the same form as that describing cupula position under the same conditions (Table 3-1). Thus one might erroneously conclude that the short time constant T_S was the short time constant of the semi-circular canal.

Similar erroneous conclusions might be drawn from frequency response analysis, assuming again that results of the present analysis are applicable to the real system. It will be noted from Fig. 5-10(a) that when the gain ratio K_1/K_2 is less than 1/T, the amplitude ratio A_v (i.e. effective slow-phase eye velocity) approximates that of an overdamped second order system for frequencies below 2 rad/sec. Phase-frequency curves (Fig. 5-10(b) show a corresponding tendency. These frequency characteristics are very similar in form to those expected from the semi-circular canal and could be fitted rather well by a transfer function such as

$$\frac{V_{E(s)}}{\dot{\theta}_H} = \frac{Ks}{(0.1s + 1)(s + 1)}$$

The lower break frequency is of course attributable to the semicircular canal, but the upper one is due to the low pass filter of Sugie and Jones. This could be the explanation for the experimental findings of Niven and Hixson (1961) who obtained by frequency response testing a similar transfer function for the human vestibulo-ocular system. Mayne (1965) has presented strong functional arguments against accepting such large values for the short time constant of the semicircular canal in man.

CHAPTER 6

BIOLOGICAL OPTIMIZATION IN THE VESTIBULO-OCULAR SYSTEM*

6.1 INTRODUCTION

This chapter describes theoretical studies of optimal saccade strategy in the vestibulo-ocular system. The work is the first step in an attempt to gain insight into the physiological rationale for the variations in saccade amplitude and frequency which occur during normal operation of the vestibulo-ocular system. The approach used here is to work backwards from a hypothesis as to the 'goal' of the system and attempt to find the strategy, governing saccade generation, which would best satisfy this goal. The analysis is made possible by use of theory recently developed for the optimal design of engineering control systems.

A mathematical model of the vestibulo-ocular system developed by Sugie and Jones (1966) has been discussed in detail in the previous chapter. The basic feature of this model, and the feature for which there is the best experimental confirmation, is that there is some mechanism such that when unforced the eyes tend to return exponentially to their resting or mid-position. Each saccade is interpreted as the result of a brief forcing pulse applied to this centering mechanism. It is shown in the previous chapter that,in consequence, (i) the velocity of the eyes during each slow-phase interval is to a significant extent dependent on the magnitude of the preceeding pulse, and (ii) the effect of repeated pulses (saccades) is cumulative. Clearly therefore the amplitude and temporal placement of saccades for a given time course of cupula movement becomes critically important if the system is to achieve efficient visual stabilization.

Sugie and Jones (1966) assumed for simplicity that the frequency of saccades could be regarded as essentially constant, with the saccade amplitude modulated by the cupula signal. These assumptions form the basis for useful analysis of the vestibulo-ocular system (Sugie & Jones, 1966, & above, Chapter 5). However, records of actual vestibulo-ocular response show considerable variation from the simple

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*This work was done in collaboration with Mr. U. Wettstein relationships suggested. Indeed, variations appear with sufficient regularity to suggest that a more complex strategy is actually involved, although it is not at all clear what the actual strategy might be.

In this connection it seems reasonable to assume that during evolution or post-natal learning the organism 'discovers' a more or less systematic way of triggering saccades which is 'good' in some sense. Presumably 'goodness' depends on some balance or 'trade-off' between the energy cost of eye movements and the accuracy of tracking in the slow phase. Since the input to the system, the cupular signal, is a velocity signal, it seems likely that the accuracy of velocity tracking is of major importance. Indeed, from studies of its function, it is clear that the system has been highly refined for velocity compensation, presumably by some adaptive or learning process.

The concepts of learning and adaptation to environment have been with the biologist for many years. There is ample evidence for example that the structure of a biological organism tends towards a configuration which is optimum in some sense appropriate to the situation or function required (D'Arcy Thompson, 1961; Rashevsky, 1960; Rosen, 1967). Optimization in dynamic biological systems has also received increasing attention recently, and there have been a number of studies showing how some such systems tend automatically to choose an operating point such that their performance is optimum (Christie, 1953; Cotes & Mead, 1960; Mead, 1960; Milsum, 1966; Milsum, 1968;). Of course such studies become exceedingly complicated with increasing complexity of the systems under consideration. However with the continuing and rapid development of theoretical knowledge about optimization and adaptive systems, appearing in the literature of engineering and applied mathematics, progressively more complex biological systems become amenable to analysis from this point of view.

In order to optimize the performance of a system there must be some procedure for adjusting the parameters controlling system response so as to produce optimum performance as judged by a specified "performance criterion". The latter is a function of the variables of the system, and may have several components, there being then a trade-off between these components in order to reach optimality. In the present system possible components of a biological performance criterion might be the energy cost of eye movements on the one hand, and the accuracy of tracking on the other, as suggested above. Frequently there are in addition known "constraints" on system performance, as for example limitations on the maximum force available, or on power consumption. Then the optimum solution is that which maximizes or minimizes, as appropriate, the performance criterion, subject to the limitations imposed by the constraints.

In any tracking system an important index of system performance is the error between actual and desired output, and an objective of design might be to minimize some average or cumulative measure of the error. Usually it is desirable to weight positive and negative errors equally, so that it is necessary to choose as a performance criterion an even function of the error, such as its absolute value, or some even power. The mean square error or integral square error is frequently chosen for this purpose, because in addition to the property of weighting, and therefore penalizing, large errors more than small, such a function often makes the analysis much simpler.

In biological optimization the performance criteria are presumably set by evolutionary pressure, and derive from the requirements of survival. The optimization processes of evolution and learning presumably operate by trial-and-error, and this same approach is used to a considerable extent in engineering applications through the medium of high speed computers. The genetic trial-and-error process has been studied quite extensively (Fisher, 1958; Kimura, 1958) and appears to be very efficient in comparison with man-made schemes (Justice & Gervinski, 1966), particularly when the performance criterion has many components. To the human designer an analytical optimization using the methods of calculus is desirable but frequently impossible in complex systems. Such is the case in the present study, in which after preliminary analysis it is necessary to resort to trial-and-error. The technique of Dynamic Programming (Bellman, 1967), in which the number of relevant trials is systematically reduced, has been used in implementation of this latter stage.

6.2 Problem Formulation

As mentioned above and in Chapter 5, the efficiency of visual stabilization by the vestibulo-ocular system depends on the magnitude and occurrence times of the saccades. It seems likely therefore that during the biological optimization processes of evolution or learning, or both, some strategy is developed to control these saccade parameters so as to achieve optimum performance. Such optimization would presumably be directed primarily towards minimizing the velocity of retinal image slip during the compensatory phase of eye movements (the slow phase), so as to achieve accurate tracking. Thus a reasonable performance criterion might be the mean square value of the velocity error, that is, the mean square velocity of retinal image slip. In the present study this performance criterion has been used, with a modified version of the Sugie-Jones model of the vestibulo-ocular system, to determine both the magnitude and the temporal placement of saccades required to produce optimum response.

The biological optimization process involved in this sytem must include other more complex components in the performance criterion. For example the energy cost of making the saccadic flicks very rapidly is probably high, but this cost must be traded off against the reduced slow-phase duration which would occur if saccadic velocity were lower. The time required, during the slow phase, for the visual system to acquire adequate information from the visual scene may act as a lower constraint on slow-phase duration, while force limitation may restrict saccadic velocity. It may plausibly be argued however that such factors are likely to be effective principally in determining the time course of the quick phases, and the overall frequency of saccades, while tracking accuracy is probably the major determinant of the amplitudes and occurrence times of saccades. Overall saccade frequency may readily be constrained in a simulation study to equal the experimentally observed frequency. As for the large anticompensatory velocity of the quick phase, it will be noted that while this clearly contributes to the actual velocity error, there is evidence that vision is suppressed during this phase of eye movement (Latour, 1962; Volkmann, 1962; Zuber & Stark, 1966). Hence a measure of greater functional and evolutionary significance would be slow-phase retinal velocity error, excluding consideration of these anti-compensatory pulses. Thus it seems reasonable, with overall saccade frequency constrained, to test whether minimization of mean-square slow-phase velocity error is adequate to explain the observed variations in saccade magnitude and placement.

These arguments may be summarized in the following hypothesis:

Hypothesis:

Minimization of the mean-square slow-phase velocity error is the major factor governing the amplitudes and occurrence times of saccades occurring in the vestibulo-ocular system; and

The effect of other possible components in the biological performance criterion may be accounted for by imposing a suitable constraint on the overall frequency of saccades.

The hypothesis is to be tested by finding the saccade amplitudes and occurence times which minimize the mean square error in the performance of the model of Fig. 6-1, which is assumed to be an adequate description of the real system. The model shown is that of Sugie and Jones (1966), modified so as to eliminate the direct dependence of the saccadic pathway on the cupular signal which is proposed by these authors (c.f. Fig. 5-1, 5-4). In the present formulation the input to the saccadic pathway is shown as a train of impulse functions,

$$p(t) = \sum_{i=1}^{\infty} C_i U_0 (t - t_i),$$

composed of impulses having amplitudes C_1, C_2, ...C_i, ..., and occurring at times t_1, t_2, ...t_i, ... respectively. The amplitudes and occurrence times of these impulses are assumed to be controlled by an unknown saccade-generation mechanism, labelled 'SG' in the figure. Dotted lines are drawn to indicate possible sources of information upon which a control strategy might be based. For generality two separate eye-centering filters have been included here, as justified for Fig. 5-4.

The hypothesis stated above implies minimization of mean square error evaluated over an infinite time interval, whereas in practice any theoretical result must be compared with an experimental record of finite length. It is convenient therefore to consider only an interval $t_1 \leq t \leq T$, containing a specified number of saccades, N, where t_1 is the occurrence time of the first saccade, and T is the occurrence time of the $(N+1)^{th}$ saccade. The problem of initialization is circumvented in a particular case by choosing t_1 and T from the experimental record under consideration. The number N is set equal to the number of saccades observed experimentally in this interval, thus providing the required

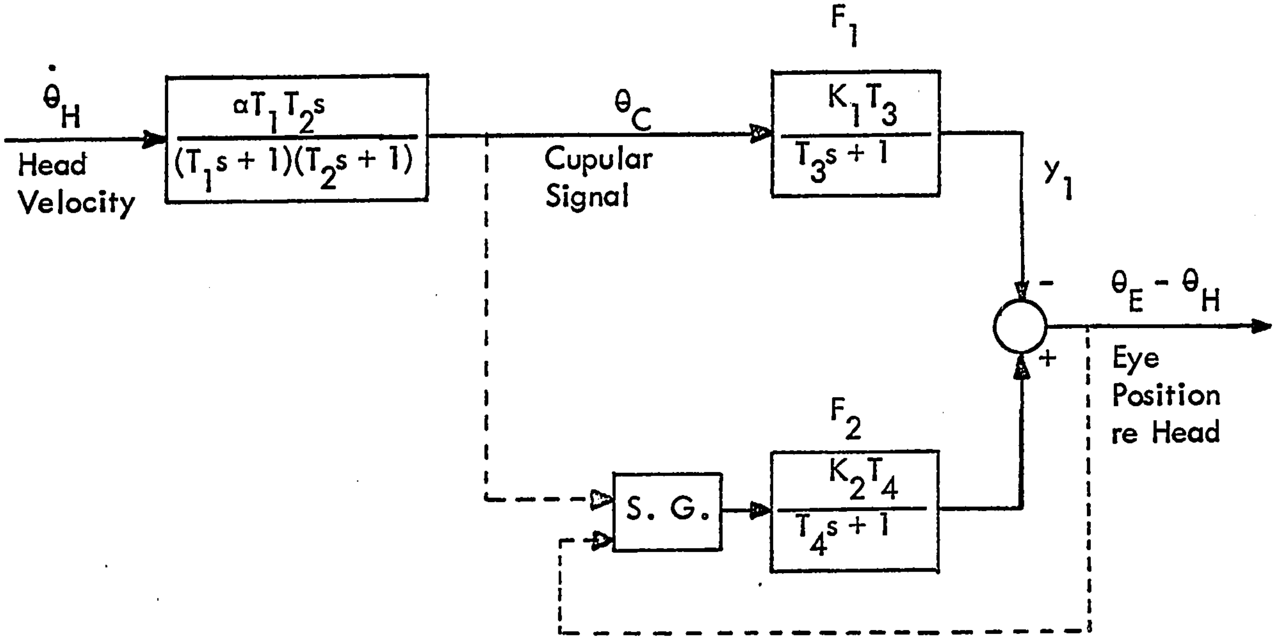


Fig. 6 - 1 MODEL OF THE VESTIBULO-OCULAR SYSTEM, MODIFIED FROM SUGIE & JONES, 1966.

The component "S. G." is an undefined Saccade Generation Mechanism, whose output is a pulse train. Possible inputs to S. G. are shown by dotted lines.
The filters F_1 and F_2 are shown with different time constants, for generality

constraint on the overall saccade frequency.

In the studies to be described here only sinusoidal head velocity inputs have been considered, and the sinusoidal frequency has been chosen such that the phase shift between head velocity and canal signal is negligible. Thus the question of whether the relevant error signal is with respect to actual head velocity or to canal signal ("perceived" head velocity) is avoided. Some computational simplification results, but this interesting question remains to be answered.

6.3 OPTIMIZATION PROCEDURE

On the basis of considerations described in Section 5.2.1, the output of the saccadic pathway may be expressed as

$$y_2(t) = \sum_{i=0}^{\infty} C_i \, e^{-a(t-t_i)} U_{-1}(t-t_i)$$

where

$$e^{-a(t-t_i)} U_{-1}(t-t_i)$$

is the response of the filter F_2 to an impulse occurring at time t_i. Thus during the $(i)^{th}$ intersaccadic interval,

$$y_2(t) = \left[y_2(t_{i-}) + C_i \right] e^{-a(t-t_i)} \quad , \quad t_i \leqslant t \leqslant t_{i+1}$$

where $y_2(t_{i-})$ is the value of y_2 immediately prior to the $(i)^{th}$ saccade.

It is convenient to define

$$D_i = y_2(t_{i-}) + C_i$$

to represent the magnitude of y_2 immediately following the $(i)^{th}$ saccade, so that the output may be represented

$$y_2(t) = D_i \, e^{-a(t-t_i)} \quad , \quad t_i \leqslant t \leqslant t_{i+1},$$

$$i = 0, 1, 2, 3, \ldots\ldots$$

The procedure to be outlined yields the optimal sequence $\left\{ D_{i_{opt}} \right\}$ from which the $\left\{ C_{i_{opt}} \right\}$ may be calculated if desired.

Differentiating this last expression yields the velocity output of the saccadic pathway, which is

$$\dot{y}_2(t) = -a D_i e^{-a(t-t_i)} + C_i U_0(t-t_i), \quad t_i \leqslant t \leqslant t_{i+1},$$
$$i = 0, 1, 2, 3, \ldots\ldots.$$

The second term in this expression represents the impulses of velocity which correspond to jump discontinuities in the position output. In the real system such jumps are of finite duration and correspond to the quick phases. However quick-phase velocity is to be ignored here, for reasons outlined in the previous section, and hence the impulses in the above expression will be ignored in calculating the mean-square velocity error. The symbol $\dot{y}_{2,s}(t)$ will be used to denote slow-phase velocity due to the saccadic pathway, i.e.,

$$\dot{y}_{2,s}(t) = -a D_i e^{-a(t-t_i)}, \quad t_i \leqslant t \leqslant t_{i+1},$$
$$i = 0, 1, 2, 3, \ldots\ldots\ldots\ldots$$

The slow-phase error velocity, or velocity of retinal image slip, is the slow-phase velocity of the eye relative to space, and may be represented as

$$\begin{aligned} \epsilon(t) &= \dot{\theta}_H(t) + (\dot{\theta}_{E,s}(t) - \dot{\theta}_H(t)) \\ &= \dot{\theta}_H(t) + (\dot{y}_{2,s}(t) - \dot{y}_1(t)) \end{aligned}$$

where $\dot{\theta}_H$ represents head velocity, $(\dot{\theta}_{E,s} - \dot{\theta}_H)$ represents slow-phase eye velocity relative to head, and $\dot{y}_1$ and $\dot{y}_{2,s}$ represent the contributions of continuous and saccadic pathways respectively to slow- phase eye velocity relative to head.

In the optimization to be performed, only a finite segment $[t_1, T]$ of the time axis is to be considered. Hence minimization of mean-square error is equivalent to minimization of the integral of the square error, or integral square error. The latter will be called the "return", and for the case of N saccades, may be expressed,

$$R_N(t_1, T) = \int_{t_1}^{T} \epsilon^2(t)\ dt$$

$$= \sum_{i=1}^{N} \int_{t_i}^{t_{i+1}} \epsilon^2(t)\ dt$$

$$= \sum_{i=1}^{N} \int_{t_i}^{t_{i+1}} (\dot{\theta}_H - a\, D_i\, e^{-a(t-t_i)} - \dot{y}_1)^2\ dt$$

$$= \sum_{i=1}^{N} R_1\,(t_i, t_{i+1}) \ldots\ldots\ldots\ldots \qquad \text{Eq. 6.1}$$

This function, to be minimized with respect to the $\{D_i\}$ and the $\{t_i\}$, is the sum of N integrals, each containing only one of the $\{D_i\}$. It is therefore possible to obtain a general expression for the optimum saccade amplitude D_i for the $(i)^{th}$ inter-saccadic interval as a function of the limits of that interval. The integral square error for the $(i)^{th}$ interval is minimized with respect to D_i by differentiating and setting the result equal to zero,

$$\frac{\partial}{\partial D_i}(R_1(t_i, t_{i+1})) = 0.$$

Let it now be assumed that

$$\dot{\theta}_H(t) = A \sin(\omega t),$$

$$\dot{y}_1(t) = B \sin(\omega t + \beta),$$

where B and β may be found in terms of known model parameters. Then upon differentiation, integration and solving for D_i, one obtains an explicit expression for the optimum saccade amplitude,

$$D_{i_{opt}} = D_{i_{opt}}(t_i, t_{i+1}, a, A, B, \beta, \omega)$$

$$= \frac{H\left[\exp(-a(t_{i+1} - t_i)) \cdot \sin(\omega t_{i+1} + \delta) - \sin(\omega t_i + \delta)\right]}{\exp(-2a(t_{i+1} - t_i)) - 1}$$

where

$$H = 2\left[\frac{A^2 + B^2 - 2AB\cos\beta}{a^2 + \omega^2}\right]^{1/2} \quad \text{.................Eq. 6.2}$$

$$\delta = \tan^{-1}(\omega/a) + \tan^{-1}\left(\frac{B\sin\beta}{A - B\cos\beta}\right)$$

When the optimal saccade amplitude is known, the minimized integral square error for the (i)th interval may be calculated as in Equation 6.1. Thus for any given sequence of saccade occurrence times, it is possible to find the optimal return for that sequence. The problem remaining is to find the optimal sequence.

It is convenient now to use the symbol $Q(t_i, t_{i+1})$ to denote the return resulting from the $(i)^{th}$ interval after optimizing its saccade amplitude. Thus

$$Q(t_i, t_{i+1}) = \min_{D_i} \int_{t_i}^{t_{i+1}} \epsilon^2(t)\, dt$$

$$= \int_{t_i}^{t_{i+1}} \epsilon^2(t)\, dt, \quad D_i = D_{i_{opt}} \quad \text{........ Eq. 6.3}$$

Then for any arbitrary sequence of N saccades in the interval $[t_1, t_{N+1}]$, the total return after optimizing saccade amplitudes is

$$R_N(t_1, t_{N+1}) = \sum_{i=1}^{N} Q(t_i, t_{i+1})$$

and the optimal return, corresponding to the optimal sequence of occurrence times, may be expressed as,

$$F_N(t_1, t_{N+1}) = \min_{\{t_i\}} \left[\sum_{i=1}^{N} Q(t_i, t_{i+1}) \right]$$

To achieve this minimization using the calculus it would be necessary to differentiate the sum in square brackets with respect to each of the $\{t_i\}$, set the results equal to zero, and solve the resulting N simultaneous equations. The equations are complex and non-linear, so that some method involving enumeration or iteration is necessary. The technique of Dynamic Programming (Bellman, 1957) has been chosen because it leads to a simple computational algorithm.

Dynamic Programming is a method of systematic enumeration derived from a simple property of multistage decision processes, of which the present case is a relatively simple example. Bellman (1957) named this property the "Principle of Optimality" and stated it as follows:

> " An optimal policy has the property that whatever the initial state and the initial decision are, the remaining decisions must constitute an optimal policy with respect to the state resulting from the first decision."

To illustrate, suppose that a given sequence of saccade occurrence times $\{t_i\}$, i=1, 2, 3, ...N, is optimal for the interval $[t_1, t_{N+1}]$. Now consider as the "initial decision" the occurrence time t_N of the $(N)^{th}$ saccade. This occurrence time is of course optimal for the interval $[t_N, t_{N+1}]$ since it is the only one possible, and clearly the remaining occurrence times $(t_1, t_2, \ldots\ldots t_{N-1})$ are optimal for the interval $[t_1, t_N]$.

From this conclusion one may argue as follows: Suppose that for the case of N-1 saccades in an interval $[t_1, \lambda]$, the optimal return $F_{N-1}(t_1, \lambda)$ were known for all possible values of λ in the major interval $[t_1, t_{N+1}]$, and that the N-1 occurrence times (the "optimal policy") corresponding to each value of λ were known also. Then determination of the optimal t_N for the N-saccade case would be a simple matter, requiring minimization with respect to t_N only. Thus the return from the N-saccade case, for arbitrary t_N, would be

$$R_N(t_1, t_{N+1}) = Q(t_N, t_{N+1}) + F_{N-1}(t_1, t_N)$$

and the optimal return

$$F_N(t_1, t_{N+1}) = \min_{t_N} \left[Q(t_N, t_{N+1}) + F_{N-1}(t_1, t_N) \right]$$

Moreover the optimal return for the (N-1)-stage case could clearly be derived from the general result of the (N-2)-stage case, and so on, reaching finally the single-stage case (one saccade in the interval $[t_1, \lambda]$ for which it is obvious that

$$F_1(t_1, \lambda) = Q(t_1, \lambda) \quad \ldots\ldots \text{Eq. 6.4}$$

Thus starting from this result, and using the recursive equation

$$F_i(t_1, \lambda) = \min_{t_i} \left[Q(t_i, \lambda) + F_{i-1}(t_1, t_i) \right] \quad \ldots\ldots \text{Eq. 6.5}$$

the general solutions to the problems of each stage are found successively as functions of λ, and used in the solution of the succeeding stage problem.

The fundamental feature of this method therefore lies in the decomposition of the more complex problem into a succession of simpler ones. The decomposition is possible because of the self-evident property of the optimal policy which is expressed by the Principle of Optimality. It should perhaps be noted that the method has immense power and versatility, although its application is sometimes difficult, as for example when the relationship between returns of successive stages is not simply additive as in this case.

6.4 COMPUTATION

A detailed outline of the steps involved in the computation is given here, and may serve to clarify the nature and advantages of the Dynamic Programming approach.

Consider the major interval $[t_1, T]$, and imagine a single saccade occurring at time t_1 with the corresponding slow-phase ending at some arbitrary time t_2, within the major interval. As t_2 is varied the optimal saccade amplitude D_i, and the return $Q(t_1, t_2)$ may be calculated as functions of t_2 from Equations 6.2 and 6.3. By Equation 6.4 the return so calculated is the optimal return.

In the computer solution the time axis is divided into a suitable number of equal increments, and a table of t_2 and the optimal return $F_1(t_1, t_2)$ is constructed, along with a table of the corresponding optimal saccade amplitudes. This completes the first stage.

In the second stage, a second saccade is introduced, corresponding to the slow-phase interval $[t_2, t_3]$. For an arbitrary value of t_3, all possible values of t_2 are considered, and the return $Q(t_2,t_3)$ due to the second slow-phase interval is calculated. The total 2-stage return is

$$R_2(t_1,t_3) = Q(t_1,t_2) + Q(t_2,t_3)$$

and is obtained simply by adding to $Q(t_2,t_3)$ the tabulated value of $F_1(t_1,t_2)$ from the previous stage. Thus for a particular value of t_3, a list is formed of the return $R_2(t_1,t_3)$ as a function of t_2. This list is scanned as it is formed, and the smallest entry is stored as the optimal return for a 2-stage process,

$$F_2(t_1,t_3) = \min_{t_2} \left[Q(t_2,t_3) + F_1(t_1,t_2)\right]$$

The procedure is repeated for all incremental values of t_3 in the interval $[t_2,t]$ and a new table is formed with the column headings t_3, $F_2(t_1,t_3)$, $t_{2_{opt}}$, $D_{1_{opt}}$ and $D_{2_{opt}}$. The table entries describe the optimal return and the optimal policy for the 2-saccade case in the interval $[t_1,t_3]$.

Up to this stage no major computational savings are evident, but such savings are very striking in subsequent stages. By the general recursive relationship of Equation 6.5, it is evident that the procedure to be followed in the $(i)^{th}$ stage is identical to that followed in the second stage. The number of calculations per stage actually decreases slightly in successive stages, since the interval over which t_{i+1} must be varied gradually shrinks.

The digital computer program used to perform these computations was written in Fortran and executed on the IBM 7044 installation at McGill University. All programming for this study was done by Mr. Wettstein.

6.5 RESULTS

Studies were made of a record of cat eye movement in response to sinusoidal rotational oscillation of head and body at 0.2 cycles per second. The record, from an experiment performed by Mr. H. Zuckerman in this laboratory, was obtained from a conscious cat restrained by means of a steel wire passed through holes drilled in the canine teeth, the drilling having been performed previously under anaesthesia. Eye movement was recorded by the method of DC electro – oculography. The experiment was performed in total darkness to eliminate interference from the visual tracking reflex.

A continuous major segment from the experimental record was divided into minor segments each containing four saccades with the corresponding slow-phase intervals. Data from each minor segment were first fitted to the Sugie-Jones model by the method of least squares, in order to determine the basic system parameters. It should be noted that an iterative modification of the usual linear least squares fitting procedure was necessary to determine the value of the time constant T_4 of the saccadic pathway, a value of 0.8 seconds being found to be satisfactory. The output $y_1(t)$ of the continuous pathway, emerged from the fitting procedure with a phase lag relative to head velocity of around 47° in each case. Canal-induced phase advance at this frequency was estimated from the data of Jones and Milsum (1966) to be 8.1°. Thus phase lag attributable to the filter F_2 was 55°, corresponding to a time constant $T_3 = 1.1$ sec. Thus the values of the filter time constants ($T_3 = 1.1$ sec, $T_4 = 0.8$ sec.) which emerged from the fitting procedure, were both very close to the value of 1.0 sec. obtained by Sugie and Jones (1966). Fig. 6-2 (a to d) shows four consecutive segments of the original record with four saccades per segment. The squares indicate the original data, and the solid line represents the best least-squares fit to the slow phase segments. The fit is quite good and increases one's confidence in the model of Sugie and Jones, since they did not test it by this means.

In Fig. 6-3 (a to d) the same four minor segments of the experimental record are shown as solid lines, and the optimum response for the respective segment as determined by the Dynamic Programming approach is shown in each case as a dashed line. Model parameters were obtained from the fitting described above, and the

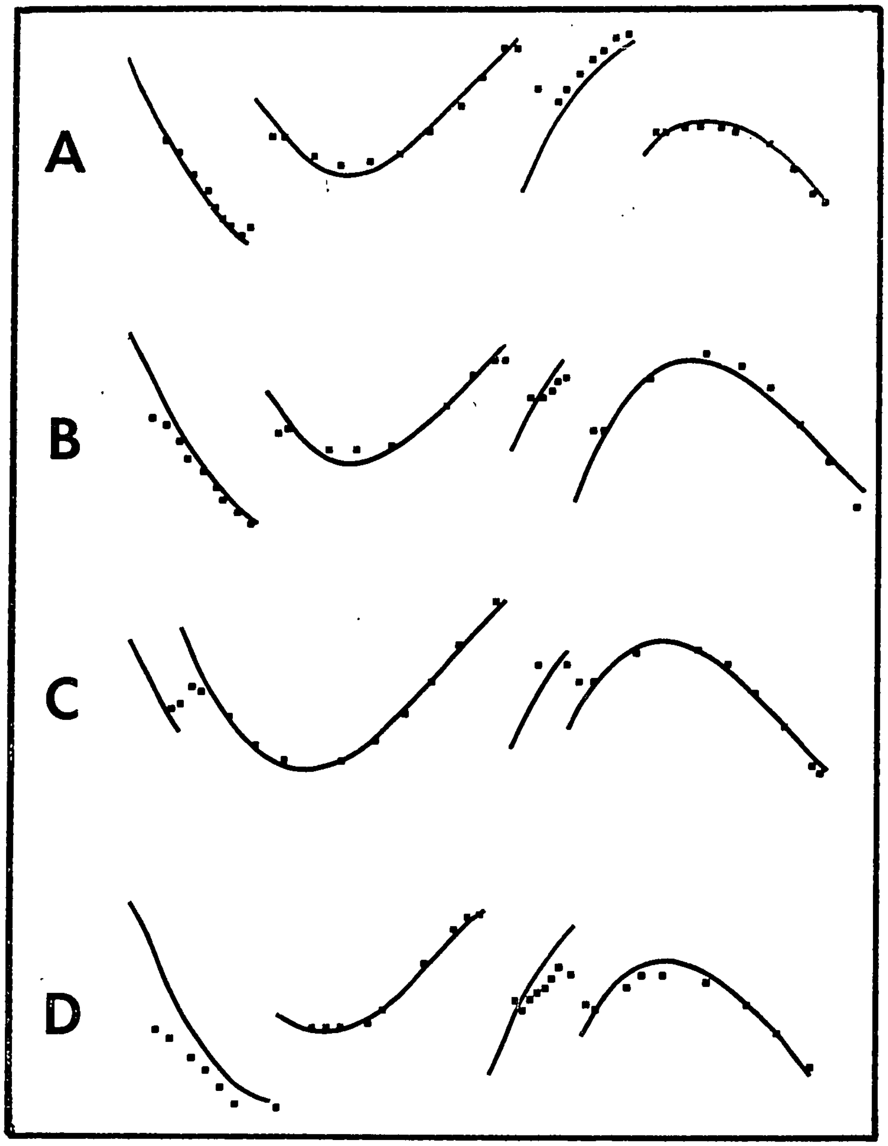


Fig. 6-2 CURVES FITTED TO RECORDS OF CAT VESTIBULO-OCULAR RESPONSE Records are consecutive segments of the response of a cat, in darkness, to sinusoidal head and body rotation at 0.2 Hz. Squares indicate points taken from the original records; solid lines were fitted by least squares iteration to find the system parameters.

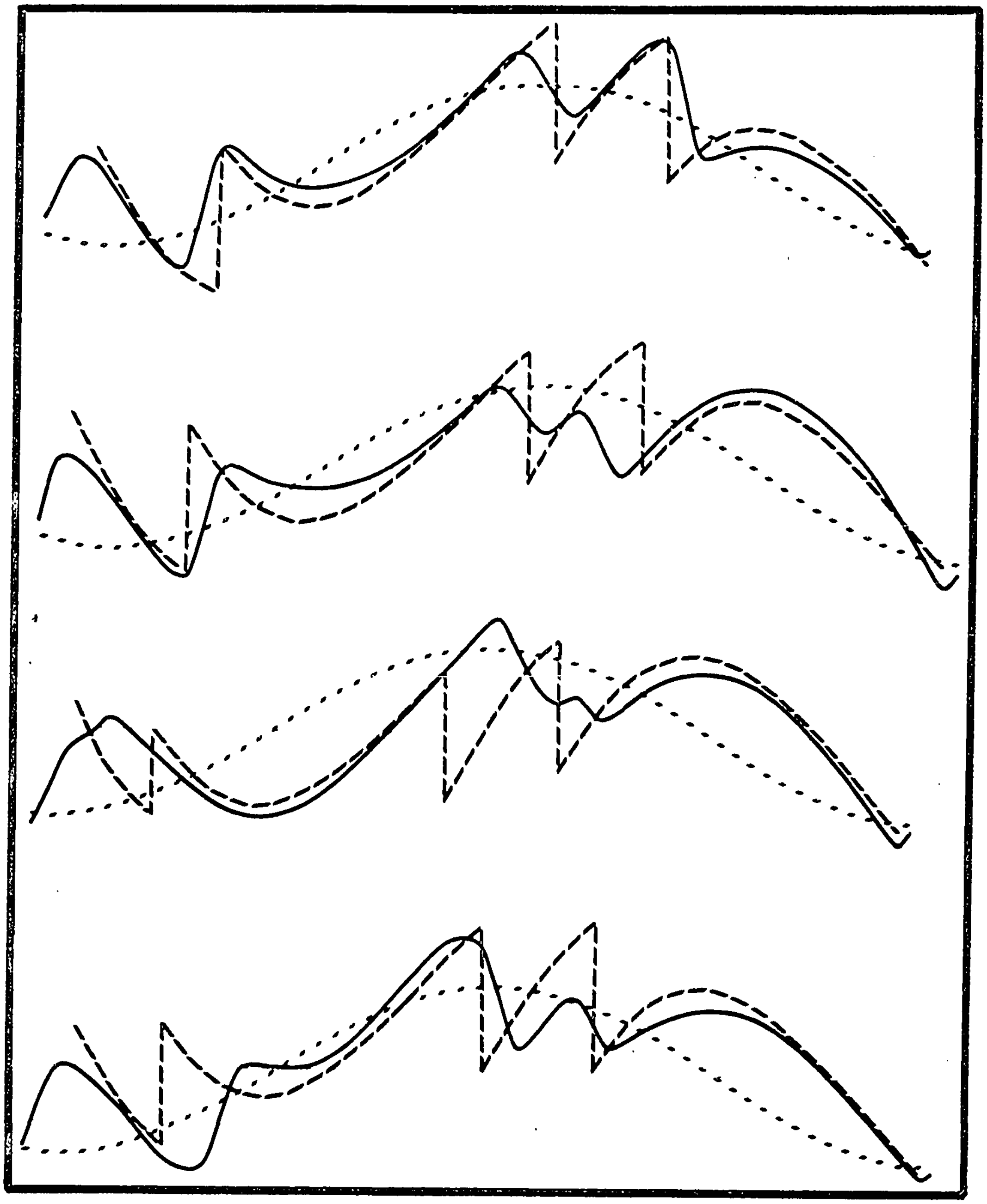


Fig. 6-3 ACTUAL vs. OPTIMUM RESPONSES OF CAT VESTIBULO-OCULAR SYSTEM.

Solid lines - actual cat eye movement, the four segments being recorded consecutively; Dotted lines - required eye velocity (equal to head velocity but opposite in sign); Dashed lines - simulated optimum system response: saccade amplitudes and occurrence times determined such that mean square velocity of image slip in the slow-phases is minimized.

optimum placement and amplitude of the four saccades were found for each segment. In the first two segments (Fig. 6.3 (a) and 6.3 (b)) the experimentally observed response is remarkable similar to the optimum response, both as regards the timing of saccades and the time course of eye movement during the slow phases. There is of course a discrepancy at the time of each saccade, since the simulated response gives instantaneous saccades. The fourth segment shows slightly greater discrepencies and the third seems to be the worst. This last one is of considerable interest however. Considering the second slow-phase interval, which is long and concave upwards, it appears that in the actual response this interval was allowed to continue past the time when a saccade "should" have occurred. There follows a short interval and a small saccade, which one is at first tempted to call abortive. However, in comparing actual response with the optimum, it appears plausible that this short interval and the ensuing small saccade are together correcting for the error resulting from the excessively long duration of the second slow-phase interval.

6.6 DISCUSSION

It may be concluded that in spite of some discrepancies the actual response of the vestibulo-ocular system is surprisingly similar to the optimum response of the Sugie-Jones model under the conditions here studied, optimality being based on the mean-square velocity-error criterion chosen rather arbitrarily as described above. The result tends at the same time to validate the model and the choice of performance criterion. There can be little doubt that a performance criterion which is some even function of the velocity error, or some estimate of it, is a critical factor in determining the performance of the system, although other factors are certainly involved.

It must be emphasised that it is not intended to suggest that the optimization procedure used here to obtain the optimum simulated response has any relation whatsoever to the biological optimization process involved in the real situation. Rather it is simply noted that the actual response in the circumstances described follows very closely the absolute optimum response.

It is interesting to consider how the biological organism might achieve such efficient performance. The two basic alternatives are (1) that there is "on-line" adaptive optimization throughout the course of normal eye movements, and (2) that the processes of evolution and/or post-natal learning result in the development of a basic control strategy which is then built into the reflex mechanism and ensures nearly optimum response during most of the conditions met with in everyday life of the organism.

On-line optimization would have to be based on a continuous flow of information as to the motion of the eyes. This presents no problem in principle, even if there were no real motion signal from eye muscles or other orbital structures, since an eye motion signal could presumably be computed with a fair degree of accuracy. In this regard Robinson has shown (1964) that the ocular globe is very heavily damped so that movement of the eye in response to extra-ocular muscle activity is not affected by mechanical loading unless this is very severe. It is hard to imagine any physiological situation in which the eye would be subject to any more than very light mechanical loading, so that eye motion should be easily defineable in terms of the neural signal to the eye muscles.

Some sort of predictive mechanism would be an advantage in achieving on-line optimization. It is well known (Young, 1962; Michael & Jones, 1966) that such prediction occurs in the visual tracking system and there are reasons for assuming that it occurs in the vestibulo-ocular system also, although this would be more difficult to demonstrate. The procedure described here for finding the optimum response of the vestibulo-ocular system to a given input may prove to be a useful approach to the question of prediction in this system.

The idea that a suitable control strategy governing saccade generation develops through evolution or learning is also attractive. Because of the normal head and eye movements of everyday life, there is ample opportunity for one or both of those two very efficient adaptive mechanisms, namely the genetic processs and/or post-natal learning, to sort out a suitable strategy. Under these conditions a more or less direct estimate of error in the vestibular signal to the eye muscles is available through vision and the visual tracking system, the latter being required to correct for the error remaining after vestibular compensation reaches its limit. The evolutionary rather than post-natal development of an optimum strategy would be difficult to prove or disprove, especially since the vestibulo-ocular system appears to be phylogenetically a very old system. On the other hand it would be most interesting to investigate the development of good vestibulo-ocular compensation during post-natal growth and development, although it might be difficult to distinguish the development of a control strategy from the development of a coordinated motor system.

These two major alternatives, on-line optimization and an optimal strategy, are of course not mutually exclusive. Rather they would probably be mutually dependent. In either case it would clearly be advantageous to the organism if the optimum condition, thought of as the minimum point on a multi-dimensional surface, were contained not in a steep-sided valley but in a shallow depression. In this way system performance would be affected relatively little by variations from the optimum strategy and by variations in system parameters, a particularly desirable characteristic in a biological system, in which such variations are probably common. The methods described here make it possible to investigate these possibilities, although no such analysis has yet been pursued in detail.

The problem posed in the first paragraph of this chapter was to gain understanding about the rationale for variations in saccade placement and amplitude, and in particular the strategy governing such variations. The rationale seems apparent, since variations such as those normally seen, must occur to achieve optimum performance. More detailed studies, taking into account other possible performance criteria, may be expected to lead to even better definition of these variations. The mechanism or strategy governing these variations remains a mystery.

PART III

EXPERIMENTAL INVESTIGATION OF SOME ASPECTS OF VESTIBULAR STABILISATION OF THE HEAD

CHAPTER 7

VESTIBULAR STABILISATION OF THE HEAD: HISTORICAL, ANATOMICAL AND THEORETICAL ASPECTS

7.1 GENERAL

The maintenance and control of the posture of the head must depend on a precise interplay of complex neuromuscular mechanisms involving sensory information from many sources. The major sensory inputs are presumably from muscle and joint receptors, from vision, and from the linear and angular accelerometers of the inner ear. Everyday experience emphasizes the great precision of this postural control and of the control of voluntary head movements. However there has been comparatively little investigation of the nature of this control, and of the relative significance of the various sensory inputs. It is evident that any serious attempt to elucidate the details of this control will have to give careful and quantitative consideration to the dynamic properties of the contributing systems.

The studies described here are related to the contribution of the vestibular system to head stabilization and are confined to the investigation of stabilization during rotational movement of the body about the vertical axis. Before proceeding it is desirable to establish a suitable terminology. The term "vestibulo-collic reflex" has come into use in this laboratory to distinguish the reflex vestibular control of neck muscle activity and head movement from the general class that has been called "cristo-spinal" reflexes by Henricksson, Dolowitz and Forssman (1962). The term "laterotorsion" used by Henricksson et al. to refer to calorically-induced head deviations about the long axis of the body seems less suitable, since it gives no indication of anatomical components involved in the system. The more specific term "cristo-collic" may in future become more suitable to distinguish rotational from linear reflex stabilization systems. However for the present the term "vestibulo-collic reflex" will be retained, as it probably has connotations for a wider audience.

There are of course dangers in any attempt to isolate a single functional component system from a larger complex dynamic system. However, certain features of the component system discussed here, i.e. the reflex semicircular canal control of horizontal rotational head movements, make this system particularly suitable for isolation in this way. Vision can of course be easily excluded in studying the role of the vestibular input, although the converse is not true for the case of head stabilization. The choice of horizontal-plane rotation also simplifies matters, since the effect of changing orientation with respect to the gravitational vector is excluded, while the effect of centrifugal force on the otolithic receptors is probably relatively small in this situation and can be minimized by keeping the head near the axis of any applied rotation of the body. The contribution of reflexes dependent on muscle and joint sensation is more difficult to eliminate. However, it is probably suitable for the present to lump these effects with the passive visco-elastic properties of neck structures, as discussed below.

The vestibulo-collic system tends to be related to the better known vestibulo-ocular system because both are important for stabilization of the visual image, the vestibulo-collic reflex apparently being particularly important in this respect in the smaller animals. The two reflex systems differ fundamentally however, according to the manner in which the sensors, the semicircular canals, are utilized in the respective systems. The canals are fixed in the head, and hence detect the output of the vestibulo-collic system. Head velocity information is thus fed back to the controlling neural centers, providing the potentiality for an error-activated mode of operation in which the head is continuously driven so as to null the canal signal and thus keep the head stationary in space. A number of possible advantages which may accrue as a result of this feature are outlined briefly here, and discussed more fully in a subsequent theoretical section.

(1) Because it uses the canal in a feedback mode, the vestibulo-collic system may be expected to perform effectively in visual stabilization over a greater bandwidth than does the vestibulo-ocular system; (2) In the maintenance of head posture, and in head movements resulting from other inputs, the vestibulo-collic reflex would appear to provide what is effectively damping of the head relative to space; (3) The active vestibulo-collic system in birds could be the

basis of an inertial navigation capability, at least for short intervals.

Study of this reflex system is complicated by the presence of feedback, since there is no simple way of estimating, for example, the magnitude of neck-muscle torques attributable to the vestibulo-collic mechanism without actually disrupting the system, a fact first emphasized by Jones and Milsum (1965). The occurence of saccades, or head nystagmus, which affect both the sensor and the effector mechanisms, results in even greater complication. Moreover, changes in arousal, and other phenomena which may produce changes in the gain of various components, have dual effects in the vestibulo-collic system. Not only is arousal found to affect saccade magnitude and frequency as it does in the vestibulo-ocular system, but from well known principles of control theory it is clear that gain changes within the feedback loop may be expected to produce changes in the dynamic parameters of the response even in the absence of saccades.

Thus, while this system, providing horizontal-plane stabilization of the head, is probably easier to study than any other component of the overall head stabilization system, it is nevertheless quite complex. Moreover there has been very little quantitative investigation of this system. Consequently the approach in the present study has been to survey briefly several major aspects of the system in the hope of providing a rational basis for more definitive studies in the future.

The organization of this third major part of the thesis is as follows. In the present chapter a historical review is followed by a detailed consideration of the relevant anatomy, and a theoretical examination of the vestibulo-collic system. Chapter 8 then describes experimental techniques used, in particular the measurement system which was devised for accurate, restraint-free recording of head movement in man and birds. Experiments in human and avian subjects, designed to test some theoretical deductions, are described in Chapters 9 and 10, as well as investigations to assess the basic functional characteristics of the response in pigeons. Experiments directed towards assessment of some of the components in the vestibulo-collic system in pigeons through study of vestibulo-ocular response and of electromyographic activity in neck muscles are described in Chapter 11. These studies have yielded some important findings relevant to the problem of saccadic mechanisms in the Sugie-Jones model (Sugie & Jones, 1966) of the vestibulo-ocular system, and have been largely responsible for the theoretical studies of the model which are described above in Chapter 6. Chapter 12 summarizes the theoretical and experimental findings.

7.2 HISTORICAL

Pigeons and other small animals were used extensively in many of the earliest experimental investigations of the function of the vestibular system (Flourens, 1824; Breuer, 1874; Mach, 1875; Stephani, 1876; Ewald, 1887). Head movement plays a major role in visual stabilization in these animals, unlike the situation in larger species (Ewald, 1887; Bartels, 1931), and thus head movement disturbances due to labyrinthectomy or canal section, as well as per- and post-rotatory head nystagmus have long been well-known phenomena. Flourens' observations, which have been repeatedly confirmed, clearly demonstrated the important influence of the vestibular system on head movements. The vestibular contribution to post-rotatory head and eye nystagmus was distinguished from optokinetic effects by Breuer, who gave a good qualitative description of the time course of head nystagmus in the blindfolded pigeon following a period of constant-velocity rotation. Brisk nystagmus starts during the rapid deceleration from constant velocity, with the slow phase in the lagging or compensatory direction. During the nystagmus, the overall position of the head deviates in the lagging direction also, and then returns very slowly towards the central position when the nystagmus ceases.

Borries (1920) commented on the remarkable sensitivity of vestibular head stabilization in pigeons, and using a more refined operative technique than Breuer, showed conclusively that rotational head nystagmus in the absence of vision was abolished by canal plugging, while optokinetic responses were unaffected. Huizinga (1935, 1936) carried forward this latter aspect and showed that following careful canal section, avoiding damage to other structures, locomotor and aerobatic ability in pigeons was regained to a remarkable extent, provided that vision was not excluded. Dunlap and Mowrer (1930) and Mowrer (1934, a,b,c, 1935) were probably the first to make objective recordings of pigeon head movement, using cinematographic and kymographic methods. Mowrer was primarily interested in central phenomena such as habituation, which he studied in detail. However he astutely observed that the function of vestibularly-driven head movements was apparently to keep the head still relative to space,and noted that the duration of post - rotational head nystagmus was significantly reduced if the rotation wasstopped during active per-rotatory nystagmus. He also investigated (1934c) the remarkable susceptibility of the vestibular head-nystagmus response to variations in "excitement" due to handling and other non-vestibular sensory inputs. Huizinga and van der Meulen (1951) using Mowrer's method of recording, confirmedmany of Mowrer's observations concerning the interaction of visual and rotational stimuli in producing head movement, and investigated in some detail variations in the waveform of per- and post-rotatory head nystagmus associated with changes in arousal. They obtained stable decerebrate pigeon preparations, some kept alive over one month, and observed that per-and post-rotatory head nystagmus in these animals lastedsignificantly longerthan in normal birds, with considerably less individual variation. The magnitude of the quick saccadic flicks of the head was generally larger after decerebration,so that the overall lagging deviation of the head seen in normal animals was almost totally absent.

There have been few significant investigations of pigeon head movement since Huizinga's studies. Schierbeek (1953) repeated much of Huizinga's work, but without the advantage of accurate objective recording. However he noted a feature of the post-rotatory response which has been found repeatedly in the present investigation, namely that the final steady position of the head some minutes after the stopping stimulus is frequently some distance away from the central position. Schierbeek also attempted to estimate pigeon semicircular canalparametersfrom the head-nystagmus response using the method of cupulometry. A fundamental error in this approach is pointed out in a later section. Aschan, Bergstedt and Stahle (1955) and Stahle (1960) made some preliminary studies of pigeon head movements associated with constant angular accelerations, using a simple electro-optical device to record head movement. Several electromyographic studies have been made by van Eyck and colleagues (1949-60) who recorded from electrodes in the neck muscles during acoustical (Tullio phenomenon) and rotational stimulation of the semicircular canal. These workers were principally concerned with the latency (1.5msec) between ampullary and neck muscle action potentials, and with the angular acceleration threshold (1.5 deg/sec^2 for 1 second).

There have been fewer studies of vestibularly-driven head movements in non-avian species. Recently Suzuki and Cohen (1964), Cohen, Suzuki and Bender (1965) have studied the effects of electrical stimulation of individual semicircular canal nerves on head movements in cats and monkeys. There were a number of studies of the reflex response in reptiles and amphibia around the turn of the century (Steiner, 1885; Loeb, 1907; W.F. Ewald, 1907; Tredelenburg and Kuhn, 1908; W. Mulder, 1911). These studies were qualitative and the results were essentially the same as those in pigeons, but they may be of some interest in future work since these and other authors have shown that in snakes, turtles and frogs, the head movement response is essentially non-saccadic, a fact which could substantially simplify studies aimed at understanding the neural control mechanism involved.

According to Utsumi, Shindo, Mukai and Yamanaka (1961), Urbantschisch (1910) was the first to describe head nystagmus in man, induced in this case by pressure on a fistulous lesion in the ear of a patient. There have been numerous similar observations. von Bekesy (1935) made a careful study of this phenomenon, obtaining a very sensitive photo-oscillographic recording of head movements in response to controlled tone bursts. Fischer and Wodak (1922) made a study of post-rotatory head, body, and arm deviations in man, and Wodak (1957) has emphasized the clinical importance of these "deiterospinal" reflexes. These workers made qualitative observations only. Head movements were in the lagging direction when they occurred but were not particularly striking. Torok (1960) recorded "vestibular latero-pulsion", i.e. lateral movements of the trunk in the seated subject following cessation of constant velocity rotation. The body movement was in the same direction as the slow phase of eye nystagmus with a slow decay back to the resting position. Average duration of the body movement was 27 seconds, or two to three times longer than the duration of eye nystagmus. Hinoki and Kitahara (1961), using a strain gauge device to indicate the occurence of head movements, noted synchronous head and eye movements in man during rotation.

Henricksson, Dolowitz, and Forssman (1962) in a series of papers reported studies on so-called "cristo-spinal" reflexes. During caloric stimulation these authors noted rotation of the head in the long axis of the body in supine subjects, in whom they recorded head movement by differential pressure measurements in two balloons supporting the head. Head movement occurred in the direction of slow-phase eye nystagmus in normal subjects, reaching a maximum value a short time before the termination of the eye nystagmus, and persisting sometimes for as long as 10 minutes. They offer no explanation for the long duration of head deviation but were impressed with the value of this new test as a clinical tool, since in certain pathological conditions there was a differential effect on the head movement response as compared with the eye movement response to caloric stimulation.

There have been a few studies of vestibularly-driven head and eye movements in newborn animals and humans which are some interest as they hint at the developmental sequence in these reflex systems. Bartels (1910) and Galebsky (1927) observed that while optokinetic responses are absent in the human newborn, there are compensatory head and eye movements in response to rotation. Saccadic flicks were absent in very young infants. Windle and Fish (1932) reported that vestibular righting reflexes and post-rotational head-turning appear in the cat embryo at approximately 55 days, whereas other righting reflexes such as body righting from a flat surface appear later. Fish and Windle (1932) and Windle and Fish (1932) found that post-rotational head deviation was present in kittens at birth but that vestibulo-ocular responses did not appear for several days. However in the newborn rabbit, Barany (1918) found vestibularly-driven head and eye movements.

Reports of subjective and objective findings in human subjects following loss of vestibular function are of interest in the present context, but are rather difficult to interpret. A particular question which arises in considering the vestibulo-collic control system is to what extent disturbing head movements are normally damped out on account of the semicircular canal feedback (Section 7.5), and one wonders whether in the absence of the vestibular influence head movements may be underdamped and hence prone to oscillation. The early experiments by Flourens, Breuer, Ewald and others (previously cited) seem to suggest that this may be the case in pigeons; Ewald in particular emphasizedthe continuous pendular head movements which occurred in his labyrinthectomized birds. However these workers used rather crude operative methods which frequently destroyed the sensory hair cells, so that the contribution of irritative symptoms cannot be ruled out. In the experiments of Huizinga (1935, 1936),who used careful canal-plugging techniques, there seems to have been little hint of oscillatory symptoms in pigeons, but Money and Scott (1962) observed pendular head movements in cats up to 10 weeks after bilateral semicircular canal plugging. In human subjects who have lost labyrinthine function,"jiggling" of the visual scene appears to be a frequent and distressing symptom (Ford and Walsh, 1936; Levin, 1939; Crawford, 1952; Cogan, 1958). Cogan describes two patients with a deficit due to streptomycin overdose in which apparent vertical oscillations of the surroundings were very pronounced, so much so that one patient at first found it necessary to hold his head still with his hands in order to be able to see. There were no horizontal oscillations . These symptoms however were apparent only in the early stages of the emergence of the syndrome and could again be conceivably due to irritation. On the other hand, their disappearance could be attributed to adaptive changes in the neural control structure, for example augmenting the stabilizing effects of neck proprioceptive mechanisms .

7.3 NEURO-ANATOMY OF THE VESTIBULO-COLLIC REFLEX SYSTEM

Since few studies of vestibular connections have been made with the vestibulo-collic reflex system specifically in mind, a careful appraisal of available information is necessary. The problem is made difficult because the central distribution of primary vestibular fibers from specific receptors is incompletely known, the best available overall study being that of Lorente de No (1933a). The major conclusions of this study are not contradicted by recent studies of vestibular nuclear unit responses to acceleratory stimuli in which the cells recorded from have been precisely localized (Eckel, 1954; Crampton, 1965, 1966; Shimazu & Precht, 1965; Jones & Milsum 1969). Lorente de No described afferent fibers from the semi-circular canals entering the superior and medial vestibular nuclei and, to a lesser extent, the descending vestibular nucleus. The superior and medial nuclei did not receive macular afferents, which were distributed to the descending, and particularly to the lateral vesibular nuclei. Other primary vestibular fibers, whose origin was unidentified by Lorente de No, also entered the lateral vestibular nucleus. Eckel (1964), and Deunsing and Shaeffer (1958) identified rotation sensitive cells in the lateral as well as other vestibular nuclei. However, Shimazu and Precht (1965), who were very critical in their definition of rotation sensitive cells, found that most such cells lay in the medial and superior vestibular nuclei, with only very few in the lateral and descending nuclei. Many, but not all of the cells isolated by the latter authors were monosynaptically excited by primary vestibular afferents. It would appear therefore that the medial and superior vestibular nuclei are of primary importance for processing of rotational information but that the descending and perhaps the lateral nuclei are also involved.

There is evidence however that only some of these nuclei are involved in relaying rotational information to the spinal cord in general and to neck muscles in particular. The descending nucleus has few if any connections with the spinal cord (Brodal et al., 1962) and the superior nucleus, according to the same authors, probably has none. The lateral vestibular nucleus has extensive ipsilateral connections to all levels of the cord via the vestibulospinal tract (Brodal et al., 1962; Nyberg - Hansen & Mascitti, 1964). Its fibers end in the medial portion of the ventral horn, and make monosynaptic and polysynaptic connections with α-motoneurones (Lund & Pompeiano, 1965) and perhaps with γ-motoneurones also (Pompeiano, 1967). However the apparent paucity of rotation sensitive units in the lateral vestibular nucleus makes one search for another major descending pathway for the vestibular control of rotational head movement, particularly in the horizontal plane. The lateral nucleus is probably very important in other aspects of head stabilization, in which the interaction of inputs from linear and angular receptors will obviously be of great significance.

The medial vestibular nucleus appears to fulfill the requirements, although the number of descending fibers appears to be small. The nature of its connections has been clarified in recent careful studies by two groups of authors. (a) Nyberg-Hansen (1964) has shown that of the vestibular nuclear group only the medial vestibular nucleus sends fibers into the descending medial longitudinal fasciculus, and that these fibers, which are mostly uncrossed, terminate in the medial portion of the ventral horn mainly in the cervical cord, seldom reaching below thoracic levels. (b) Wilson, Wylie and Marco (1968a,b) report that while there are more cells in the medial nucleus with fibers entering the ascending than the descending medial longitudinal fasciculus, the great majority of cells with descending axons are excited monosynaptically by primary vestibular afferents, as compared with less than half of the cells with ascending axons. Very little spatial summation is required for monosynaptic firing. Almost half of the cells in this nucleus, including some activated monosynaptically, are also activated polysynaptically by vestibular afferent fibers.

The medial vestibular nucleus and descending medial longitudinal fasciculus thus provide a direct, low-threshold pathway from rotational receptors to cervical cord, although the fibers are of small diameter (Nyberg-Hansen, 1964) and few in number (Nyberg-Hansen, 1964; Wilson et al., 1968a).

Physiological considerations provide a further basis for arguing that the medial vestibular nucleus may be especially important for rotational head stabilization, and particularly for stabilization in the horizontal plane. This nucleus makes extensive connections to the oculomotor nuclei and its importance for ocular stabilization seems clearly established. The fact that the requirements for visual stabilization in the horizontal plane are especially demanding, at least in terrestrial animals, and the obvious importance of coordinating head and eye compensation, suggests that descending fibers from the medial nucleus are in fact largely concerned with head movements involved in visual stabilization.

Other less direct descending vestibular pathways also exist but details of these connections have not been well defined. For example the lateral vestibular nucleus receives extensive connections from the fastigial nuclei of the cerebellum and also from the cerebellar cortex, especially the anterior vermis, which is know to receive primary vestibular afferents (Brodal & Howik, 1965). The medial vestibular nucleus receives similar but less extensive connections. Vestibulo-reticulospinal connections are another alternative. However these indirect connections appear unsuitable as a primary pathway for reflex control of head movement.

There have been some findings which suggest the existence of primary vestibular afferents descending into the cervical cord without synapsing in any nuclear region. Gernandt & Gilman (1959, 1960) recorded potentials in the radial nerves in cats in response to electrical stimulation of the labyrinth, and found, in addition to a delayed variable wave, an early spike of 2-3 msec. latency, whose form was relatively unaffected by anoxia and intravenous barbiturate infusion. The early spike was prominent in the contralateral radial nerve but also present ipsilaterally. It was unaffected by cutting or stimulating the medial longitudinal fasciculus, but the contralateral spike was obliterated by a mid-line longitudinal section just below the obex. The early spike was not seen in recordings from lumbar ventral roots. These authors argued that the early spike was due to crossed and uncrossed primary vestibular fibers making monosynaptic connections with cervical motoneurones, and cited unpublished anatomical observations of Rasmussen which seem to agree with their findings. Curiously Gernandt and Proler (1965) found a somewhat greater latency (5 msec.) in the response of the spinal accessory nerve to vestibular stimulation.

Brodal et al. (1962) are apparently skeptical of the idea of direct primary vestibulospinal connections. However it is clear that existing pathways are rapidly conducting. Goto, Tokumasu and Cohen (1965), and Cohen (1966) recorded neck muscle activation electromyographically in response to electrical stimulation of the contralateral cristae, and observed latencies of 8-10 msec. in the cat. Van Eyck (1953) recorded ampullary action potential activity and contralateral neck EMG in a pigeon with a Tullio fistula in response to a single click stimulus. The latency observed was only 1.5 msec.

Connections to the spinal cord in avian species have not been studied in great detail but there is reason to suppose that the situation is in general similar to that in mammals. The avian brain shows considerable interspecies variation in gross morphology though probably differences in connections are relatively minor (Ariens-Kappers, Huber & Crosby, 1936). The major differences between avian and mammalian brains appear to be the following (Ariens- Kappers et al. 1936; Romer, 1955): (a) The cerebrum is very small in birds, forming a thin shell around the dominant basal ganglia; (b) the avian optic tecta, corresponding to the superior corpora quadrigemina of mammals, are very large and contain the first synapse in the visual pathway; (c) the avian cerebellum is small, consisting mainly of the phylogenetically-older vestibular portions, i.e. the vermis, flocculus and nodulus. However lateral portions of the cerebellar cortex, which tend to be non-foliated, have been shown to be homologous in structure and connections to the cerebellar hemispheres of mammals (Goodman, Horel & Freeman, 1964).

The avian vestibular nuclear group is complex, and descriptions as well as nomenclature vary considerably. The description given here corresponds to that of Ariens-Kappers et al. (1936). A more recent description is given by Stengelin (1965) but this is concerned largely with morphology of the nuclear groups rather than with their connections. A tangential vestibular nucleus is found in birds lying in the course of incoming VIIIth nerve fibers, and corresponds to the interstitial nucleus (Brodal et al., 1962) of higher forms, though it is somewhat larger. The ventrolateral vestibular nucleus is agreed to correspond to the lateral vestibular nucleus (Deiter's) in mammals, and sends many fibers into the spinal cord. A large dorsolateral vestibular nucleus is described and is thought to be part of Deiter's complex. It is said to receive some primary vestibular afferents and to make extensive connections with the cerebellum. Descending and superior vestibular nuclei in birds appear to correspond to nuclei of the same name in mammals. The dorsomedial or triangular nucleus in birds may be related to the medial vestibular nucleus in mammals but there appears to be doubt about this since some authors found no primary vestibular fibers entering the dorsomedial group in birds (Ariens-Kappers et al., 1936).

The question of a primary pathway for the vestibulo-collic reflex cannot be answered in detail for birds. Descending fibers in the vestibulospinal tract and medial longitudinal fasciculus are described, but the latter are said to derive from the dorsolateral nuclei on both sides. Direct primary vestibular afferent connections with the spinal cord are also reported (Ariens-Kappers et al., 1936)

7.4 FUNCTIONAL ANATOMY OF HEAD ROTATION IN MAN AND BIRD

The mechanics of head rotation are very complicated owing to the multiple articulations and muscles involved, and a brief consideration of the anatomy is desirable. The emphasis here will be on functional anatomical features relating to rotation in the horizontal plane when the body is in a normal standing posture. Descriptions of human anatomy are based on the standard text by Johnston, Davies and Davies (1958), and avian anatomy is described on the basis of an early publication by Shufeldt (1890). The latter applies specifically to the raven, which belongs to a more highly evolved avian order (Passeriformes) than does the pigeon (order Columbiformes) (Romer, 1955). However, they are both of approximately the same size and body configuration so that Shufeldt's work is probably adequate for the present purpose.

In man the atlanto-occipital joint, and all but one of the cervical intervertebral joints, are specialized for movements of flexion and extension, and to a lesser extent lateral flexion. Individually these joints permit relatively little rotation. In the atlanto-occipital joint, rotation is restricted because of the upward concavity of the articular surface of the atlas. In cervical intervertebral joints below the first, the superior articular facets are directed upwards and backwards, thus severly restricting rotation in particular and also lateral flexion. However some rotation does occur at each of these joints so the total is still appreciable. In contrast the first cervical intervertebral joint or atlanto-axial joint is highly specialized for rotation about the axis of the vertebral bodies. Other movements at this joint are greatly curtailed by the close articulation of the odontoid process of the axis into the ring formed by the anterior arch and transverse ligament of the atlas. Rotation at thoracic intervertebral joints, whose articular facets are almost parallel with the vertebral axis, may also contribute to head rotation to a small extent.

Movements of the vertebral column are limited by extensive ligamentous attachments. Prominent in the cervical region is the Ligamentum Nuchae, a thick band running from the external protruberance of the occipital bone to the spine of the seventh cervical vertebra, where it becomes continuous with the interspinous ligament. A fan-shaped fibrous lamina extends from Ligamentum Nuchae to the posterior midline portions of the cervical vertebrae. Also import are the thick Ligamenta Flava which run posteriorly between the lamina of adjacent vertebrae. These ligaments and other fibrous structures forming the capsules of joints are elastic, the Ligamenta Flava being particularly notable in this respect. Hence limitation of movement is not abrupt but graduated, and the ligaments, together with the muscles, provide a passive restoring force tending to bring the head towards its "resting position".

The majority of muscles controlling head movement are located posteriorly because of the unbalanced support provided for the skull by the atlanto-occipital joint. In general, muscles producing rotation are involved in other movements also. An important exception in man is the Inferior Oblique, a fleshy muscle running between the transverse process of the atlas and the spine of the axis. Each of these bony processes is long and massive, providing strength and leverage, while the nature of the atlanto-occipital joint prevents the lateral flexion which might be expected owing to the slightly oblique orientation of the muscle. The short Rectus Capitis Posterior Major, and the longer Splenuis Capitis and Longissimus Capitis work to fairly good mechanical advantage in rotation when the head is initially facing ahead, but are primarily extensors. Similar considerations apply to the anterior neck muscles. Rectus Capitus Anterior, Longus Cervicis and Longus Capitis provide flexion and some rotation; Sternocleidomastoid produces rotation and lateral flexion. Rotation of cervical vertebrae appears to occur largely as a result of head rotation, although the Scalene muscles and Splenius Cervicis also contribute through their attachments to the vertebrae.

In the raven and pigeon there are about twice as many cervical vertebrae as in man, resulting in considerably greater mobility. Atlanto-axial and atlanto-occipital joints are similar to those in man. The differences in neck musculature largely correspond to the greater length and mobility of the neck. In addition some considerable functional differences result because the upper portion of the cervical spine in birds is curved with a foward instead of a backward concavity. This curvature appears to result in a great mechanical advantage in rotation for some muscles.

The major muscles of the side of the neck in the raven are shown in Fig. 7.1, which is reproduced from Shufeldt. Fig 7.2 shows the cranial attachments of some of the muscles. Near the occupital ridge are inserted three muscles significant for rotation, the Complexus and Rectus Capitis Anterior Minor superficially, and deep to them the Rectus Capitis Posterior Major. Complexus originates from the transverse processes of upper cervical vertebrae, and Rectus Capitis Anterior Minor winds round the side of the neck from its origin on the anterior surfaces of the upper cervical vertebral bodies. Rectus Capitis Posterior Major is large despite its single origin from the spine of the axis. Two muscles, Trachelomastoideus and Rectus Capitis Lateralis, arise from the transverse processes of the upper cervical vertebrae and insert side by side on the inferior surface of the skull, anterior to the foramen magnum and fairly near the midline. In the neck the Obliquus Colli, see in Fig. 7.1, appears to be important for rotation, arising on transverse processes and winding up and back to insert on or near spinous processes two or three segments above. The Longus Colli Posticus is a complex muscles in three parts. Two portions arise from the spines of the first two thoracic vertebrae, and of these, one belly inserts into the transverse process of the atlas, and others insert on the dorsal surfaces of the seventh to eleventh cervical vertebrae near the spinous processes. A third portion included under the name Longus Colli Posticus arisesfrom the spines of the second to the seventh cervical vertebrae and inserts into the transverse process of the atlas.

The complexity of neck anatomy and musculature has a number of implications for the study of reflexes involving these muscles. The neural programming required to produce coordinated motion of the head must be very complex indeed, and obviously records of the activity in a single muscle must be interpreted with caution since it would not be surprising to find that a given muscle was active only during a portion of the movement. In birds and

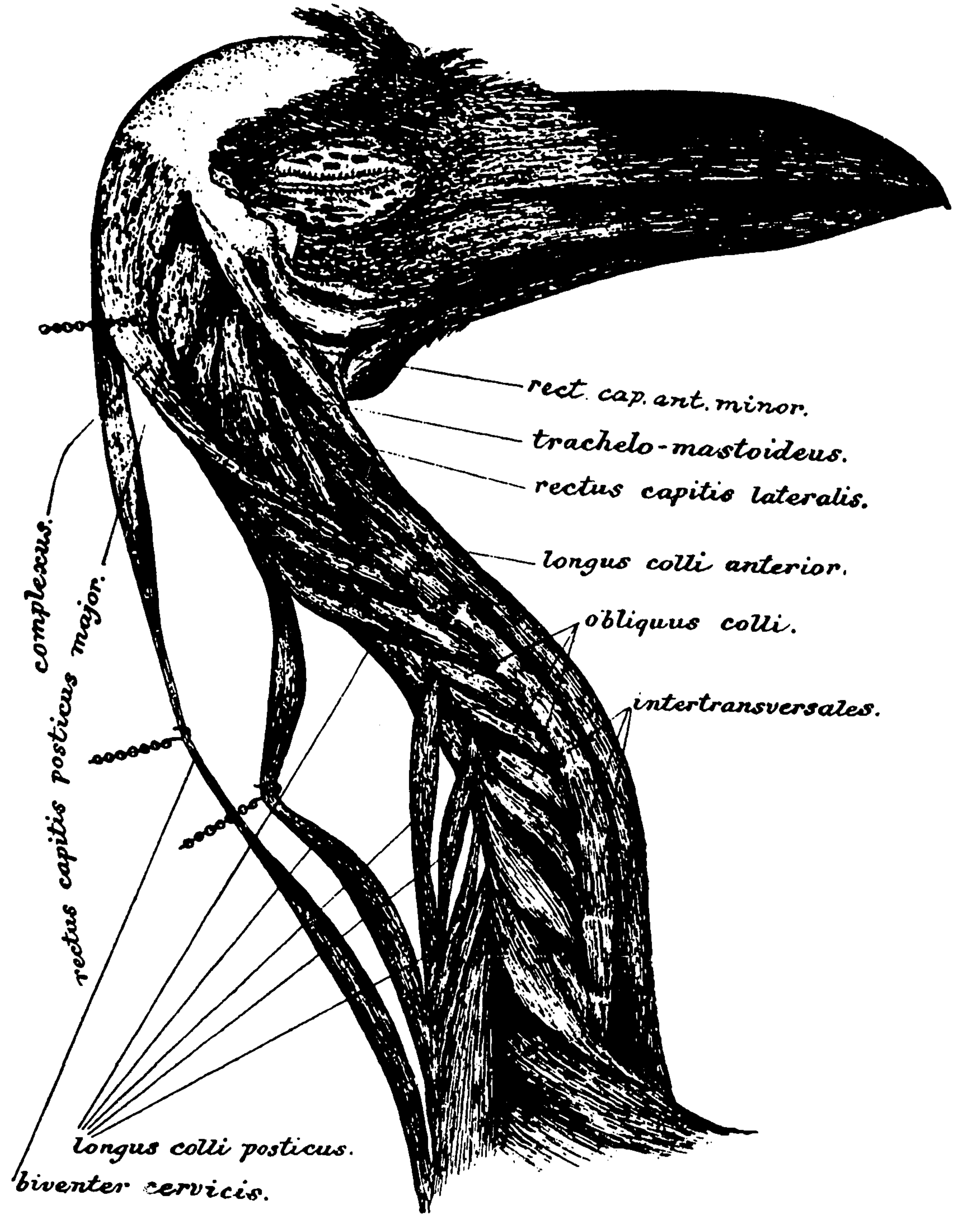


Fig. 7-1 MUSCULATURE OF THE LATERAL ASPECT OF THE NECK IN THE RAVEN (from Shufeldt, 1890)

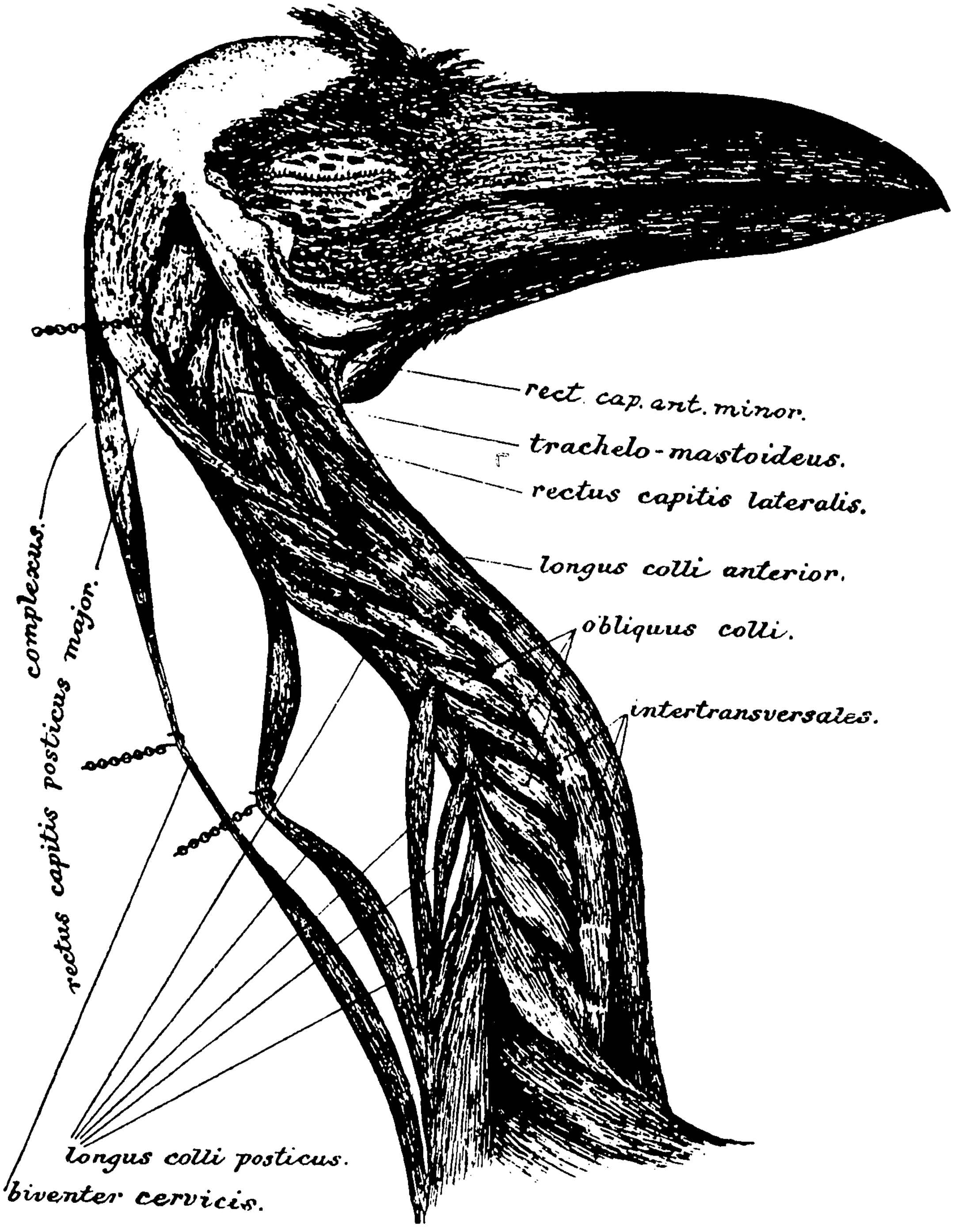


Fig. 7-1 MUSCULATURE OF THE LATERAL ASPECT OF THE NECK IN THE RAVEN (from Shufeldt, 1890)

perhaps in man it seems not unlikely that considerable differences in the speed of contraction will be found in different muscles, some of which may be involved primarily in quick, repositioning motions, while others may be slow and operate mainly in a stabilizing role.

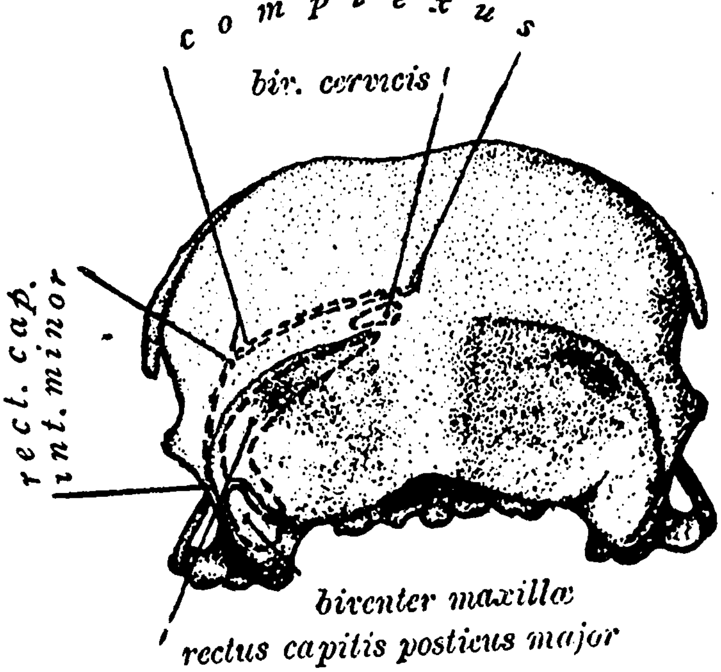


Fig. 7-2 POSTERIOR VIEW OF THE SKULL OF THE RAVEN, SHOWING ORIGINS OF MUSCLES (from Shufeldt, 1890)

7.5 THEORETICAL ASPECTS OF HEAD MOVEMENT CONTROL

7.5.1 General

Because of the complexity of head movement control systems it is useful, before proceeding to experimental investigations, to set down the known facts about the system under consideration and to make whatever inferences are possible as to its nature. Such facts and conjectures may be conveniently summarized as information-flow or block diagrams, on the basis of which tentative hypotheses as to system performance may be proposed for experimental verification.

The system to be considered is the horizontal cristo-collic reflex control system, which provides rotational stabilization of the head in the horizontal anatomical plane (of the head). The fact that such stabilization occurs is firmly established by previous work reviewed in Section 7.2. At the risk of overemphasis it is noted again that the system is necessarily of the error-activated type, since the anatomical location of the semicircular canals (i.e., in the head), ensures that the canals sense head motion relative to space, and hence continuously monitor system output. The reflex produces, as necessary, head movements relative to body which provide a degree of head stabilization relative to the environment ("space") in the face of disturbance inputs such as body rotation or external forces applied to the head. In the natural environment,such external forces might,for example,occur as a result of high ambient air velocity, especially in the case of flying birds, or during running in terrestrial animals. It seems clear that a prime function of such head stabilization is to contribute to visual image stabilization during body rotation. However since the system stabilizes the head relative to a fixed inertial coordinate system, it could concievably contribute to a short-term inertial navigation capability which might be of value to flying animals under extreme conditions.

The stabilizing role of active head-on-body motion is most apparent in the situation in which there are no other CNS commands to produce head movement. The absence of such commands may be considered equivalent to a command to keep the head stable, that is, to keep some parameter of head motion as near zero as possible. It is pertinent to ask what parameter or parameters are to be stabilized. A reasonable conjecture, based on arguments similar to those applied in consideration of the vestibulo-ocular system (Chapters 5 & 6), is that head velocity relative to space (absolute head velocity) is the primary variable, but that there are in addition some restrictions on head position relative to the body. Since the semicircular canal is presumably the most significant source of absolute rotation information in the feedback path, and since the canal signal, to the best of available knowledge, is interpreted as a velocity signal, it seems most reasonable to assume that absolute head velocity is the principal controlled variable. Moreover for the purpose of visual image stabilization the vestibulo-collic system as well as the vestibulo-ocular system appears to serve as a back-up stabilization system for the visual tracking reflex. The latter, as Young (1962) has shown, is severely limited in the velocity of target motion which it can cope with. Hence velocity stabilization of the head and eyes relative to space must be highly desirable, if not essential, during rapid body movements.

Using these considerations as a basis, it is possible to construct a tentative model of the inertial head stabilization system (vestibulo-collic reflex) for horizontal-plane rotation, starting with the simpler condition in which there are no saccades. Experimental justification for this simplification comes from the observation of completely non-saccadic responses in anaesthetized and decerebrate pigeons (Chapter 10). The system is assumed to consist of four basic components, namely (1) the 'plant', represented by the dynamics of head on neck; (2) the 'feedback transducer', being in this case a complementary pair of integrating angular accelerometers, the semicircular canals; (3) the neural 'comparator' and control network; and (4) the 'actuator', made up of one or more pairs of complementary neck muscles. An information-flow diagram of the system is shown in Fig. 7-3. The plant receives two inputs, a muscle torque τ_M, and the rotational velocity of the body, $\dot{\theta}_B$. Its output, absolute head velocity $\dot{\theta}_H$, is also the system output, and is fed back by the semicircular canals to a hypothetical neural comparator. Its output is the difference between the hypothetical

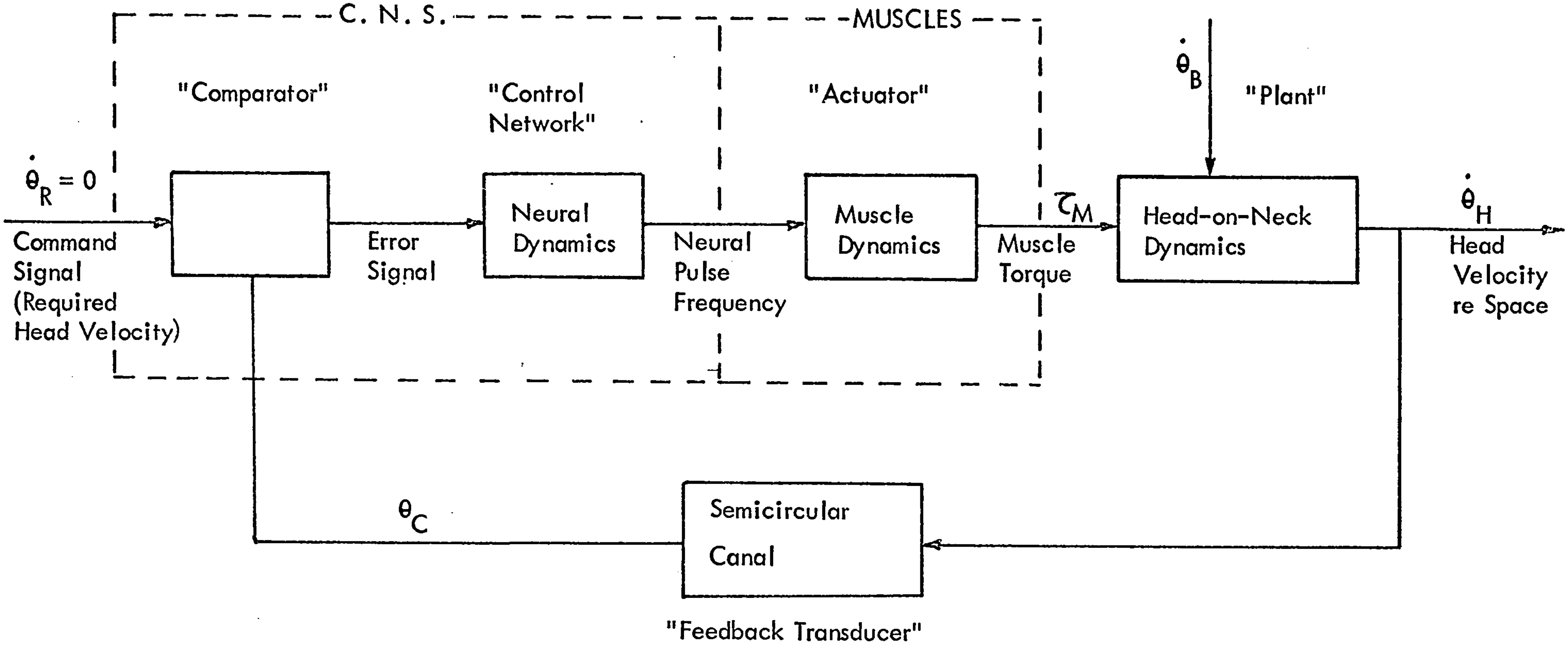


Fig. 7 - 3 INFORMATION FLOW DIAGRAM FOR THE VESTIBULAR CONTROL OF HEAD MOVEMENT

command signal (required head velocity, $\dot{\theta}_R$) and the actual head velocity as estimated by the semicircular canals. This error signal is, potentially at least, processed by a neural control network before emerging as a neural pulse sequence to drive the actuating muscles.

7.5.2 Evaluation of System Components

Proceeding now to a more detailed consideration of the individual components, it is convenient first to consider head-on-neck dynamics. As a first approximation these may be modelled using linear components. Taking moments about the center of head rotation, it is assumed that the head has a moment of inertia J, and that the passive mechanical connections between head and neck may be approximated as to function by linear viscous and elastic elements in parallel, with coefficients b and k respectively. It seems likely that spring stiffness actually increases with angular deviation of the head, and viscous retardation in the real system presumably depends to a considerable extent on instantaneous muscle properties. Moreover this single-link model of the complex, multi-link mechanical structure of the neck may seem a gross oversimplification. However in this discussion it is intended primarily to develop a concept of the overall structure of the control system, and for this purpose such simplified modelling is probably adequate.

A physical analogy of this representation of head-on-neck dynamics is shown schematically in Fig. 7-4. The body is assumed to have much greater inertia than the head so that body motion is insignificantly affected by viscous and elastic retarding torques and by the active muscle torque τ_M. Summing all torques acting on the head yields the equation of motion of the head about the vertical axis,

$$J\ddot{\theta}_H = -b(\dot{\theta}_H - \dot{\theta}_B) - k(\theta_H - \theta_B) + \tau_M \quad \text{.................Eq. 7.1}$$

This is Laplace-transformed assuming zero initial conditions, and rearranged to give

$$Js\dot{\theta}_H(s) = -(b + k/s)\,[\dot{\theta}_H(s) - \dot{\theta}_B(s)] + \tau_M \quad \text{............Eq. 7.2}$$

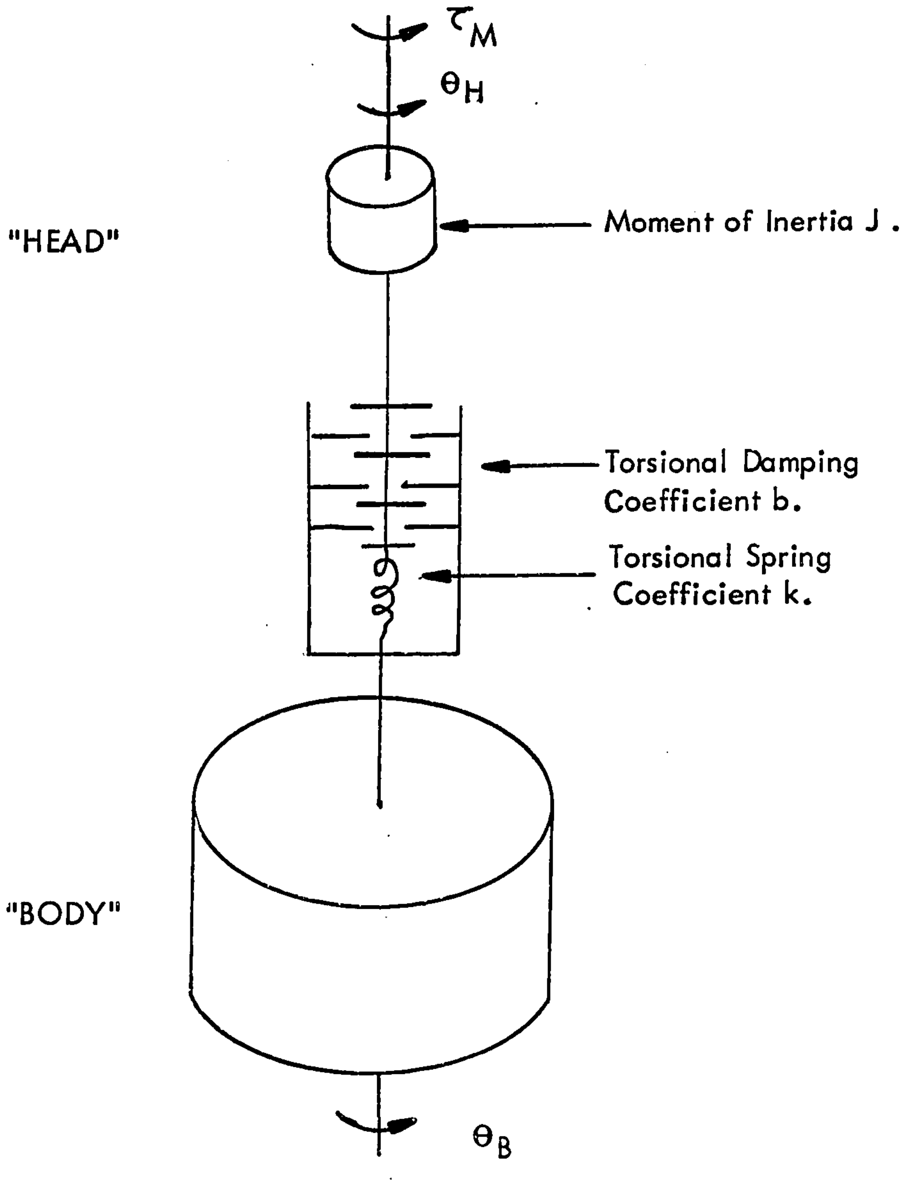


Fig. 7-4 PHYSICAL ANALOGY FOR PROPOSED HEAD ON NECK DYNAMICS

The relationship is summarized in the block diagram of Fig. 7-5. It will be noted that head movement relative to space results from the action of two torques, one due to muscle contraction (τ_M), and another, called τ_{BH} and described by the first term on the right hand side of Eq. 7.2, being transmitted through the neck structures as a result of head motion relative to body.

The effect of proprioceptive feedback from the neck muscles and joints must also be considered, and it is convenient for present purposes to think of these as part of the 'plant' dynamics. Reflex muscle activity due to such feedback would affect the value of τ_M, which may thus be considered to have two components, due to proprioceptive and vestibular influences respectively, i.e.,

$$\tau_M = -\tau_P + \tau_V$$

If the relationship between the stretch-reflex torque τ_P and relative head velocity is described by the transfer function G(s), then Eq. 7.2 may be rewritten

$$Js\,\dot{\theta}_H = -(b + k/s)(\dot{\theta}_H - \dot{\theta}_B) - \tau_P + \tau_V$$

$$= -(b + k/s + G(s))(\dot{\theta}_H - \dot{\theta}_B) + \tau_V \quad \ldots\ldots\ldots\ldots\ldots\ldots \text{Eq. 7.3}$$

The equivalent block diagram is drawn in Fig. 7-6. The nature of the transfer function G(s) is unknown, but if it is assumed that the torque τ_P is proportional to the signal from muscle-spindle receptors, it seems likely that the effect of adding G(s) in Eq. 7.3 is basically to increase the effective values of the viscous and elastic coefficients b and k. The argument is based on the fact that muscle spindle responses contain components related to muscle length and to rate of change of length. Thus the relationship between relative head position and stretch reflex torque might be crudely approximated as

$$\frac{\tau_P}{\theta_H(s) - \theta_B(s)} = s\,G(s)$$

$$= K_P(cs + d)$$

Substitution in Eq. 7.3 would yield

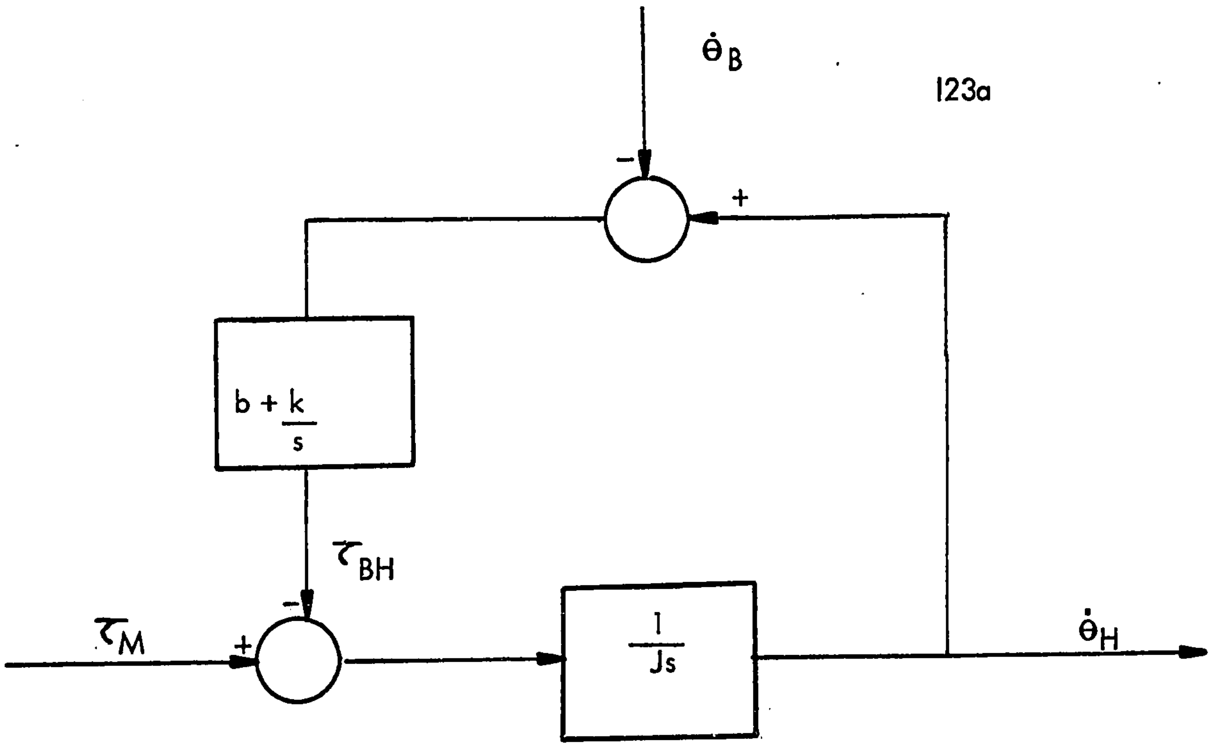


Fig. 7-5 MODEL FOR PASSIVE HEAD-ON-NECK DYNAMICS

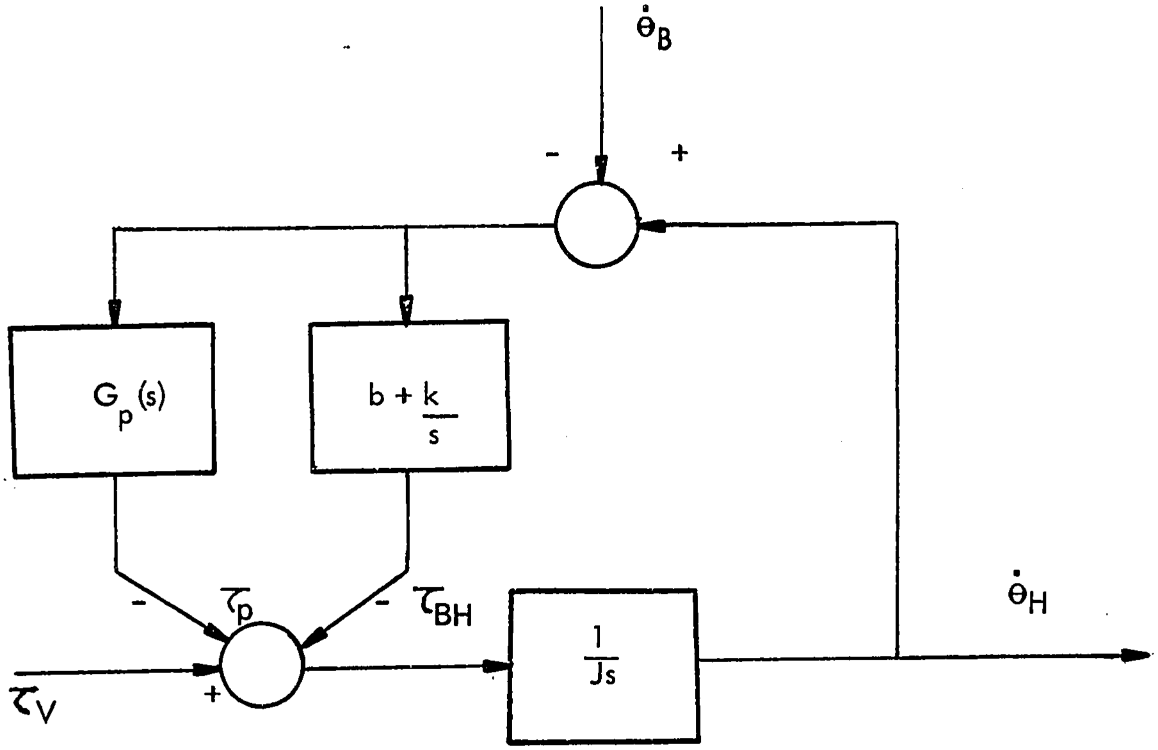


Fig. 7-6 MODEL OF HEAD-ON-NECK DYNAMICS MODIFIED TO INCLUDE PROPRIOCEPTIVE REFLEX EFFECTS

$$Js\,\dot{\theta}_H = -\left[(b + K_p c) + (k + K_p d)/s\right](\dot{\theta}_H - \dot{\theta}_B) + \tau_V$$

$$= -(b' + k'/s)\,(\dot{\theta}_H - \dot{\theta}_B) + \tau_V \quad \ldots\ldots\ldots\ldots\ldots\ldots\text{Eq. 7.4}$$

In this expression b' and k' are the new effective viscous and elastic terms.

Head-on-neck dynamics are represented in this form in Fig. 7-7, which is a block diagram of the entire vestibulo-collic system for the non-saccadic case. The primed parameters b' and k' are retained to serve as a reminder that proprioceptive as well as passive factors are to be taken into account in the representation. It will be noted that absolute head velocity could be equivalently described as

$$\dot{\theta}_H(s) = \frac{1}{Js^2 + b's + k'}\left[(b's + k')\,\dot{\theta}_B(s) + s\,\tau_V(s)\right] \quad \ldots\ldots\text{Eq. 7.5}$$

There is little available evidence to indicate what are suitable parameter values for this second order model of the 'plant', but it may be possible to infer roughly to what extent the system is damped in the absence of canal feedback. The results of extirpation experiments in animals are somewhat conflicting, as are the largely subjective reports of the effects of loss of labyrinthine function in humans, but after reviewing these findings (Section 7.2) it is clear that there is a significant tendency for oscillatory head movement to occur involuntarily in these cases, particularly in the early stages of the deficiency. The tendency has been noted especially in vertical planes, in which the problem of stability is complex compared to the horizontal plane owing to the inverted-pendulum effects and otlithic influences. However horizontal-plane oscillation has also been described, (eg. Money & Scott 1962) and suggests sub-critical damping of horizontal-plane head-on-neck dynamics.

The semicircular canal is represented in the feedback pathway of Fig. 7.7 by the customary second-order overdamped transfer function. Threshold and saturation non-linearities have not been included, although these effects, as well as terms to account for adaptation and possibly habituation, would probably have to be included in a more exact analysis.

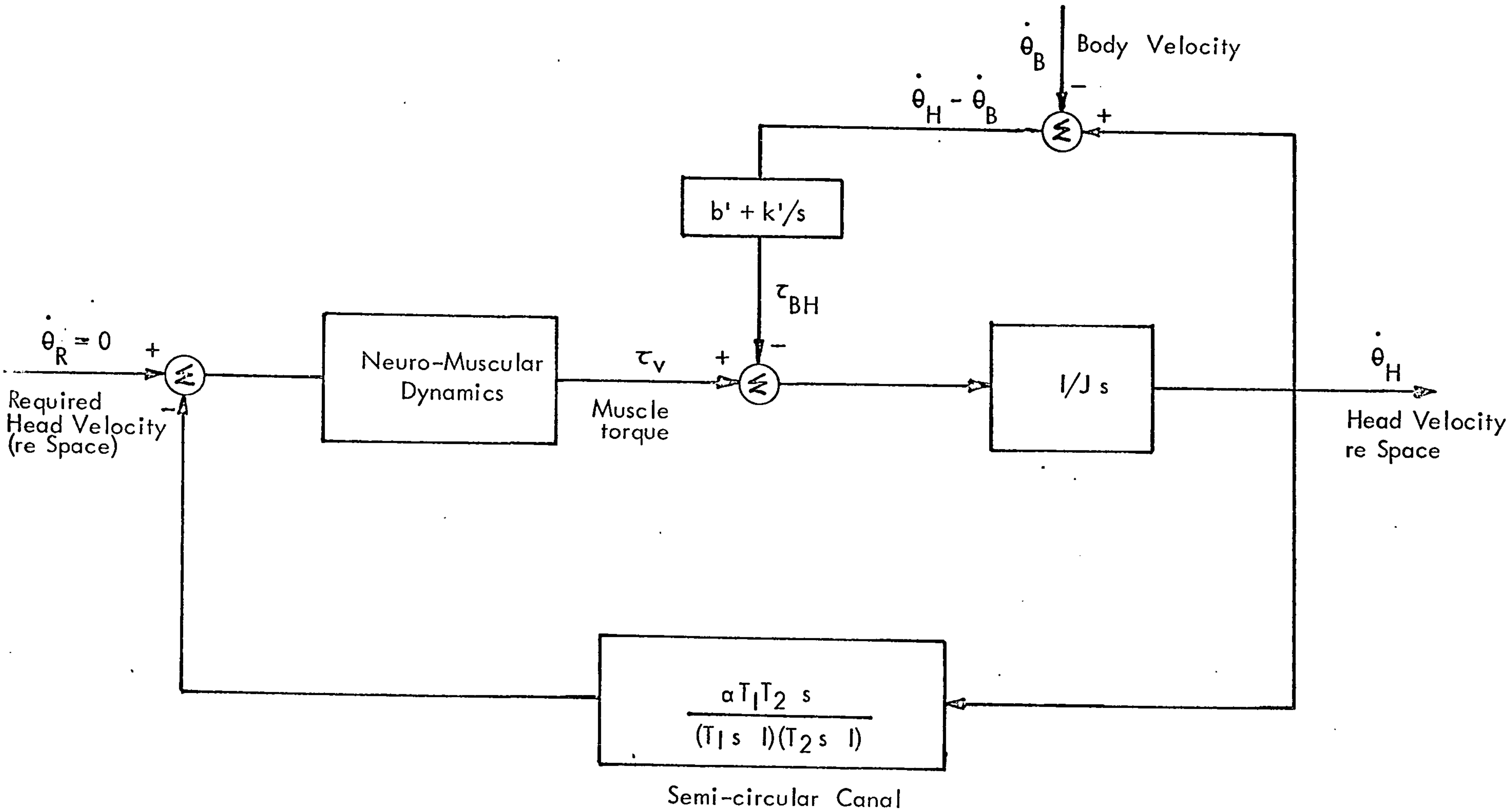


Fig. 7-7 ELEMENTARY BLOCK DIAGRAM OF THE VESTIBULO-COLLIC REFLEX SYSTEM FOR THE NON-SACCADIC CASE.

Representation of the 'comparator','controller' and 'actuator' can only be in the most general terms at the present time since so little is known about them. Th existence of a comparator in this system may be debated, but its inclusion is useful for conceptual purposes,and its representation in Fig. 7.7 as a summing element rather than some more complex operator may readily be justified as an abstraction which clarifies its functional role (Milsum ,1966). A hypothetical neural 'controller', shown following the comparator, is included to account for any neural delays or dynamics which may exist. Muscle or 'actuator' dynamics are represented perhaps optimistically as on operator having a single input and single output,i.e., neural firing frequency and muscle torque respectively. In fact it would be difficult in a detailed study to separate muscle dynamics from those of head-on-neck. However further consideration of this particular aspect would entail a very substantial diversion, besides which there is no immediate possibility of experimentally resolving the system in such detail at the present time. The simple representation of Fig. 7.7 is more useful conceptually and is at least plausible as an approximation.

Evidently no detailed prediction of system performance characteristics is possible on the basis of this model, since much vital information is missing. Moreover there has been no consideration as yet of possible mechanisms of saccade generation and of their effects on system performance. However this elementary formulation of the problem gives some insight into the nature of the system and leads to a rational experimental approach. There can be little doubt that future investigation of saccadic mechanisms will be substantially facilitated if a reasonable working model of system operation in the non-saccadic mode can first be worked out.

7.5.3 The Role of Canal Feedback

A fundamental step in understanding this reflex system is to evaluate the effect of semicircular canal feedback. To do this, 'plant' performance must first be assessed in the absence of feedback. The open-loop dynamic relationship between head velocity and body velocity is given by the first term in Eq. 7.5, and may be rewritten,

$$\frac{\dot{\theta}_H(s)}{\dot{\theta}_B(s)} = \frac{Ts + 1}{\frac{s^2}{\omega_0^2} + \frac{2\zeta s}{\omega_0} + 1}$$

or, rearranging,

$$\frac{\dot{\theta}_H(s) - \dot{\theta}_B(s)}{\dot{\theta}_B(s)} = \frac{-Js^2}{\frac{s^2}{\omega_0^2} + \frac{2\zeta s}{\omega_0} + 1}$$

where

$T = b'/k'$

$\omega_0 = (k'/J)^{1/2}$

$\zeta = (b'^2/4\,Jk')^{1/2}$

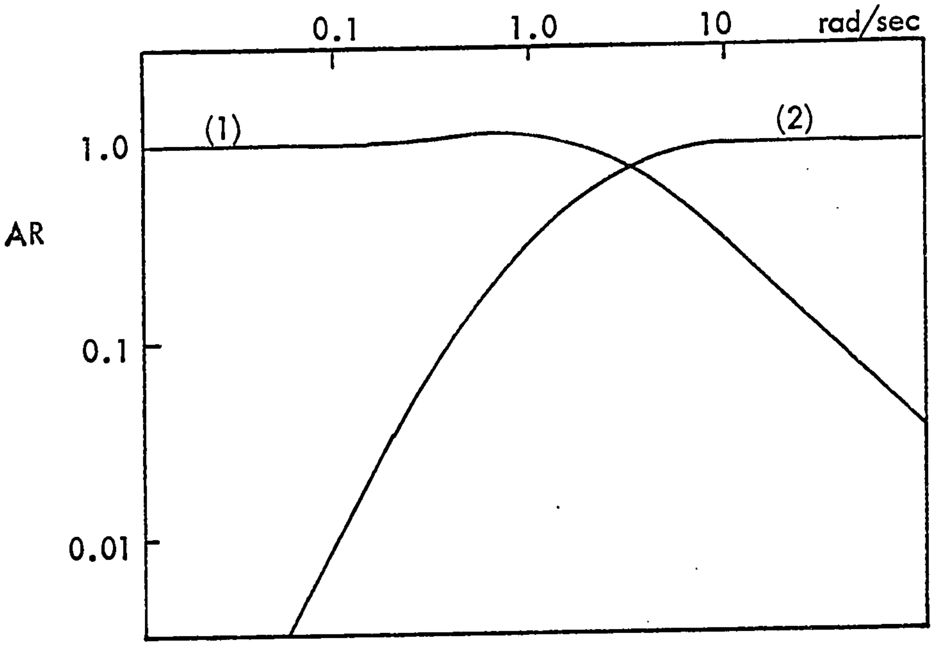
Here ω_0 and ζ are respectively the undamped natural frequency and damping ratio of the system. The amplitude-ratio portions of the corresponding Bode frequency response plots for a slightly underdamped and a slightly overdamped system are shown in Fig. 7.8, parts (a) and (b) respectively. Now the requirement for head velocity stabilization relative to space is that

$$\frac{\dot{\theta}_H(s)}{\dot{\theta}_B(s)} = 0,$$

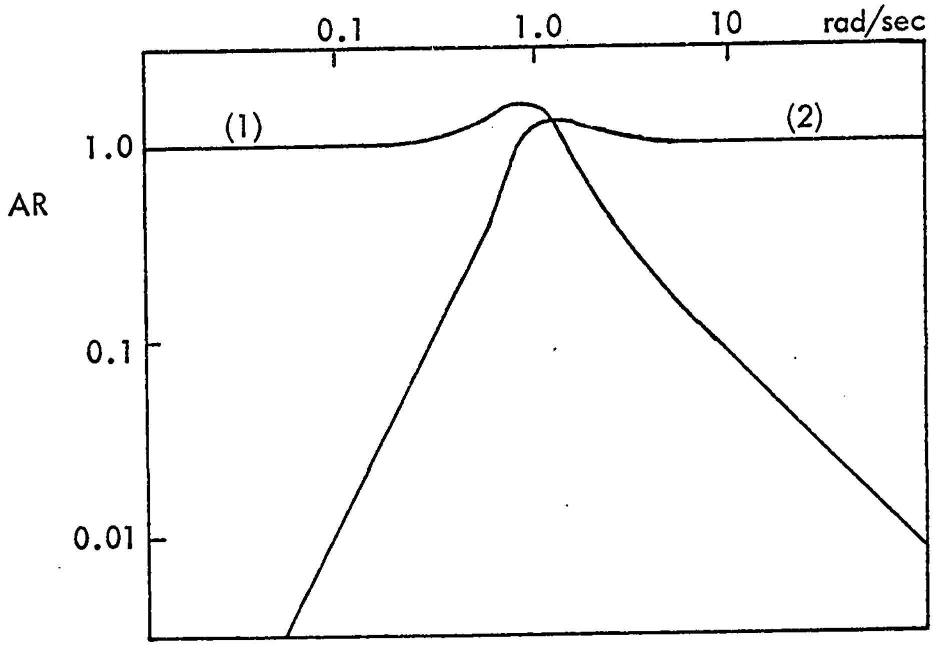
or correspondingly,

$$\frac{\dot{\theta}_H(s) - \dot{\theta}_B(s)}{\dot{\theta}_B(s)} = -1.$$

The second order plant evidently meets these requirements even in the absence of feedback provided the frequency of body movement is significantly greater than the undamped natural frequency (Fig. 7.8). This conclusion may seem surprising



(A) - damping ratio 1.6



(B) - damping ratio 0.4

Fig. 7-8 Bode Plots of Amplitude Ratio (AR) vs. Normalized Frequency for two possible models of head on neck dynamics. Curves (1) - AR of absolute head velocity ($\dot{\theta}_H$) and body velocity($\dot{\theta}_B$); curves (2) - AR of relative head velocity ($\dot{\theta}_H - \dot{\theta}_B$) and body velocity. Frequency is normalized relative to undamped natural frequency.

initially since it means that canal information is not necessary to insure good inertial head stabilization at high frequency of body rotation. However the conclusion is independent of the model and may be derived from simple physical reasoning; at high frequencies head inertia is the dominant dynamic influence and tends to prevent absolute head movement in space. The function of canal feedback is therefore presumably to improve performance in the low-frequency portion of the spectrum. It will be noted that in theory improved low-frequency performance could also be achieved, without canal feedback, by reducing the negative feedback of proprioceptive information about relative head-on-body position. Such reduction would decrease the effective value k' and hence lower the natural frequency. However the resulting loss of coupling stiffness between head and body would have profound deleterious effects on other systems, such as the control of relative head deviation in the horizontal plane. In fact it seems probable that the labyrinthectomized subject in the course of adaptation to his deficiency learns to augment rather than reduce the effects of proprioceptive feedback from the neck. This, while increasing the natural frequency of the head and hence further reducing low-frequency head stabilization relative to space, would make it possible to lock the head to the larger mass of the body. The latter can of course be stabilized voluntarily in ordinary situations by simply standing still.

Some further comments on the possible effects of canal feedback are in order, if only to emphasize the complexity of the system as compared with the vestibulo-ocular reflex. Let it be assumed, temporarily, that the neural 'controller' and the 'actuator' in Fig. 7.7 contribute no dynamic effects in the frequency range of interest, and have an overall gain equal to K_N. Then for the hypothetical case in which the feedback transducer is a pure velocity sensor with gain K_C, the torque τ_V will be

$$\tau_V = -\theta_C(s) = -K_C K_N \dot{\theta}_H(s)$$

and it is easy to show that

$$\frac{\dot{\theta}_H(s)}{\dot{\theta}_B(s)} = \frac{b's + k'}{Js^2 + (b' + K_C K_N)s + k'} \qquad \text{...........Eq. 7.6}$$

The coefficient of s in the denominator is augmented compared to that in the plant transfer function, the effect being equivalent to the addition of damping of the head relative to space. In the frequency range of accurate velocity transduction by the semicircular canals, the effect of canal feedback would be similar provided the assumptions about 'controller' and 'actuator' dynamics are at least approximately true. Even if these assumptions are invalid however, Eq. 7.6 nicely emphasizes an important general conclusion which will be very obvious to the reader familiar with control theory. The effective viscous term in the denominator of Eq. 7.6 is $(b' + K_C K_N)$, and varies with the static gain of various components in the feedback loop. In the more general case other parameters such as the effective inertial and spring terms may be functions of loop gain, which may therefore have drastic effects on the dynamic characteristics of the closed-loop system. In the biological system loop-gain may be expected to vary substantially with factors such as arousal. This may make the system more versatile in its biological role, but adds considerably to the problems of system identification.

7.5.4 Saccades

There remains the question of saccades, which will be considered only briefly. There is no doubt that the horizontal cristo-collic reflex system can operate in a non-saccadic mode (see above), and though it does not necessarily follow, it seems likely that the loop of Fig. 7.7 remains closed at all times during saccadic head movement. One is inclined to regard the saccades as resulting from an additional input to the actuator, this saccadic input being in the form of pulses. A possible scheme is shown in Fig. 7.9, in which a postulated saccade generation mechanism, labelled "S.G.", receives vestibular and neck-proprioceptive inputs,and outputs pulses to the actuator (muscle). It is highly probable that the mechanism is closely linked to that responsible for saccade generation in the vestibulo-ocular system, since vestibularly-driven head and eye saccades are synchronous in the pigeon (Section 11.4) and nearly so in man (Section 9.2). Functional considerations suggest that saccadic mechanisms in the visual tracking system may also be closely related. Further study of saccadic mechanisms thus becomes a most interesting prospect, and should eventually lead to useful clinical applications in the diagnosis of various neurological disorders, owing to the wide ramifications of neural connections in the three systems.

7.5.5 Suggestions for Experimental Studies

In this section the vestibulo-collic system has been considered theoretically at some length as a prelude to the accounts of experimental studies which follow in Chapters 8 and 9. The principal experimental problems are thereby clearly delineated, and a number of hypotheses emerge for testing.

The following experimental approaches are proposed as the logical outcome of the theoretical considerations presented:

1) To examine overall system response, both (a) in the normal saccadic case, and, (b) using appropriate pharmacological measures and/or small input amplitudes, the non-saccadic case. The former could reasonably be analyzed in terms of the variations in slow-phase head velocity,for a direct quantitative comparison with the vestibulo-ocular response. On the other hand characteristics of the non-saccadic response would be particularly useful in obtaining a mathematical model, owing to the analytical simplifications which result if saccades are excluded.

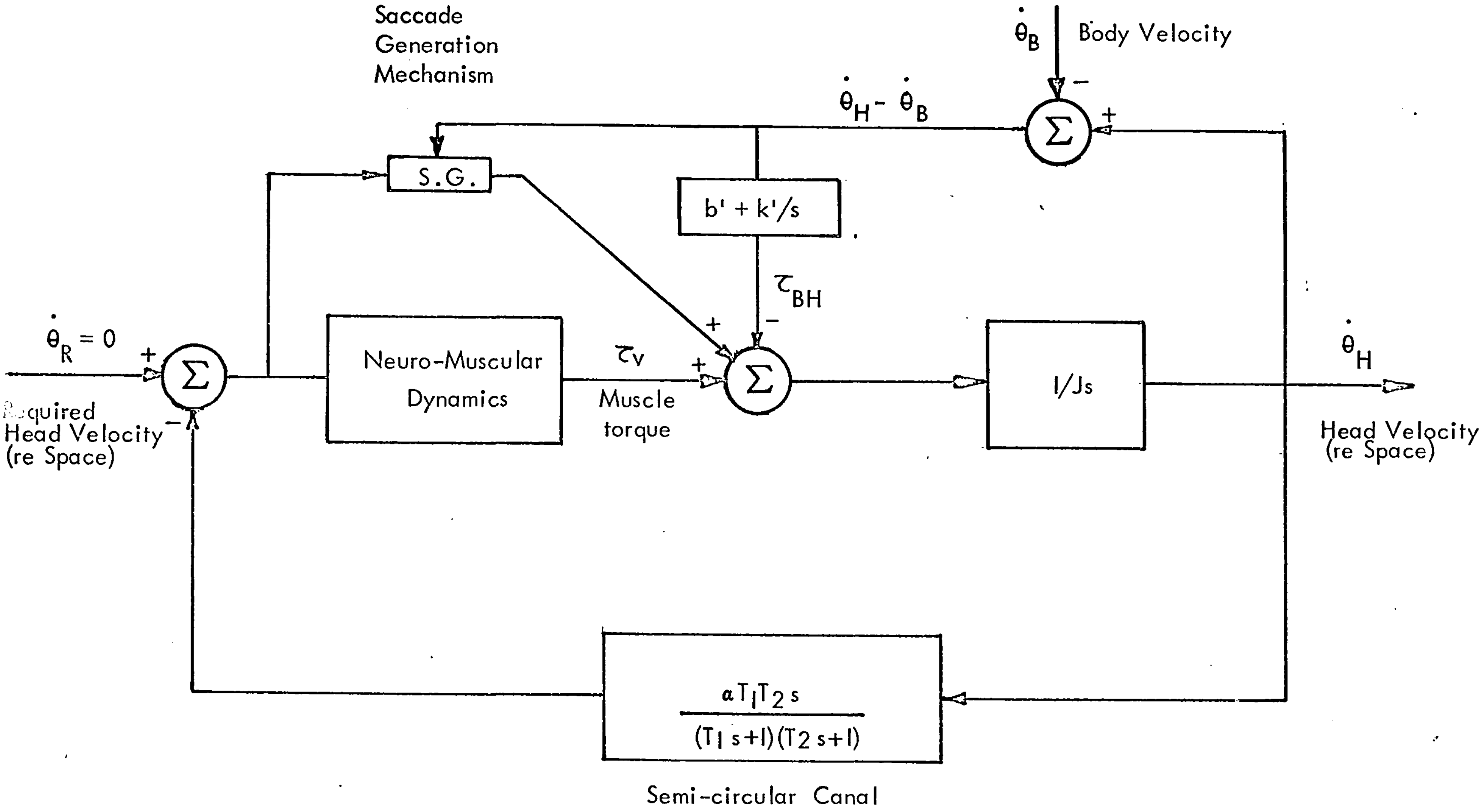


Fig. 7-9 ELEMENTARY BLOCK DIAGRAM OF THE VESTIBULO-COLLIC REFLEX SYSTEM

S. G. is a postulated saccade generation mechanism, recieving proprioceptive and vestibular inputs (the latter via the error signal). Dynamic effects of proprioceptive reflexes are lumped with passive neck dynamics.

2) To examine and characterize responses of isolated components or groups of components within the feedback loop. (a) Semicircular canal characteristics might be estimated initially through analysis of vestibulo-ocular response, and subsequently verified by appropriate electro-physiological experiments. (b) "Plant" dynamics (head-on-neck) could be analyzed by recording head motion during body rotation after plugging the semicircular canals and thus breaking the feedback loop. Similar experiments after curarization or cervical dorsal root section might aid in distinguishing the various factors contributing to head-on-neck dynamics, such as purely mechanical properties of the neck, muscle properties and proprioceptive reflexes. (c) Properties of the neural "comparator-controller" and muscle "actuator" could be examined in combination by measuring isometric head torque during body rotation, making allowances for canal dynamics in the analysis, and information about neural mechanisms alone might be otained from recordings made in appropriate motor nerve pathways during rotation with head fixed to the turntable. Modification of these experiments by severing cervical dorsal roots might give further information about the role of proprioceptive reflexes.

3) The problem of saccade-generation mechanisms in this system might be approached by simulation of various possible schemes after a mathematical model of closed-loop non-saccadic response is worked out.

In addition to these suggestions for experimental study, three hypotheses emerge from the preceding theoretical discussion and require testing. These are:

1) That dynamic characteristics of the vestibulo-collic system response,and hence response parameters such as time constants, will vary with loop gain and therefore depend on the level of arousal.

2) That the vestibulo-collic system may have significantly greater bandwidth than the vestibulo-ocular system or the semicircular canals, the region of accurate head stabilization being extended in both high and low frequency ranges.

3) That in contrast to the situation in the vestibulo-ocular system, the time constants characterizing vestibulo-collic response will all be different from the time constants of the semicircular canal, except perhaps at certain specific values of the loop gain.

In the experimental studies described below, overall vestibulo-collic system response has been examined in man and, to a greater extent, in pigeons, and semicircular canal parameters in the pigeon have been estimated through analysis of the vestibulo-ocular response. Without exception the results support the hypotheses stated above.

CHAPTER 8

EXPERIMENTAL APPARATUS & METHODS

8.1 GENERAL

Human and animal subjects were exposed to rotational stimulation in the horizontal plane on one of two servodriven turntables equipped with slip-rings for the transmission of electrical signals from turntable to recording apparatus. A potentiometer and tachometer attached to the shaft of each turntable provided an indication of turntable angular position and velocity respectively.

Angular head movement was measured without restriction using the method of a search coil in a magnetic field. A uniform field was produced by two large field coils mounted on the turntable. A light search coil on the subject's head then picked up by magnetic induction a voltage proportional to the sine of the angle between coil and field. A home-made curve-following function generator was used to linearize the trigonometric relationship. The resulting signal was proportional to the angular deviation of the head relative to the turntable over a range of 160° with an accuracy of 3%. An analog computer was used to differentiate the head position signal when head velocity information was desired, and also to perform the appropriate on-line algebraic operations necessary to obtain records of head position or velocity relative to the stationary surroundings.

Eye position relative to head was measured in man and pigeons using the principle of electro-oculography. Electromyographic activity in the neck muscles of pigeons was recorded and analysed in a conventional manner.

Appropriate output signals were amplified, monitored on an oscilloscope and recorded on paper and/or on magnetic tape using FM techniques. Occasionally records were also made on Polaroid film using an oscilloscope camera.

8.2 TURNTABLES

Two different turntables were used, one for human and one for pigeon experiments. These were both of the same overall design but the latter, whose design and construction was finalized during the course of this work, incorporated some modifications and improvements and was capable of more rapid response.

The first table (Fig. 8-1), which will henceforth be referred to as Table "A", has been extensively used in this laboratory by Dr. G. Melvill Jones and others. It was designed for use in human experiments in the configuration shown, the subject being seated on the bicycle saddle and holding on to the upright bar. The transverse support, T, and field coils, C, were added for the present experiments, the former being provided as a chest support for the subject, to restrict movement of the torso relative to table. By replacing the upright bar and bicycle saddle with a flat horizontal surface, the same turntable could also be used for animal work, but in the present series of experim ents Table "B" was used for this purpose (see below).

Turntable A was driven through a two-stage reducing friction drive by a D.C. velocity servo-motor (Servomex Controls Model MC .43) and was capable of speeds up to 360°/sec in either direction. The motor controller was driven by a function generator to produce triangular, square-wave and sinusoidal variations in table velocity, and gave excellent results at the frequencies used in the human experiments described below.

The second turntable (Table B, Fig. 8-2) was designed for animal work only. The design was similar to Table A with some improvements, i.e. an improved slip-ring assembly, and reduced moment of inertia of moving parts. Also, provision was made for easy conversion from the servo-controlled mode of operation to a spring-operated mode in which the table operated as a tuned mechanical system at higher frequencies of oscillation than it was otherwise possible to obtain.

In the servo-controlled mode the table was driven by a motor (similar to that used in Table A) through a friction reducing drive. In this mode, torque limitations due to the motor and friction drive restricted the sinusoidal response to about 0.5 Hz, above which frequency distortion of the waveform became intolerable. In the table's spring-operated mode, the motor was used to drive, through a reduction gear, an eccentric arm of variable length (labelled A in Fig. 8.2). Rotation of this arm at constant angular velocity provided a very nearly sinusoidal linear displacement of the cords, C, sufficient to maintain steady oscillation in the mechanical oscillator composed of the turntable and the springs, S. In

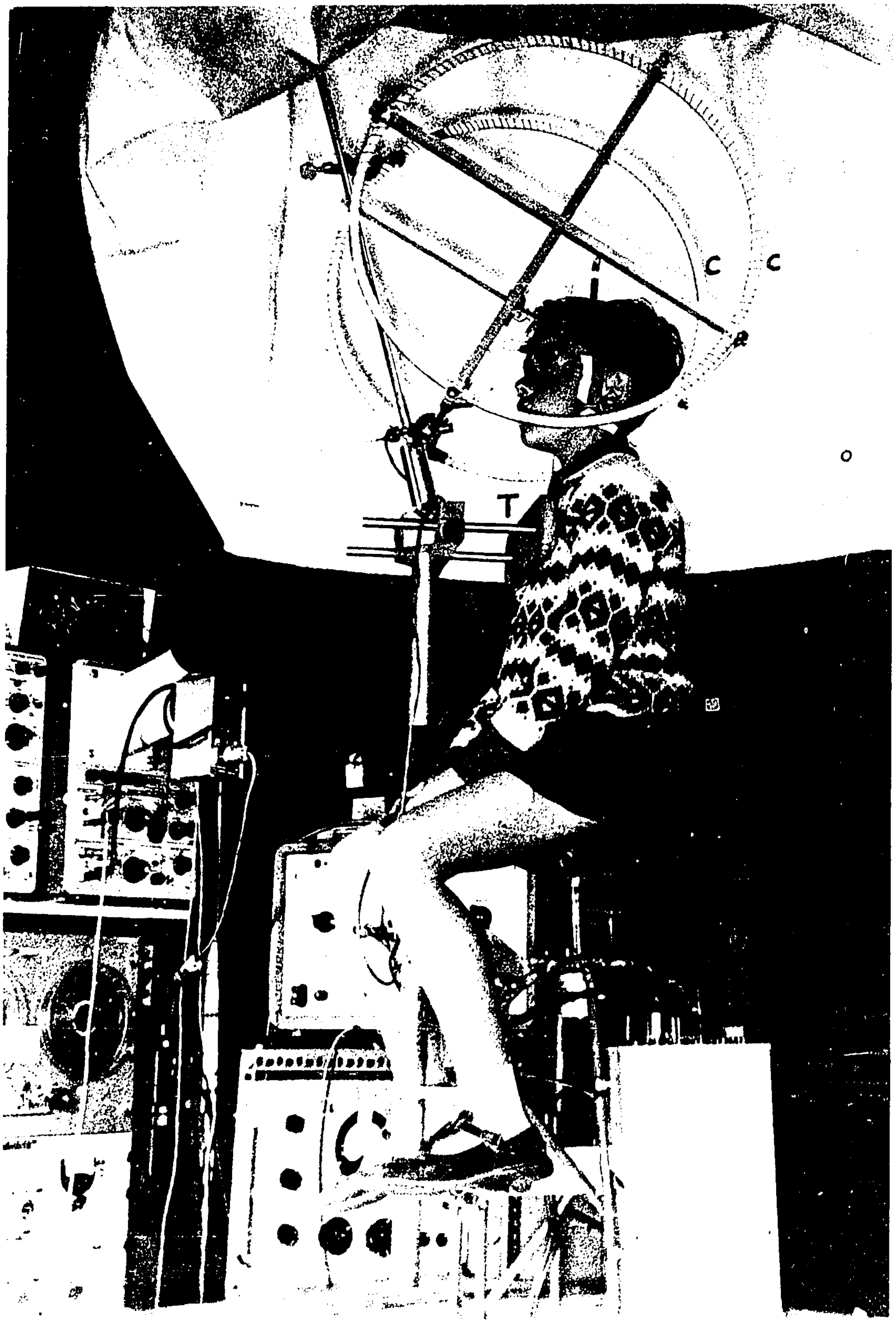


Fig. 6-1 SUBJECT SEATED ON TURNTABLE "A"

Transverse support (T) helps to prevent shoulder movement when the subject holds onto the upright bar. Pick-up coil on the subject's head lies within the magnetic field produced by current in the field coils(CC). Motor and drive mechanism are below the bottom of the picture.

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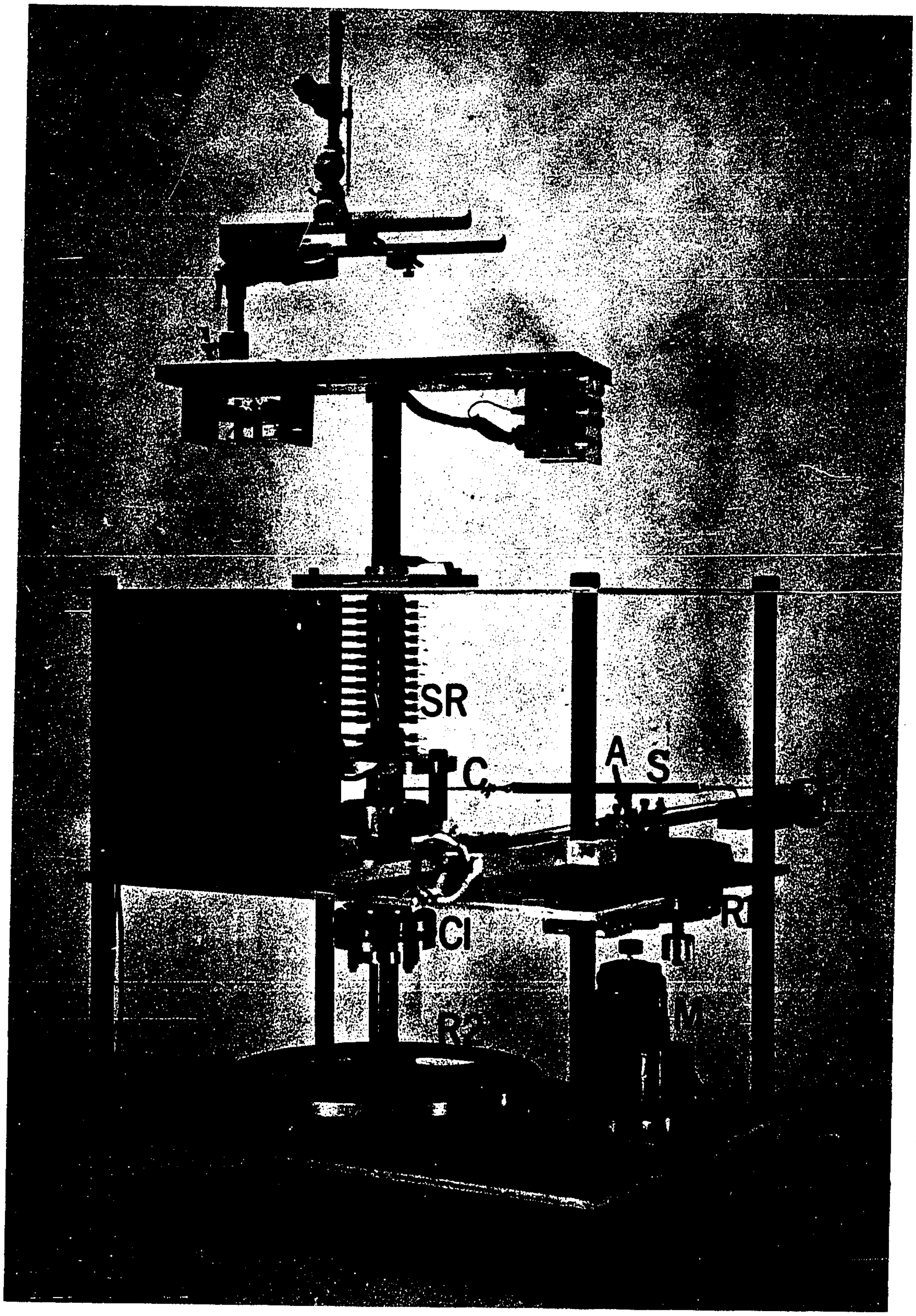


Fig. 8-2 PHOTOGRAPH OF TURNTABLE "B",USED FOR ANIMAL EXPERIMENTS
M - motor, R1 - reducing gear, R2 - reducing friction drive, Cl - clutch,
SR - slip rings, C - cords, S - spring, Cr - crank, T -tachometer.
(for explanation see text)

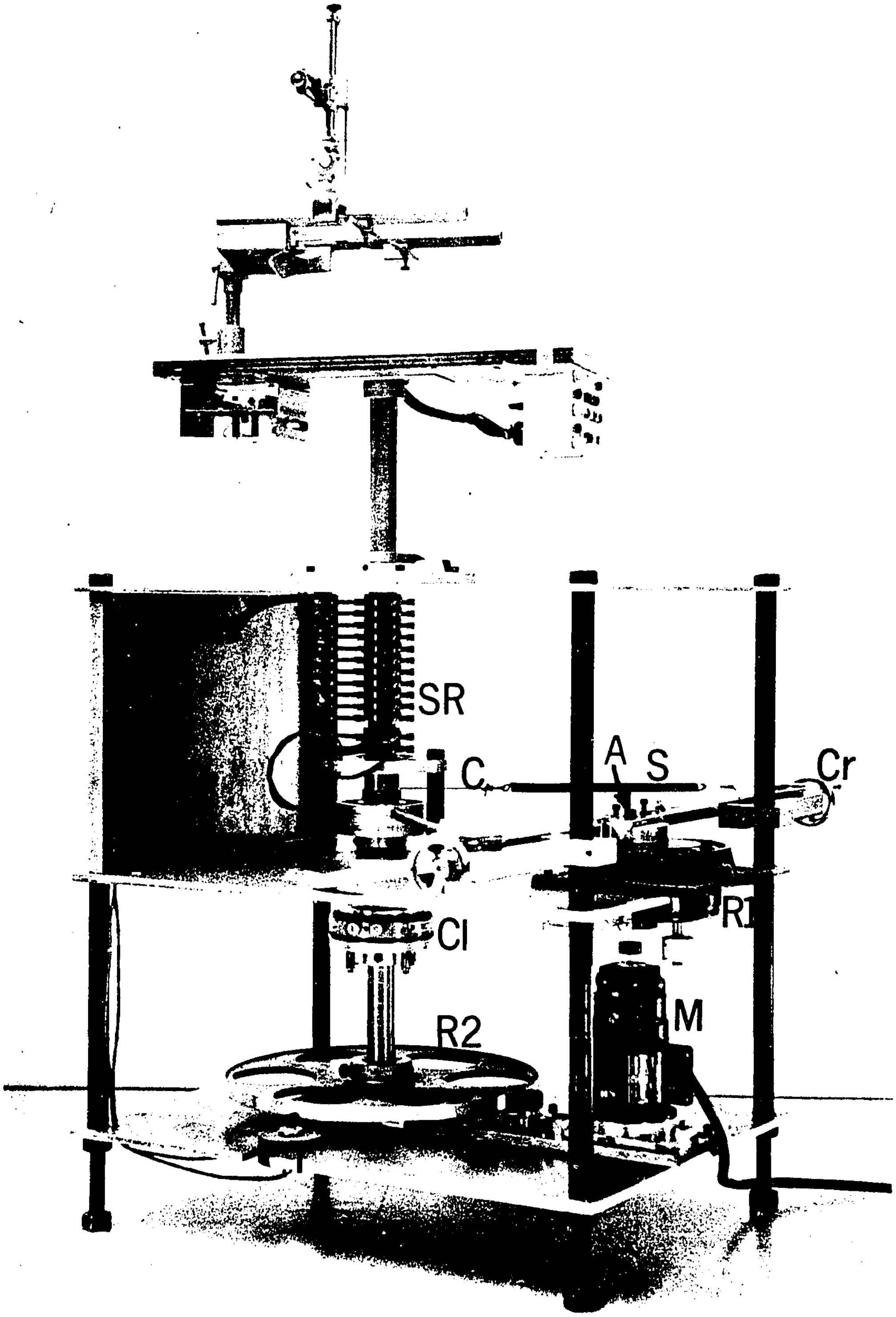


Fig. 8-2 PHOTOGRAPH OF TURNTABLE "B",USED FOR ANIMAL EXPERIMENTS
M - motor, R1 - reducing gear, R2 - reducing friction drive, Cl - clutch, SR - slip rings, C - cords, S - spring, Cr - crank, T -tachometer.
(for explanation see text)

practice the cords were attached to a dummy shaft mounted on separate bearings coaxial with the main shaft of the turntable. The two shafts were connected by a magnetic clutch when oscillation was desired. The cranks seen in Fig. 8-2 were included to facilitate the insertion of stiff springs.

The mechanical oscillator so produced was very lightly damped and had a high resonant peak. Thus at resonance, high-amplitude oscillation could be obtained with a small forcing oscillation, and distortions in the waveform of the forcing oscillation had little effect on the waveform of turntable motion. Amplitude changes were easily produced, either by changing the length of the eccentric arm, A, or by slight off-tuning. The latter was accomplished by altering the speed of eccentric-arm rotation, bringing about major changes in amplitude with very minor alterations in frequency of oscillation. Changing the frequency of resonance was more difficult, the most satisfactory procedure being to insert springs sufficiently stiff to ensure resonance at the highest frequency desired, and then to increase the table's moment of inertia with weights to bring about a progressive reduction in the resonant frequency. Using a combination of the direct drive and tuned oscillation modes of operation it was possible to achieve sinusoidal table oscillation of acceptable amplitude in the range 0.008 - 3.0 Hz.

Position and velocity of the turntable were monitored by means of a potentiometer attached to the main shaft , and a tachometer making a friction contact with a large wheel attached to the main shaft. Slip rings were made of bronze with brushes, of which there were two per slip-ring, made of copper-impregnated carbon and mounted on leaf springs.

8.3 MEASUREMENT OF ANGULAR HEAD MOVEMENT

8.3.1 Introduction

Angular displacement of the head relative to the turntable was measured in pigeons and in human subjects using the method of a search coil in a magnetic field. Two large field coils, fixed to the rotating turntable, were energized by a table-mounted oscillator to produce a high-frequency alternating magnetic field which was highly uniform in the region of the head. A light search coil mounted on the head picked up a voltage proportional to the sine of the angle between the plane of the coil and the magnetic field. After suitable processing an electrical signal was obtained which was proportional to angular displacement over a total range of 160°.

The method has previously been used to measure eye movement, both in this laboratory, and by Robinson (1963) who gives a detailed description of his apparatus. It has two great advantages in addition to high sensitivity, namely (1) There is no mechanical restriction to head movement since the search coil can be very small and is attached to the turntable by a very fine loose wire; and (2) The output is entirely unaffected by linear movements of the coil provided the magnetic field is uniform.

8.3.2 Principle of Operation

If a plane coil of N turns and area A is placed in a uniform magnetic field H parallel to the horizontal Y-axis (Fig. 8-3), then by Faraday's Law, an electromotive force e_1 will be induced in the coil, such that

$$e_1 = -\mu N \frac{d}{dt}(H A \cos \alpha)$$

where μ is the magnetic permeability of air, and α is the angle between the normal to the coil and the Y-axis. If H is sinusoidal, $H = H_0 \sin \omega t$, then

$$e_1 = -\mu N A H_0 (\omega \cos \omega t \cos \alpha - \sin \omega t \sin \alpha \frac{d\alpha}{dt})$$

The sinusoidal frequency of the field appears as a multiplicative factor in the first term, and hence if the frequency is large the second term may be ignored, yielding,

$$e_1 \approx -\mu N A H_0 \omega \cos \omega t \cos \alpha$$

which is an alternating potential whose amplitude is proportional to $\cos \alpha$.

Some form of phase detection is required if the angle α is greater than 90°, since a change in the sign of $\cos \alpha$ will lead to phase reversal of e_1. Phase detection is accomplished by placing a second, stationary coil in the field such that the amplitude of its output, e_2, is always greater than or equal to e_1. The

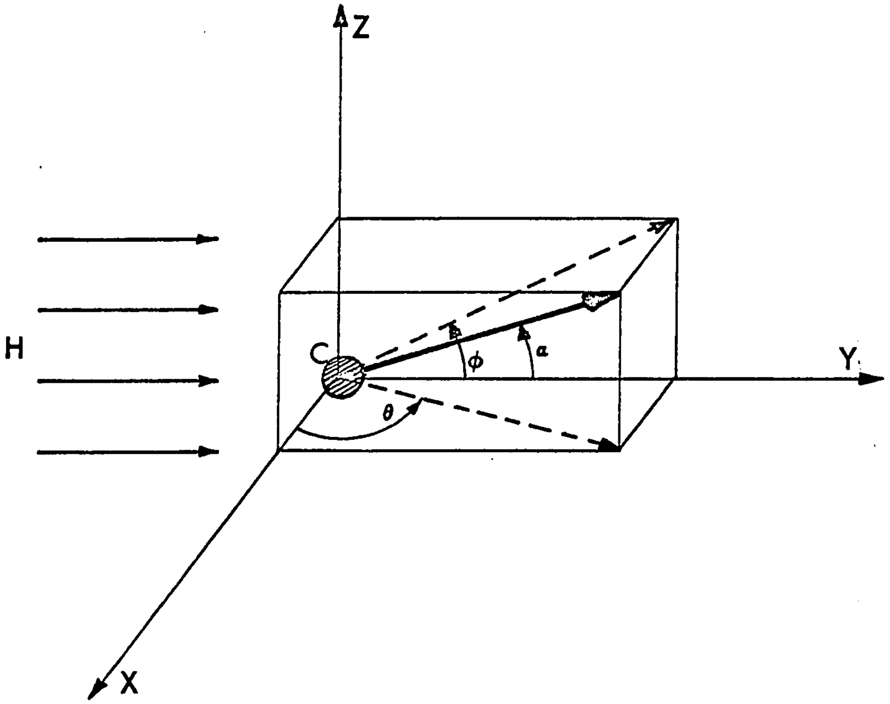


Fig. 8 - 3 DEFINITION OF ANGLES AND AXES FOR DISCUSSION OF ELECTROMAGNETIC HEAD MOTION DETECTOR

'H' indicates the direction of the magnetic field; the normal to the coil 'C' makes an angle α with the Y-axis.

sum of the amplitudes of the outputs from the two coils will always be different from zero, and may be represented

$$\begin{aligned} e &= e_1 + e_2 \\ &= b + c \cos \alpha \end{aligned}$$

where b and c are constant for a given set-up. Rectification and filtering of e then yields a DC voltage proportional to cos α.

The angle α is the angle between the magnetic field and the normal to the search coil. Since in the present study only rotations in the horizontal X-Y plane were of interest, it is desirable to express e in terms of the angles θ and ϕ (Fig. 8-3). Thus,

$$e = -\mu N A H_0 \sin \theta \cos \phi$$

Clearly rotation of the coil about the Y-axis will not affect the output. The angle ϕ representing rotation about the X-axis, could make an unwanted contribution, but if ϕ is kept small its contribution is relatively insignificant. The error is less than one percent of maximum output if ϕ is less than eight degrees, and less than five percent if ϕ is less than 18 degrees.

8.3.3 Generation of the Magnetic Field

The field was produced by two coaxial circular coils, each of 25 cm. radius and separated by 25 cm. Each coil consisted of 50 turns of No. 22 SWG insulated copper wire wound on a light, laminated-cardboard rim and supported by wooden cross braces (Fig 8-1). This coil arrangement, was chosen as one providing a very uniform field near the center of the region enclosed by the coils.

Design of the oscillator to drive the coils was based on several considerations. A high frequency of oscillation was desirable in order to obtain an output of reasonable amplitude, and also to facilitate filtering in the demodulation stage and in other low-level measurements in which interference from the field might be a problem. To avoid the gross interference which might occur if the coils were energised via the slip-rings it was necessary to use a battery-operated oscillator mounted on the turntable. To minimize power requirements and hence the added weight of large batteries the system was operated at a frequency near the resonant frequency of the coils, which was about 165 k Hz. A crystal-controlled oscillator was used to minimize frequency drift which would have a significant effect on field strength owing to the high resonant peak. To offset the effect of any residual drift in frequency the coil system was tuned to have a resonant frequency slightly less than the oscillator frequency. Thus field strength would decrease with increasing frequency whereas the induced e.m.f. in the pickup coil would tend to increase with increasing frequency, and the two effects would counteract each other.

Field uniformity in a coil system such as that used here, i.e., the so-called Helmholtz configuration, has been investigated by Nagoaka(1921) and by Montgomery and Terrell(1961). From the graphs of Nagoaka, and the tables of Montgomery and Terrell, it emerges that the radius of the sphere centered about the field center, within which the magnitudes of the axial and radial components of the magnetic field differ by less than 0.1% from their magnitudes at the field center, is 0.172 times the coil radius. For a deviation less than 1%, it is found from Nagoaka's graphs, confirmed by calculations by the author, that the corresponding sphere has a radius of 0.3 times the coil radius. With a coil of radius 25 cm., the sphere of 1% uniformity is thus 15 cm. in diameter. It will be noted that this is a relatively much larger region of field uniformity than that obtained by Robinson(1963), who used a coil separation equal to the coil diameter.

8.3.4 Arc-Sine Function Generator

The output of the search coil yielded, after rectification and filtering, a d.c. voltage, proportional to the sine of the angle (θ) between the magnetic field and the plane of the coil. For small angles the approximation $\sin\theta = k\theta$ could be used with small error (less than 2% for angles less than 20^0).

To extend the useful range of the device a curve-following function generator was constructed, having an output proportional to the arcsine ($\sin^{-1}$) of the input. The principle of this method of function generation is well known.

A mask shaped like the required function is placed on the face of an oscilloscope operating in the X-Y mode. A photo-electric device is placed in front of the oscilloscope face, and its output is fed with high gain to the Y-axis of the oscilloscope, driving the oscilloscope beam downwards so that the spot is constrained to move only along the edge of the mask. Horizontal movement of the spot, brought about by an X-axis signal, is now always associated with a vertical deflection. This deflection,and consequently also the signal reaching the vertical.deflection plates, is related to the X-axis input signal by the function defined by the mask.

The arc-sine function generator employed was constructed using a Tektronix 502A oscilloscope with a short-persistence blue phosphor to ensure rapid response. A photomultiplier tube (RCA 931A) having maximum sensitivity in the blue-to-ultraviolet range was fixed in front of the oscilloscope face on a camera-mounting cone. The mask used was a 4" x 5" negative transparency obtained by photgraphing a large scale drawing of an arcsine function. This type of mask was used in preference to a mask cut by hand, in order to reduce noise due to irregularities of the edge of the mask. The photomultiplier output was fed into the Y-axis amplifier of the oscilloscope, and the input signal fed into the X-axis amplifier. The vertical axis output of the oscilloscope, incorporating a cathode follower output stage, was taken as output of the device.

Linearity and frequency response of the function generator were assessed by operating on the sinusoidal output of a precision low-frequency waveform generator (Servomex Controls Ltd., Crowborough, Sussex, England, Type LF51, Mark II). When the input amplitude was properly adjusted, the output was a triangular wave with some distortion near the peaks,corresponding to regions where the slope of the arcsine function is nearly infinite. The straight segments of the triangular wave, corresponding in their extent to an angular excursion of $\pm 80^{\circ}$, deviated from the best-fit straight line by less then 3 per cent at frequencies up to 1000 Hz.

8.3.5 Pick-Up Coil

The pick-up coil used for human subjects was 1.5 cm in diameter and consisted of about 30 turns of No. 32 SWG insulated copper wire wound on a plexiglass holder. It was mounted on a steel wire frame shaped to fit snugly over the head (Fig. 8-4). The coil fitted into a slot on top of a two-piece plastic post on top of the wire frame. The post separated the coil from the small field distortion produced by the steel wire, and also provided a means of adjusting the angular position of coil relative to head.

Slip of pickup coil relative to head was assessed during voluntary head shaking by comparing coil output with the output from an angular potentiometer connected to a dental bite by means of a small double parallelogram such as those used in drafting tables. The results at different frequencies are shown in Fig. 8-5. A small amount of slip is seen to occur at the highest frequency, this being the maximum frequency of voluntary head shaking in this subject.

In pigeon experiments a coil 0.75 cm in diameter was used, having about 50 turns of No. 36 SWG insulated copper wire. This was attached to the top of the head, after removing feathers, by means of collodion and a small strip of gauze passed through the center of the coil.

In human and animal experiments the pickup coil was mounted so that, with the head in its resting position (eyes shut),the plane of the coil was vertical with its axis in the antero posterior axis of the head. In both human and avian subjects, particularly the latter, the nose or beak tended to tilt down when at rest with eyes shut, bringing the horizontal semicircular canal approximately into the horizontal plane of the earth. Position of the pick up coil was correspondingly adjusted.

8.4 METHODS OF RECORDING EYE MOVEMENT

Changes in eye position were recorded in human and avian subjects by the method of D.C. electo-oculography. The technique is the subject of a recent review by Shackel (1967). Basis of the measurement is the normal corneo-retinal potential, a standing potential between anterior and posterior poles of the

Fig. 8-4 PHOTOGRAPH OF SUBJECT WEARING APPARATUS FOR HEAD AND EYE MOVEMENT DETECTION

P - pick-up coil; H - steel wire holder for pick-up coil; E - electrode for electro-oculographic recording of eye movements.

Fig. 8-4 PHOTOGRAPH OF SUBJECT WEARING APPARATUS FOR HEAD AND EYE MOVEMENT DETECTION

P - pick-up coil; H - steel wire holder for pick-up coil; E - electrode for electro-oculographic recording of eye movements.

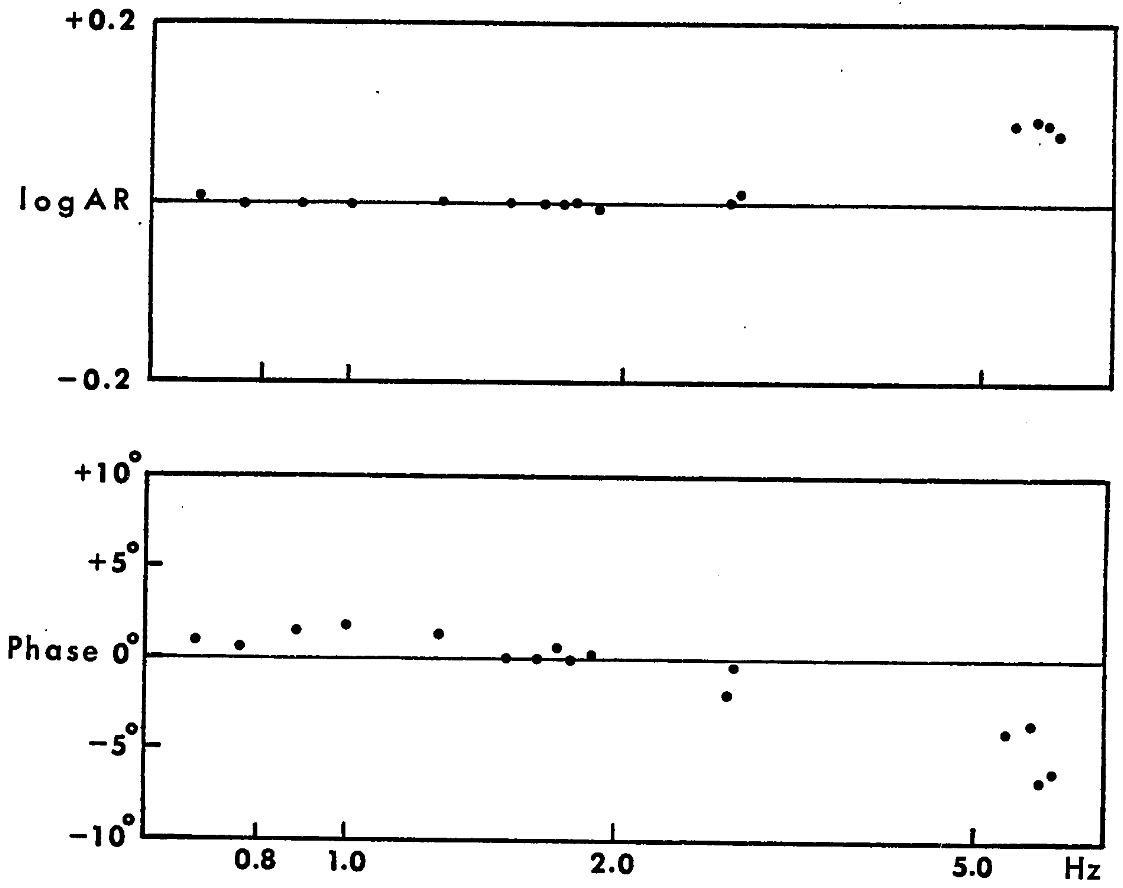


Fig. 8-5 RESULTS OF AN EXPERIMENT TO TEST FOR SLIP OF THE PICKUP COIL RELATIVE TO THE HEAD.

Amplitude ratio and phase of the pickup coil output relative to a potentiometric measurement of head position, during voluntary head shaking.

ocular globe. Changes in orientation of the globe result in changes in the potential recorded by electrodes placed on either side of the eye. The potential change is linearly related to angular position of the eye for excursions up to about 30° from the center.

In human subjects the potential was recorded using rubber suction cup electrodes (Shackel, 1958) with the silver/silver chloride contact poles surrounded by a jelly made of 0.2% Agar in 0.9% saline.

In pigeons a modification was necessary owing to the small size of the head. The electrodes consisted of silver wire 0.5 mm in diameter. These were freshly chlorided and covered with a polyethylene sleeve leaving only the tip exposed. After induction of anaesthesia and removal of feathers a small incision was made in the skin near the eye and about 0.5 cc. of the agar-salt jelly described above was injected with a syringe into the subcutaneous space. The electrode was placed with its tip in the center of this volume of jelly, taking care to ensure that no portion of the bare chlorided wire was in contact with skin or other tissue. Owing to the wide separation of the eyes in the pigeon electrodes were placed around one eye only, one anterior and one posterior to the orbit and a third midway between the other two in the midline of the skull. The center electrode was grounded and recordings were made differentially via sliprings, using a D.C. amplifier (Tektronix Type 3A3).

In initial pigeon experiments there was considerable difficulty in obtaining good records of eye movement because of pronounced electro - myographic-type activity occurring at the time of each quick, saccadic flick of the eye. It became apparent that this was due to contraction of a long thin muscle originating on the skull near the posterior margin of the orbit and inserting into the skin of the neck in the lower cervical region. The muscle is called Dermatemporalis by Shufeldt (1890). In all subsequent experiments this muscle was cut and the remnant scraped away from its bony attachment. Subsequent recordings, though never as noise free as one might hope, were nevertheless free of gross contamination by electromyographic activity.

8.5 OPERATIVE AND ANAESTHETIC METHODS IN PIGEONS

The birds are in general relatively easy to handle, since they become quite docile when blindfolded. Ether anaesthesia is readily induced using a small nose cone. Following this tracheotomy is desirable, especially if it is planned to use a head holder involving constraints near the nares, which may result in hypoventilation. Anaesthesia is then maintained by placing a small amount of ether in a polyethelene squeeze bottle and delivering a few squirts of the vapor so collected into the tracheal cannula. Artificial respiration may be applied where necessary using a similar squeeze bottle filled with air or oxygen.

The effect of ether administered by the squeeze bottle in this way is commonly rather rapid initially and quite prolonged. Not infrequently the depth of anaesthesia seems to increase slowly for a time after the rapid initial effect, and respiratory difficulties may result. In comparison with the cat, is it in the author's experience rather difficult to "blow off" excess ether by artificial respiration in the pigeon. Money (personal communication) has made a similar observation. The effect may be due in part to the large air spaces found in the bones of pigeons and other flying birds.

In the decerebration experiments described below the pigeons were initially anaesthetized with ether. The skull overlying the forebrain is very thin and may be removed using the tip of a scalpel to break off successive small pieces. Use of a dental burr is far more satisfactory as it almost completely prevents bleeding. In the experiments described the brain-stem was divided anterior to the optic lobes and care was necessary to avoid damage to these large protrusions.

CHAPTER 9

EXPERIMENTAL INVESTIGATION OF VESTIBULARLY DRIVEN HEAD MOVEMENTS IN MAN

9.1 INTRODUCTION

The experiments described here were designed primarily to investigate whether or not the vestibulo-collic reflex is active in adult human subjects and in particular whether nystagmoid head movements would occur with suitable vestibular stimulation. A secondary objective, that of discovering the detailed nature of vestibular control of head movement in man, was largely abandoned when it was found that the response in human subjects was somewhat erratic.

A total of eleven normal human subjects were studied. Seven were exposed to step changes in angular velocity of the body, and all were exposed to sinusoidal rotational oscillation at a frequency of 0.01 Hz with eyes closed. Head position, and in some subjects eye position also, were recorded by methods previously described (Chapter 8). Low frequency components are prominent in both of the types of input used, so that the semicircular canal signal could be expected to differ considerably from the relevant input, thus making obvious any vestibular contribution to the response. Further more it was found that such slowly changing stimuli made it possible to see clearly the relatively slow head nystagmus which occurred in some subjects.

9.2 RESULTS

9.2.1 Responses to Step Changes in Table Velocity

Seven subjects were exposed to step changes in angular velocity of the turntable with <u>eyes closed</u> and head free to move. In four subjects the response of the head to this manoeuvre was a small compensatory movement immediately after the velocity change, followed by a gradual smooth return to near the resting position (Fig. 9-1). Three subjects however showed obvious per- and post-rotational head nystagmus with a gradual decay in slow-phase head velocity. Figure 9-2 is a record of such a response from an experiment in which eye position was recorded as well as head position.

It will be noted that head nystagmus is coincident with a slowly-changing net head deviation in the lagging or compensatory direction. The net deviation of

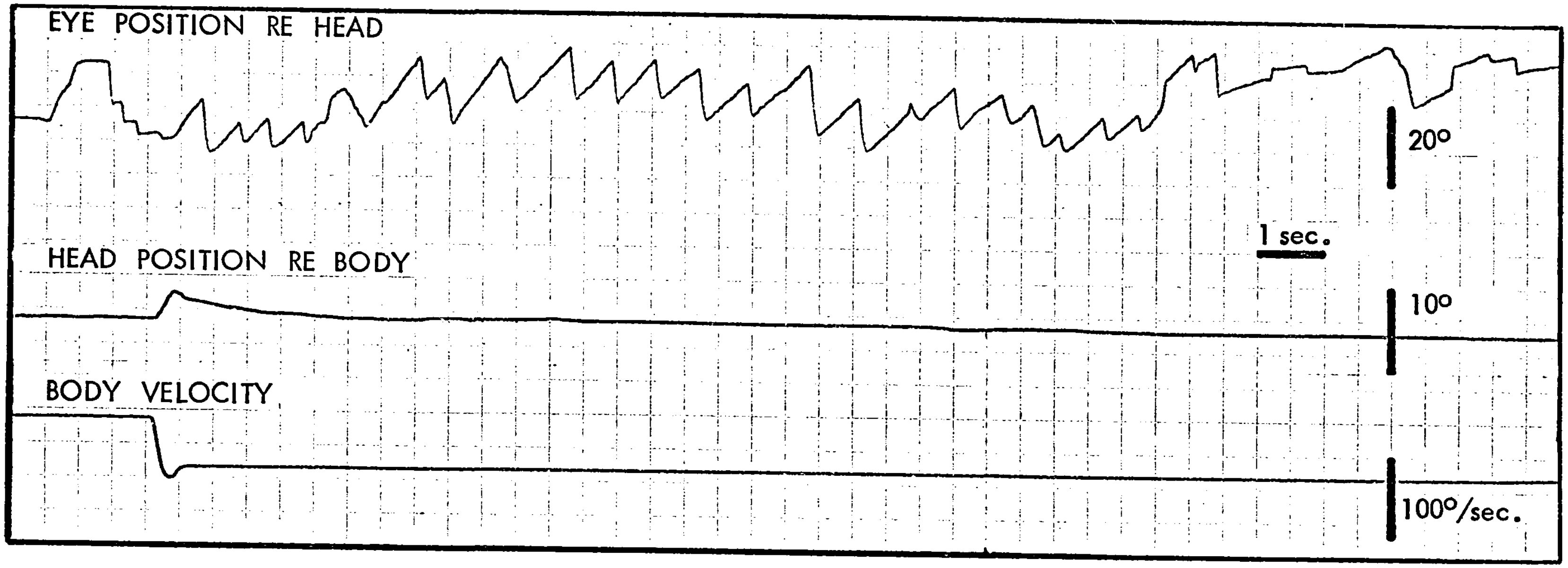
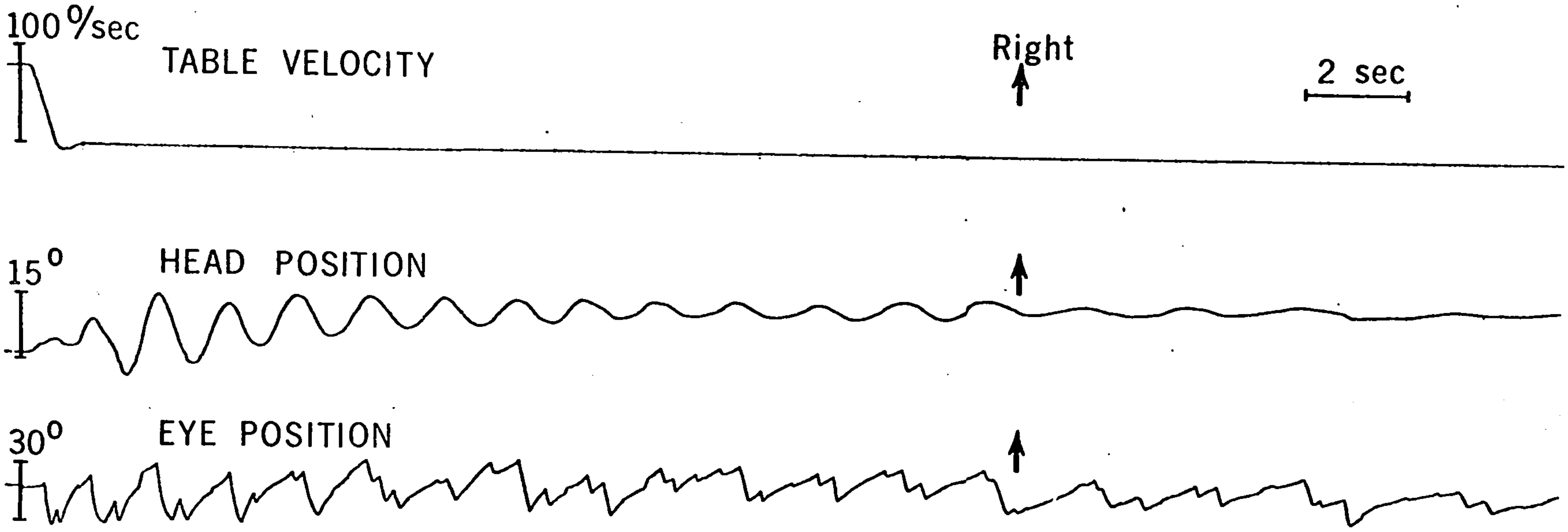


Fig. 9 - 1 RECORDING OF HEAD AND EYE MOVEMENT IN HUMAN SUBJECT EXPOSED TO STEP CHANGE IN ANGULAR VELOCITY OF THE BODY, WITH EYES CLOSED AND HEAD FREE TO MOVE.

The head movement in this subject is not saccadic, but consists of a small compensatory movement, followed by a slow return to the resting position.



Response to angular velocity step in man with eyes closed

Fig. 9 - 2

the head has a rather variable time course, but tends to reach its peak as the nystagmus dies away, following which the head returns very slowly towards its starting position. The observation that net head deviation is in the lagging direction is in accordance with the earlier descriptions of post-rotational head nystagmus in lower animals (Breuer, 1874; Ewald, 1887; Dunlap & Mowrer, 1930; Schierbeck, 1953; Aschan et al., 1955), and with records of head movement in pigeons described in the next chapter. It contrasts with the anti-compensatory or leading direction of "mean eye position" described by Jones (1964) and Mishkin & Jones (1966). The slow return of the head to center is similar to the slow return described by Henricksson et al. (1962) following caloric stimulation in man.

The interplay between head and eye nystagmus, as illustrated in Fig. 9-2, is of considerable interest. It is quite striking to note in this example that while the frequency of eye nystagmus is three to four times greater on the average than that of head nystagmus, the occurrence of a saccadic flick of the head is almost always associated with a particularly large eye saccade. Similarly during a slow-phase head movement there is usally a long slow phase of eye movement, uninterrupted by saccades. This suggests that generation of head and eye saccades is closely related. Such a relationship probably has important functional significance in the normal cooperation of the vestibulo-ocular and vestibulo-collic systems, since it means that intermittently the eye gets a longer look at a single visual target then would otherwise be possible.

A third feature of interest emerges from Fig. 9-3, in which slow-phase head and eye velocities (calculated from successive slow-phase slopes) from the experiment of Fig. 9-2 are plotted as functions of time. The relative magnitude of the step change in table velocity (80°/sec) is indicated by an arrow on the vertical axis. During the first few seconds after the step, compensation by the head clearly makes a very significant contribution to stabilisation of the eye relative to space. In this case, which appears to be typical for the few subjects exhibiting this pattern of response, initial slow-phase head velocity is somewhat more than half the table velocity. Slow-phase head velocity tends to decay faster than the overall

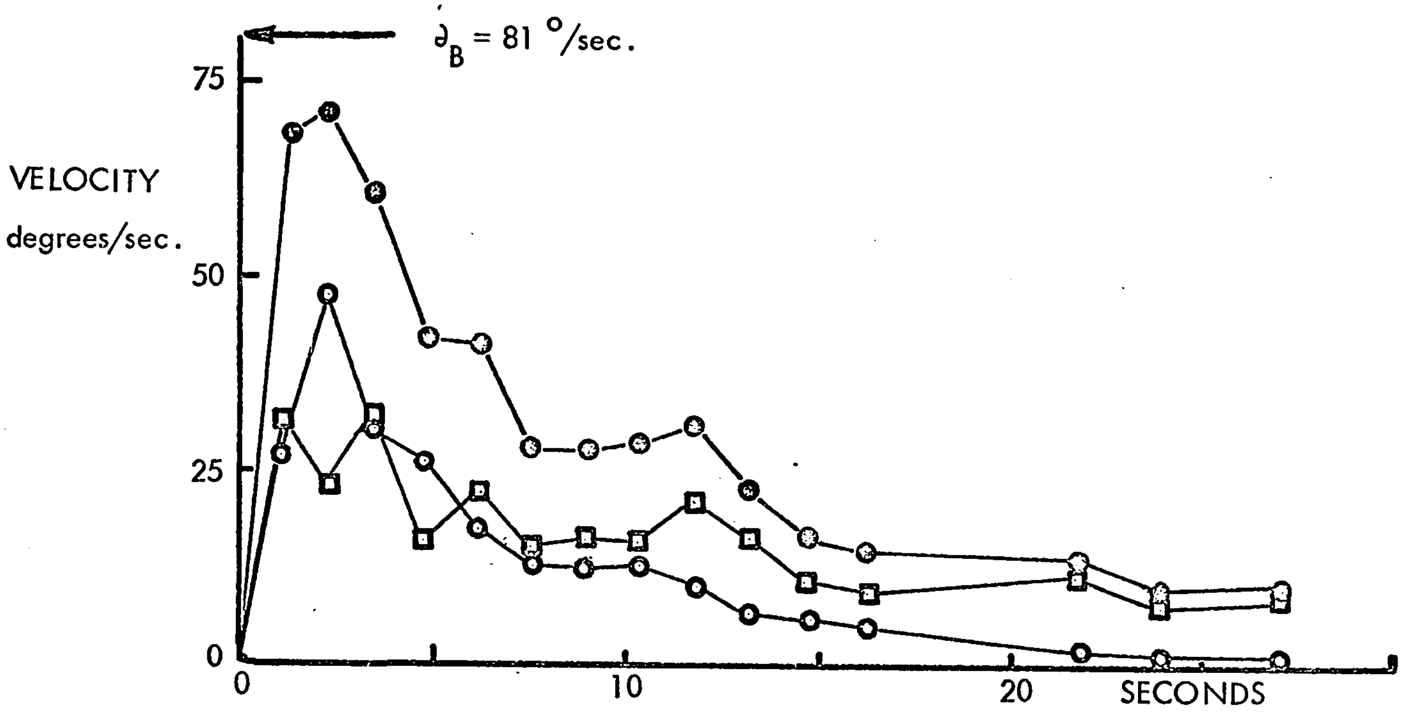


Fig. 9 - 3 SLOW-PHASE HEAD AND EYE VELOCITY IN MAN FOLLOWING A STEP CHANGE IN TABLE ANGULAR VELOCITY (81 degrees/second) Head and eye movement recorded simultaneously; head free, eyes shut. Open circles - velocity of head-on-body; Squares - velocity of eye-in-head; Closed circles - velocity of eye-in-space.

slow-phase velocity of eye relative to table, and in the late portions of the response the relative contribution of the head is small. However the initial portion of the response is probably more indicative of the contribution which head compensation can potentially make during the short, sharp body movements of everyday life. It should be noted also that the contribution by head compensation continues to be significant after head saccades begin, so that controlled vestibulo-collic reflex action is implicated, and not simply the passive head stabilization which results because of head inertia.

9.2.2 Responses to Sinusoidal Rotational Oscillation

Eleven subjects were exposed to low frequency sinusoidal rotational oscillation (around 0.01 Hz) with peak table velocities of 50 - 120°/sec. With head free and eyes open all subjects spontaneously produced rythmic nystagmoid head movements after a period of acclimatization to the apparatus. With eyes shut five subjects continued to show head nystagmus, although it was somewhat less regular. These subjects stated that there seemed to be a strong automatic drive producing head movement. Of the five, two subjects produced a sustained nystagmoid pattern with distinct slow and fast phases (Fig 9-4). The nystagmus shown by the other three subjects was not sufficiently maintained during the long stimulus cycles to permit useful quantitative analysis. Records from the two responsive subjects were analyzed by measuring slow-phase slopes to permit plotting of slow-phase velocity for comparison with table velocity.
In both cases head velocity was phase-advanced by about 30°. In contrast the phase-advance observed in the vestibulo-ocular response in four subjects at nearly the same frequency but with head fixed to the turntable was about 60° (Table 9-1). This latter value agrees with that obtained by extrapolation from the data of Niven and Hickson (1961) and of Miery (1965) and should indicate roughly the phase shift in the canal signal at these frequencies. Thus the vestibulo-collic response in these subjects showed a considerable reduction in the effect of low frequency canal errors, at least as far as phase is concerned.

At first sight the results obtained using sinusoidal inputs may seem to contradict those obtained using step inputs. Reduced phase shift in the low

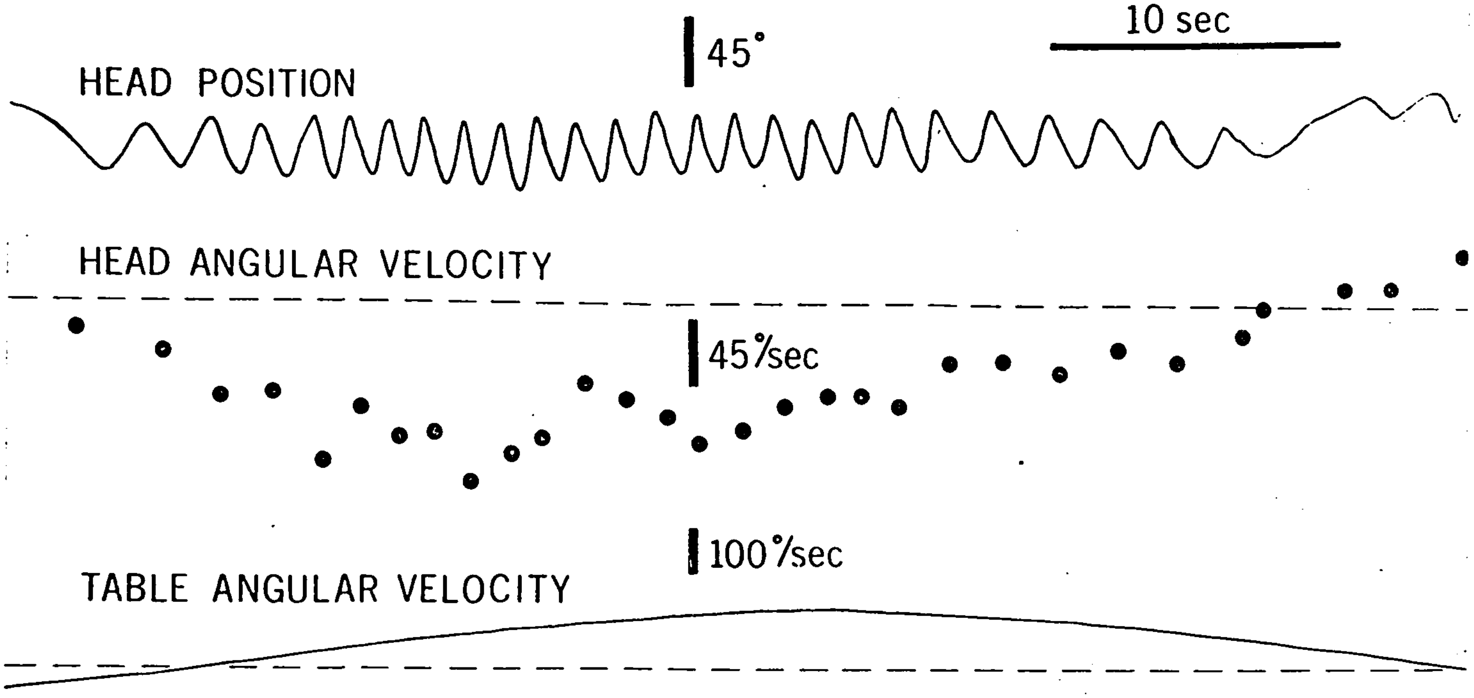


Fig. 9 - 4 HEAD-MOTION RESPONSE OF HUMAN SUBJECT (EYES CLOSED) TO SINUSOIDAL ROTATIONAL OSCILLATION AT LOW FREQUENCY (0.011 Hz.)

Top trace - head position relative to table($\theta_H - \theta_B$); Center trace - slow-phase head velocity relative to table, calculated from slopes; Lower trace - table (body) velocity.

TABLE 9 - 1

COMPARISON OF NYSTAGMUS PHASE SHIFTS DURING SLOW OSCILLATION

Vestibulo-Ocular System			Vestibulo-Collic System		
Subject	Periodic Time	Phase ± S. E.	Subject	Periodic Time	Phase ± S. E.
T. C.	94	46 ± 3.0	J. O.	85	26 ± 3.2
U. W.	96	64 ± 3.9	J. O.	86	31 ± 6.3
J. M.	100	54 ± 1.5	J. M.	105	27 ± 1.8
R. B.	120	61 ± 1.4			

frequency sinsusoidal response of the vestibulo-collic system might be taken to mean that the system has a long-time constant which is longer than that of the semicircular canal or the vestibulo-ocular system. Yet following a step input, slow-phase head velocity decayed rather rapidly, as shown in Fig. 9-3. However while head nystagmus was usally over within one minute, head deviation persisted with a much slower decay for some minutes, the corresponding velocity being too small to resolve in our records, although it clearly became reversed in sign. A similar overshoot in velocity was observed in the step response of the pegeon's vestibulo-collic system (see Chapter 10). In the presence of such an overshoot the semilogarithmic slope of the initial decay in response is not representative of any system time constant, as shown by Young (1968) and discussed in Section 4.3.2. For this reason no attempt has been made to fit a time constant to the step-response data in man. It should be noted however that compensatory eye nystagmus was observed to persist after the cessation of head nystagmus (Fig. 9-2), a fact which strongly suggests that the slow decay of head deviation was associated with a residual vestibular signal and not due to central phenomena alone.

9.3 CONCLUSIONS

These experiments demonstrate that head nystagmus does occur in man, and there can be little doubt that it was vestibularly-driven in these circumstances. During low frequency oscillation the phase advance of compensatory head velocity was found to be considerably less than that expected fromthe semicircular canal with head fixed at the same frequency. Thus as theory predicts, the vestibulo-collic reflex system, presumably because of its feedback mode of operation, apparently is capable of manifesting less phase error than its transducer, the semicircular canal.

In the response to a step change in angular velocity of the body, it was found that in the first few seconds of the response compensatory head movements can make a major contribution to the overall stabilization of the visual image by combined eye and head movements. This suggests that during rapid angular movements of the body, compensation through vestibularly-controlled head movement may play an important role. During turbulent flight the aircraft pilot is exposed to just such high frequency angular movements, and it might be of interest to evaluate the effect of the inertia added by the flying helmet on such compensation.

The feedback nature of the vestibulo-collic system, which makes it so fundamentally different from the vestibulo-ocular system, may have important implications in the consideration of life in a rotating satellite. In this situation, angular head movement out of the plane of satellite rotation would result in an erroneous canal signal due to well known "cross-coupling" effects. In the absence of head compensation, an erroneous eye response would be generated, but this would die away with the usual time constant of cupula restoration. However if a compensatory head movement occurred, it would also be erroneous, and moreover would generate a further, still erroneous canal signal due again to cross-coupling effects. It is not clear what the outcome of this would be, but it seems possible that a progressive build-up of error could occur, leading to severe disorientation and inappropriate postural adjustments.

Investigation of the human vestibulo-collic system has not been pursued further in this study because, while it is clear that the reflex is active in man, the response of human subjects was variable. It therefore seemed more useful to proceed to a more detailed quantitative investigation of the system in pigeons, in which the response is known to be more pronounced and repeatable, although quantitative studies and analyses are lacking.

CHAPTER 10

THE HORIZONTAL VESTIBULO-COLLIC REFLEX IN THE PIGEON

10.1 INTRODUCTION

This chapter describes studies of rotational head movement in the pigeon in response to vertical-axis rotation of the body. The experimental approach differs from that of previous investigators in several respects. In particular a more refined method of recording head movement has been developed and utilized, responses of the same animal to several different input waveforms have been studied, and a start has been made on the problem of identifying the dynamic nature of some of the functional components of this feed-back control system. These and other differences stem from a fundamentally different objective. Previous investigators were largely concerned with demonstrating the existence of vestibular control of head movement, or with inferring from this reflex response information as to the characteristics of the semicircular canals. In the present investigation however the emphasis has been on the nature of the reflex mechanism itself, including as a major objective the development of a realistic mathematical model of the pigeon vestibulo-collic system. The term realistic is used here in the sense that functional components of the model should have a sensible relation with physiological components. Such realism, or isomorphism is essential, at least on an elementary level, if the results of animal work are to be useful in the evaluation of the corresponding system in man. In practice, largely owing to complexities introduced by the occurrence of saccades, the results here reported do not permit exact mathematical modelling. However they do clarify the functional characteristics of the vestibulo-collic response, so that a quantitative comparison of the potential contributions of the vestibulo-collic and vestibulo-ocular systems to visual image stabilization is now possible.

As in the case of the vestibulo-ocular system, it appears useful to consider slow-phase response velocity as the functionally important output variable, and to use this as an index of the efficiency of stabilization under different conditions. This parameter is easy to obtain, either by measuring slow-phase slopes in the records of head position, or directly from records of head velocity, and has the advantage that it is familiar as a concept to most biological workers in this field. Moreover it emerges that a transfer-function approach can be used, with restrictions, to provide a rough general description of observed input-output relations when slow-phase velocity is used as the output variable.

Mention has been made in Section 7.3 of the possible effects of arousal on the operation of the system. The form as well as the magnitude of the response of a feedback control system to a given input are subject to variation if the 'loop gain' changes. Since the brain stem forms part of the vestibulo-collic control loop, it may be concluded with near certainty that arousal will have significant effects on system response. For this reason quantitative studies have been made under conditions designed to reduce arousal variations as much as possible; such conditions being most readily achieved by minimizing non-vestibular sensory inputs, especially acoustical inputs, in the conscious, intact pigeon. In addition a brief investigation has been made of experimental preparations which might be suitable for studying the system at different levels of arousal.

10.2 METHODS

Common domestic pigeons were blindfolded by closing the eyelids with black adhesive tape. The legs and wings were then bound with tape, and the birds were taped in place on the turntable (Table B. of Chapter 9) with the head always over the axis of rotation.

The primary variables recorded were table position (θ_B) and velocity $(\dot{\theta}_B)$, and head position relative to table $(\theta_H - \theta_B)$, measured by methods described in Sections 9.2 and 9.3. Absolute head position (i.e. relative to space) (θ_H) was obtained in some experiments by on-line addition of table position and relative head position. In other experiments head velocity relative to table $(\dot{\theta}_H - \dot{\theta}_B)$ was obtained by on-line differentiation using a second order differentiating filter programmed on a Pace TR-20 analog computer.

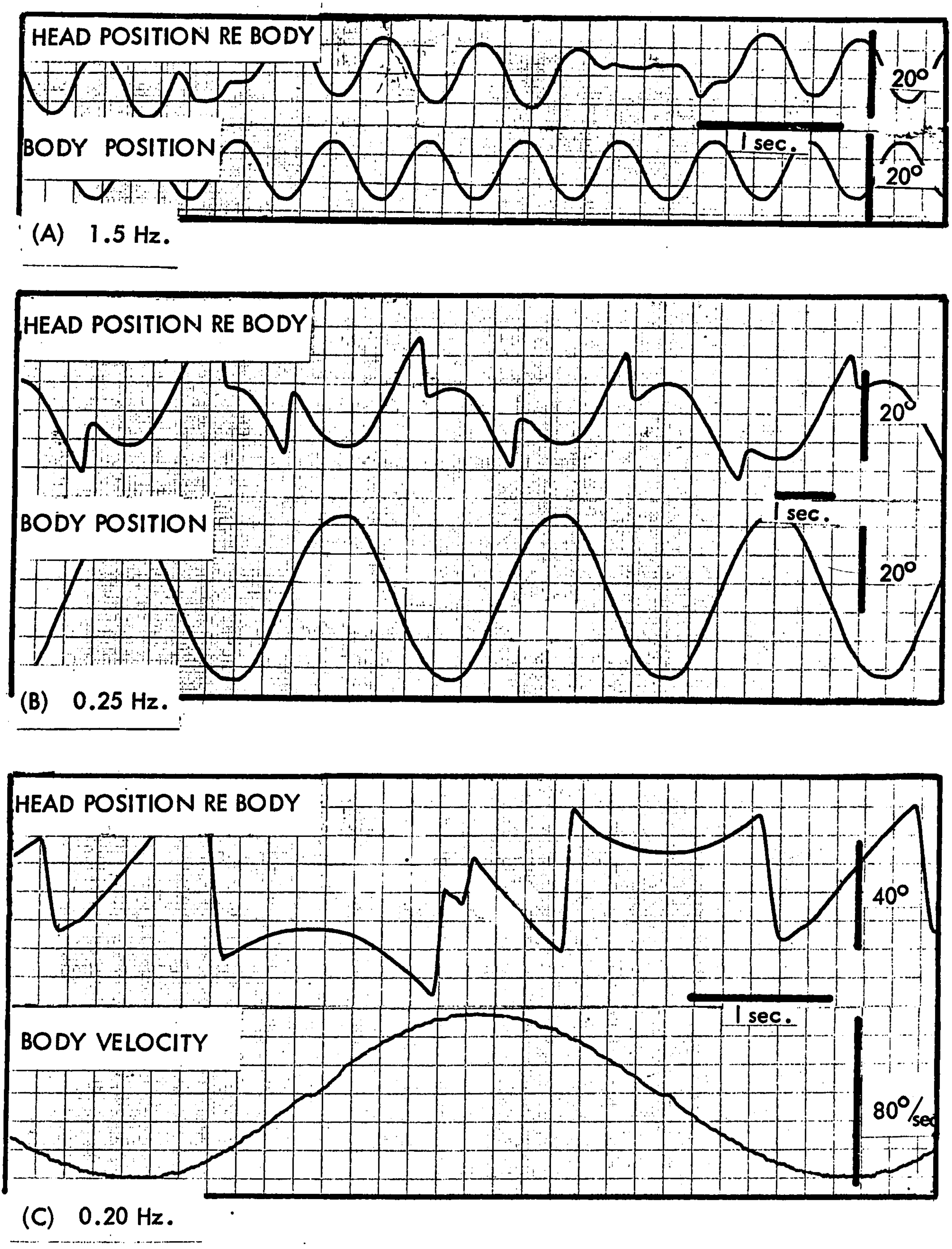
It should be noted that head velocity and head position relative to table are so defined that each has an algebraic sign opposite to that of table velocity and position respectively, when head motion is in the compensatory direction.

10.3 GENERAL FEATURES OF THE RESPONSE

Since the response of the pigeon vestibulo-collic system is relatively unknown, it seems pertinent to present a number of illustrations of the response and to discuss its characteristics in some detail. Dramatic changes in the pattern of head movement occurred in response to sudden noise and hence, for the sake of clarity, responses which occurred in the absence of noise and other disturbances will be discussed first.

Fig. 10-1 illustrates typical records obtained in a number of different pigeons exposed to sinusoidal oscillation at various frequencies in the absence of vision. In each record the upper trace represents head position relative to table (body), and the lower trace represents table position or velocity as indicated. One is immediately struck by the remarkable resemblance between these responses and those of the vestibulo-ocular system. The saccadic pattern is superficially similar, and, as in records of eye nystagmus, it is frequently apparent that a prominent Fourier component of/the position waveform is at the input frequency. Also reminiscent of the vestibulo-ocular response is the finding (Figs. 10-1A, 10-2A) that at high sinusoidal input frequencies compensation is very good but saccades are infrequent.

On closer examination however significant differences are found between the responses of the two systems. In the vestibulo-collic responses shown in Fig. 10-1 it will be noted that the fundamental Fourier component (at the input frequency) of the head position record always lags the sinusoid of body position, often by more than 90 degrees, and correspondingly lags body velocity by about 180 degrees. This is readily apparent to the observer during an actual experiment, in which head nystagmus is seen to occur in the lagging quadrant. This phenomenon is particularly striking in the response to a step change in table angular velocity (Fig. 10-5), and contrasts sharply with the corresponding phenomenon in the vestibulo-ocular system. In the latter case as Jones (1964), and Mishkin and Jones (1966) have pointed out, overall eye deviation tends to lead head position during sinusoidal stimulation, and

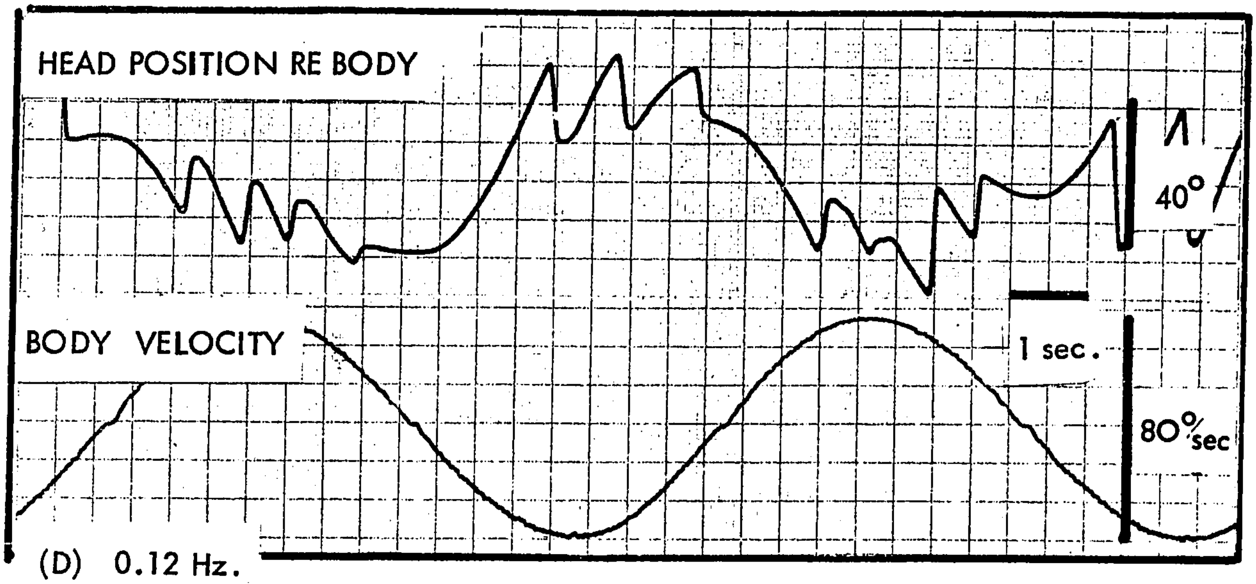


(A) 1.5 Hz.

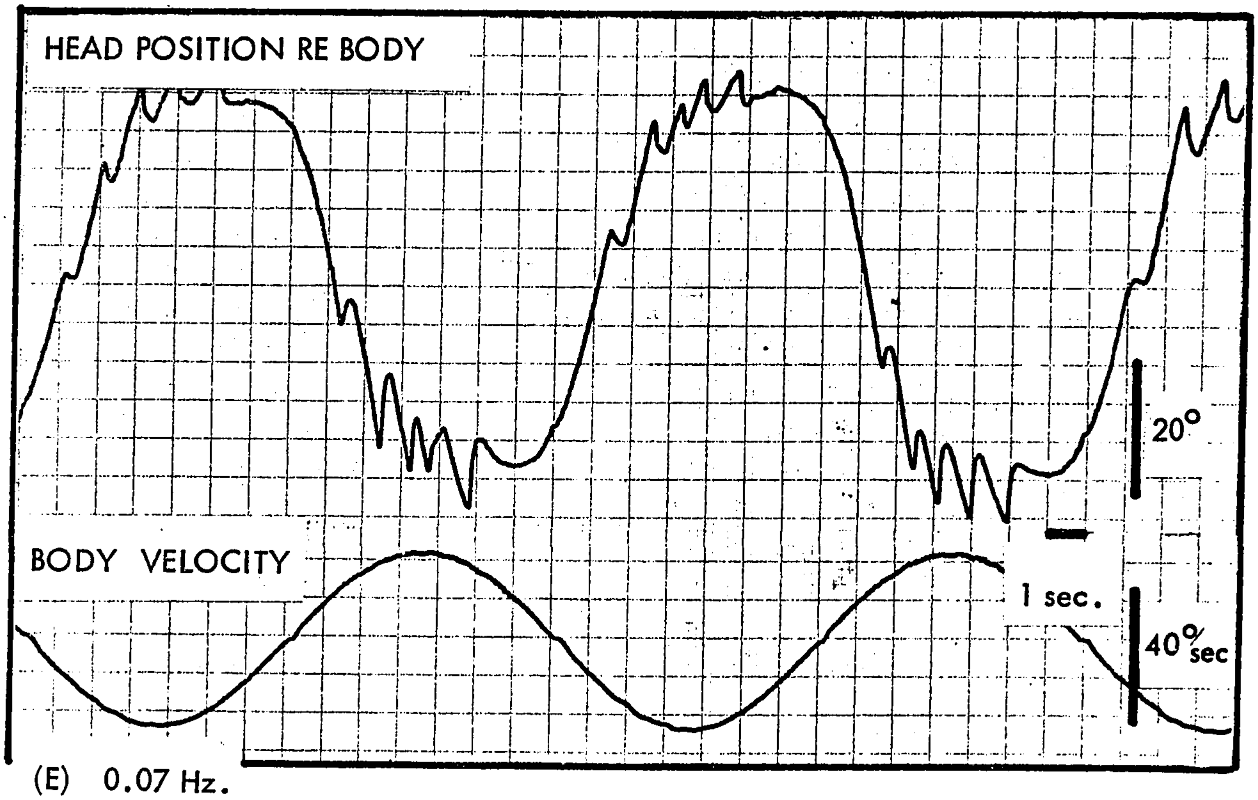
(B) 0.25 Hz.

(C) 0.20 Hz.

Fig. 10-1(a,b,c) RESPONSES OF THE HORIZONTAL VESTIBULO-COLLIC REFLEX SYSTEM IN CONSCIOUS UNDISTURBED PIGEONS (EYES SHUT) TO SINUSOIDAL ROTATIONAL OSCILLATION.

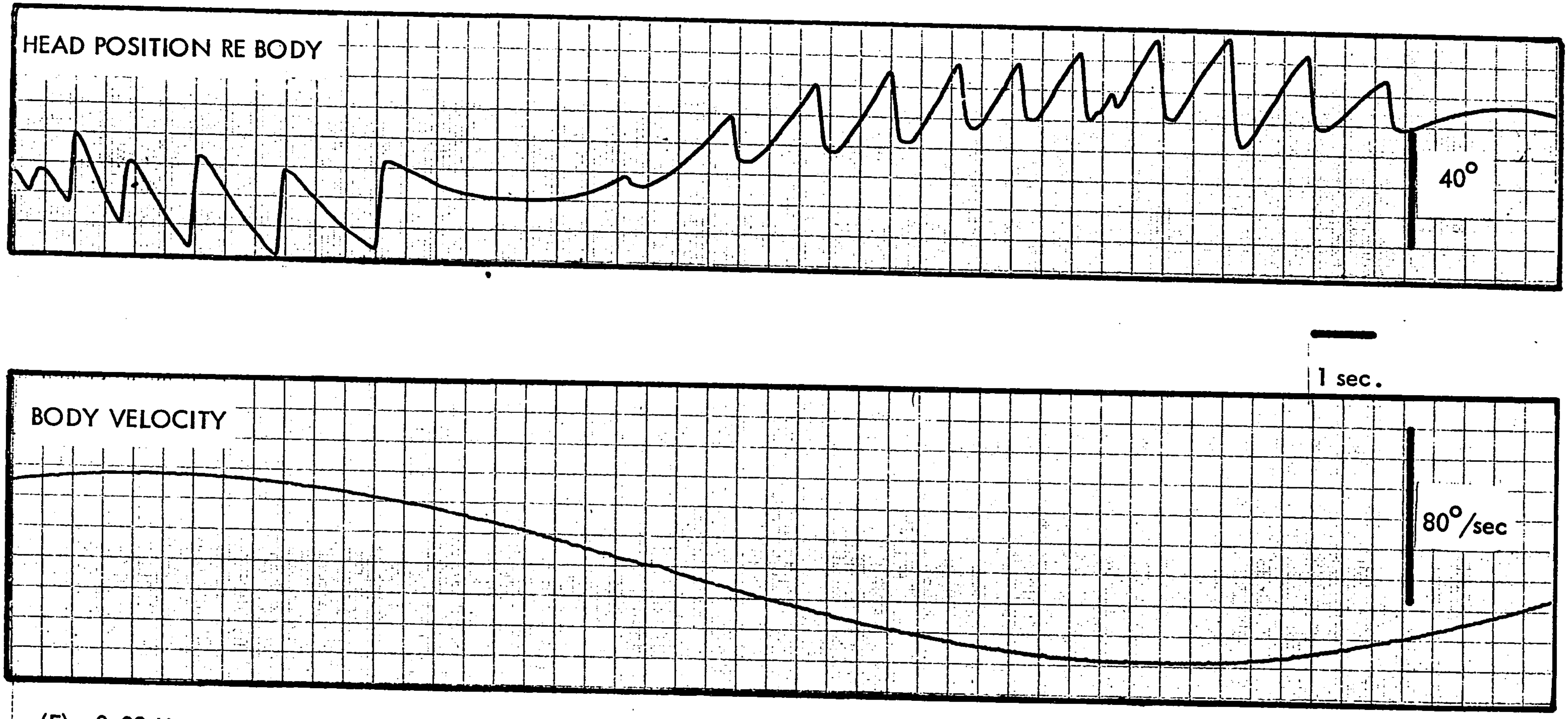


(D) 0.12 Hz.



(E) 0.07 Hz.

Fig. 10-1 (d,e) VESTIBULO-COLLIC RESPONSES OF UNDISTURBED CONSCIOUS PIGEONS TO SINUSOIDAL ROTATION (EYES SHUT)



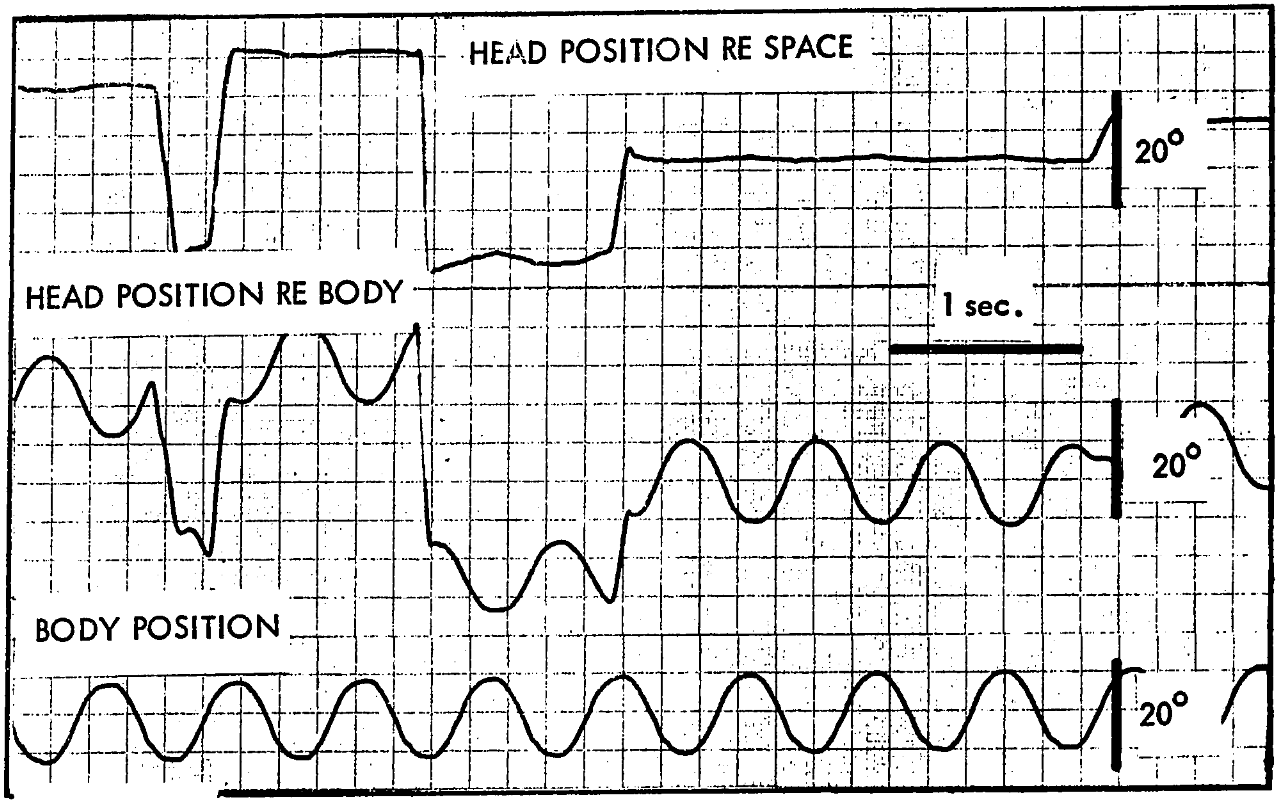
(F) 0.03 Hz.

Fig. 10-1 (f) VESTIBULO-COLLIC RESPONSE OF UNDISTURBED CONSCIOUS PIGEONS TO SINUSOIDAL ROTATION (EYES SHUT) there is a corresponding tendency in the step response for saccadic activity to draw the eye in the leading direction.

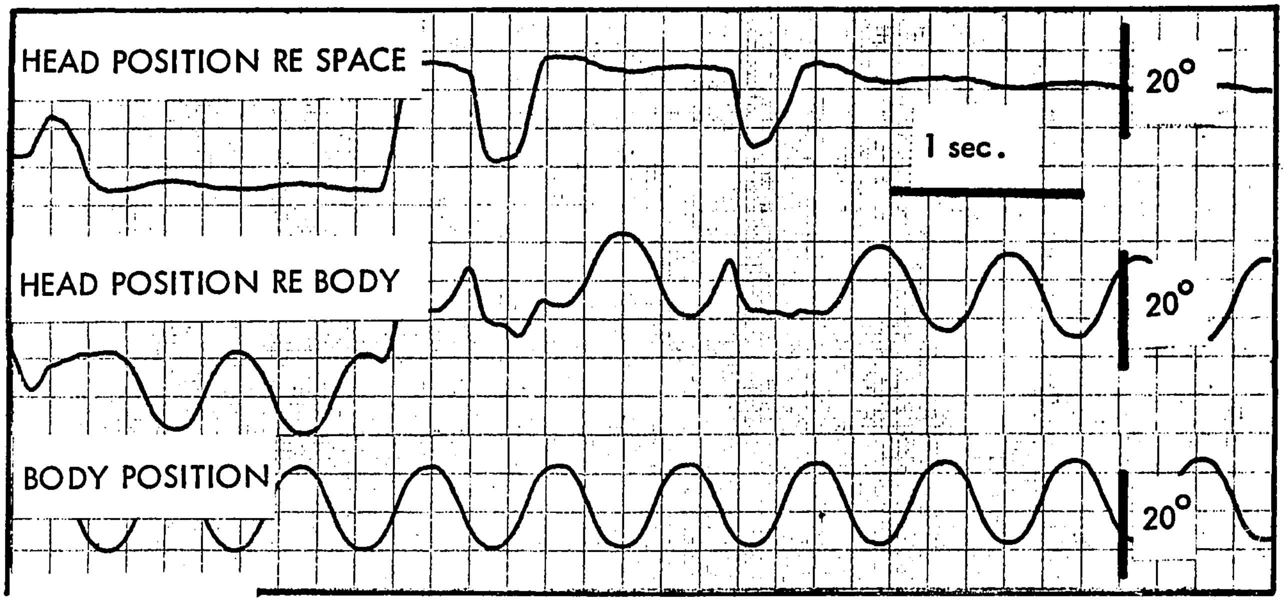
Another characteristic of the vestibulo-collic response to sinusoidal inputs which is unusual in the corresponding vestibulo-ocular response is exemplified in Fig. 10-1E. Here saccadic activity is maximal immediately before compensatory (slow-phase) head velocity reaches zero. After this point, the "turnover" of the head position record, there is a fairly long interval without saccades, during which the head is carried into the opposite quadrant before saccadic activity resumes. This feature was rather characteristic of the responses to low-frequency sinusoidal inputs, although it was not always as striking as in this particular case.

The accuracy of slow-phase tracking in the vestibulo-collic system at high frequencies (0.5 Hz. and above) was found to be very remarkable. In Fig. 10-2 are shown a number of records from experiments in which head position relative to space was obtained by on-line algebraic summation of the measured head position relative to table $(\theta_H - \theta_B)$ and the table position (θ_H). Fig. 10-2A, obtained with an input frequency of 1.5 Hz., is from the same stretch of record as Fig. 10-1A, but in this case the uppermost trace is head position relative to space. Head stabilization between saccades was almost perfect under these circumstances, a feature which is particularly striking since there was no visual input. Fig. 10-2B was obtained somewhat later in the same experiment when the pigeon was apparently more drowsy; head stabilization was a little less precise although still excellent. Fig. 10-2C was obtained with an input frequency of 0.25 Hz. and in this case the error in slow-phase head velocity relative to space was more pronounced. The error increased progressively as the frequency of stimulation decreased (Section 10.4).

Fig. 10-3 shows some examples of records in which the velocity of head relative to table was obtained by on-line analog differentiation. In each case the slow-phase segments of the head velocity curve could be joined to form a fairly smooth sinusoidal curve, phase advanced relative to table velocity. The duration of saccadic flicks in the differentiated trace is somewhat exaggerated owing to the filtering necessary to overcome the increased noise which appears upon differentiation. An interesting and unexplained phenomenon is noted in Fig. 10-3C and to a lesser



(A) 1.5 Hz.



(B) 1.5 Hz.

Fig. 10-2 a,b. VESTIBULO-COLLIC RESPONSES IN UNDISTURBED CONSCIOUS PIGEONS, SHOWING VARIATIONS IN HEAD POSITION RELATIVE TO SPACE.

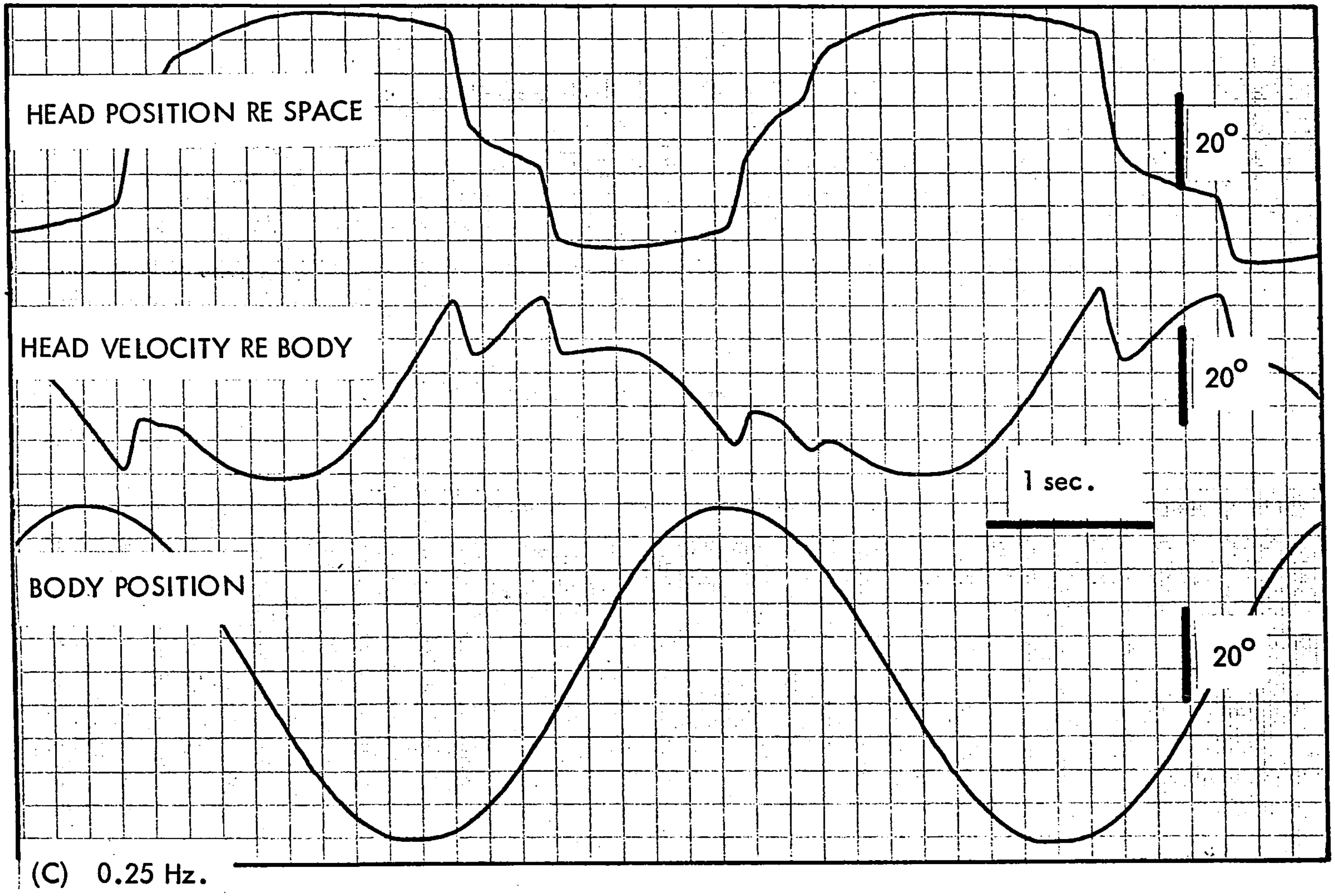
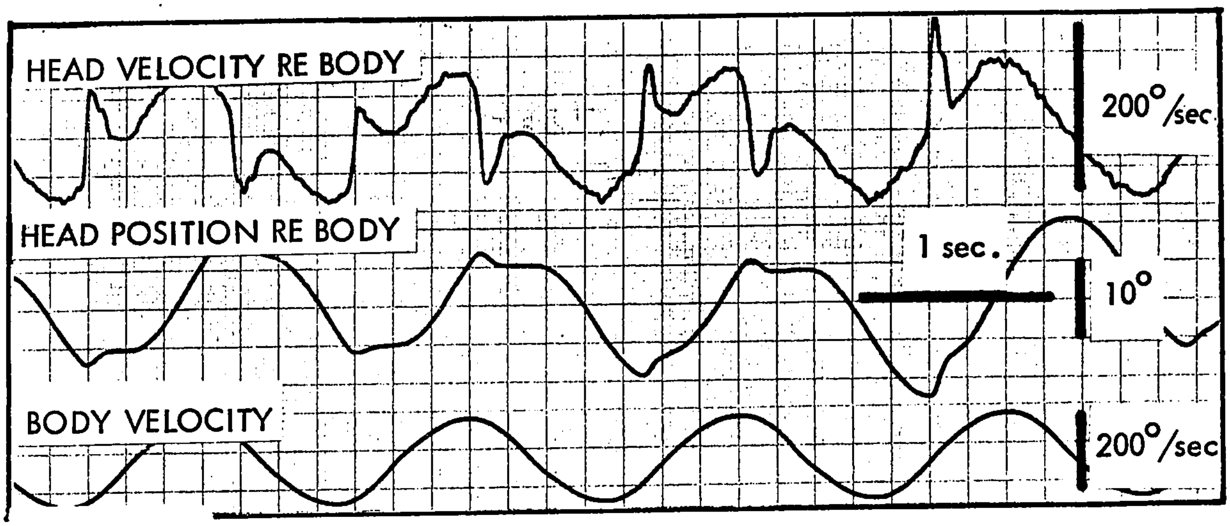
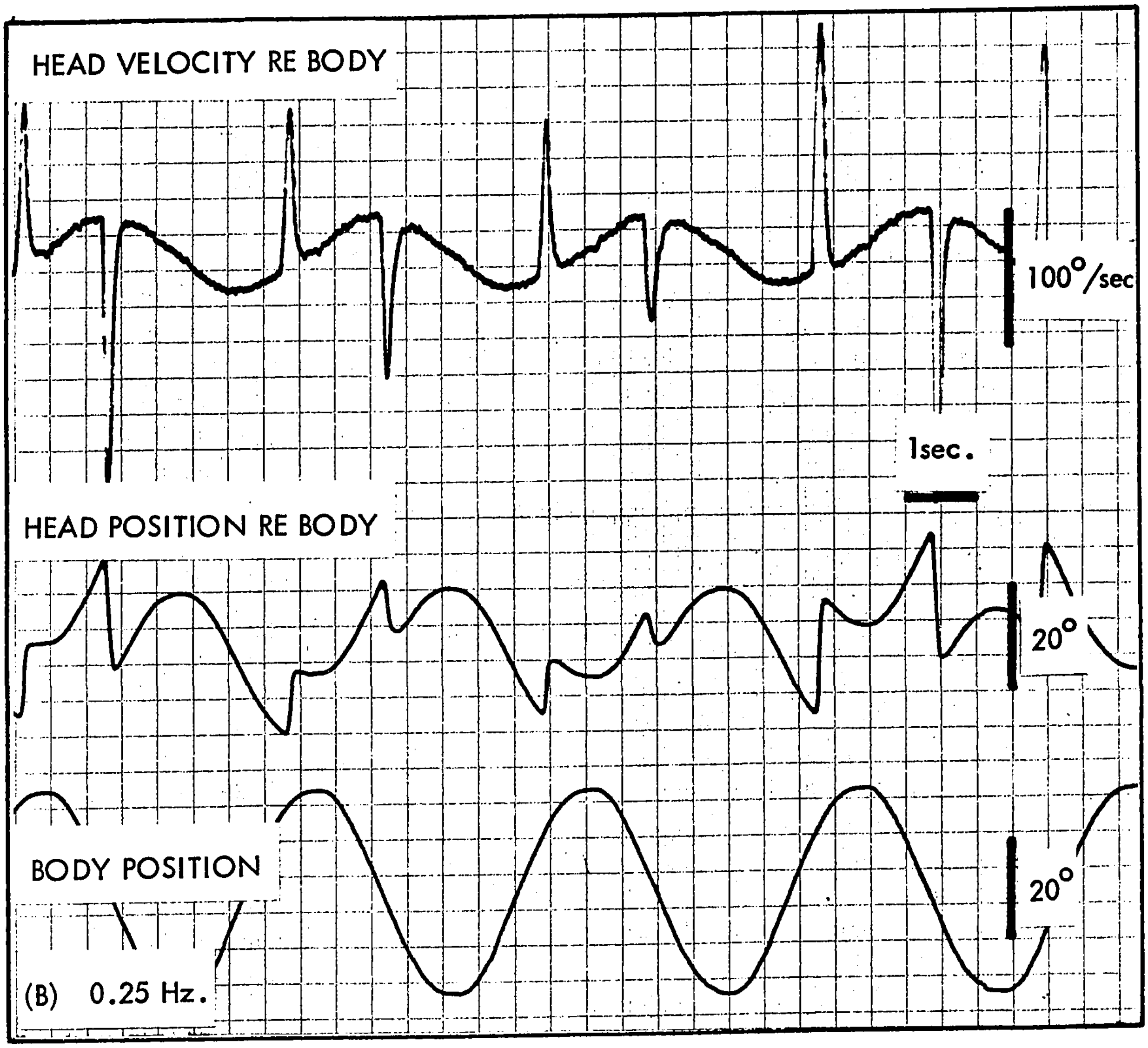


Fig. 10-2 c. VESTIBULO-COLLIC RESPONSE IN UNDISTURBED CONSCIOUS PIGEON SHOWING VARIATIONS IN HEAD POSITION RELATIVE TO SPACE.



(A) 0.7 Hz.



(B) 0.25 Hz.

Fig. 10-3 a, b VESTIBULO-COLLIC RESPONSES IN UNDISTURBED CONSCOUS PIGEONS (EYES SHUT) SHOWING VARIATIONS IN HEAD VELOCITY RELATIVE TO TABLE.

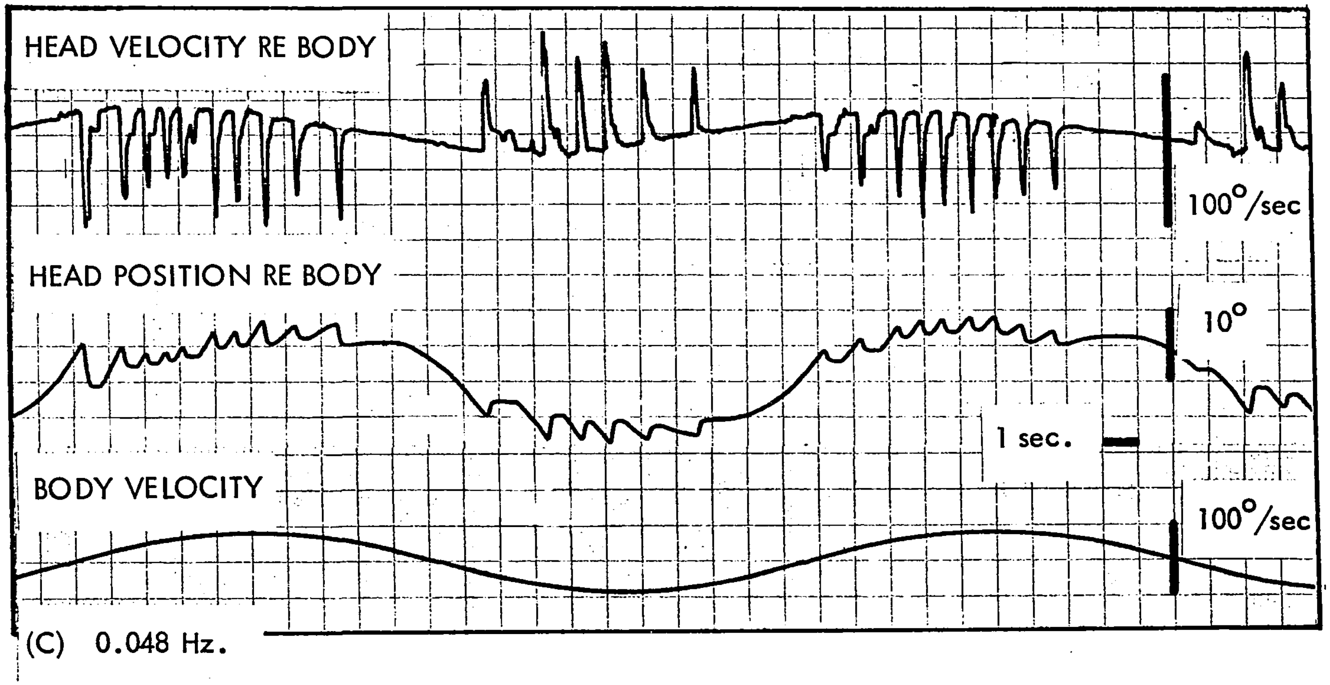


Fig. 10-3 c VESTIBULO-COLLIC RESPONSE IN UNDISTURBED CONSCIOUS PIGEON extent in Fig. 10-3A, in which after some saccades there is a brief interval during which head velocity (relative to table) tends to be zero. It was at first thought that this phenomenon might be due to the resistance offered by the very thin wire leading from the pick-up coil mounted on the pigeon's head, but it was found that changing the arrangement of the wire had no effect. The phenomenon was observed in a number of experiments although never in the highly aroused pigeon (Fig. 10-4). No satisfactory explanation has emerged.

The effects of a sudden loud noise on the response to sinusoidal inputs are shown in Fig. 10-4. In each case the noise consisted of repetitive clapping or tapping lasting for the duration of the solid bar shown in each of the three records. The effect of noise was sudden and striking. Typically the saccades became very large and of high velocity, their frequency decreased , and the whole pattern of head movement changed as a result. The approximate sinusoid of slow-phase head velocity became of greater amplitude, and its phase advance relative to table velocity tended to become less. In addition following the noise, it was frequently found that slow-phase head velocity was augmented after each saccadic flick (Fig. 10-4, A and B). This contrasts with records obtained in the undisturbed pigeon, in which post-saccadic velocity augmentation was not usually apparent, but is reminiscent of vestibulo-ocular response, in which augmentation of slow-phase eye velocity following saccades is a characteristic feature. Unfortunately the effect of noise was short-lived, even when the sound stimulation was continued, so that it was not possible to obtain a sustained response of the type occurring immediately after the noise.

Typical responses of undisturbed pigeons to step changes in table angular velocity are shown in Fig. 10-5. In each case the response begins with a compensatory head movement whose velocity is very nearly equal to the magnitude of the step change in table velocity. Following this there is a period of about 20 sec. during which the head, while remaining in the lagging quadrant, makes vigorous nystagmoid movements. Slow-phase head velocity decreases gradually, and at the end of this period it changes sign and the head moves very slowly back towards its central position. During this return phase, there are typically very few

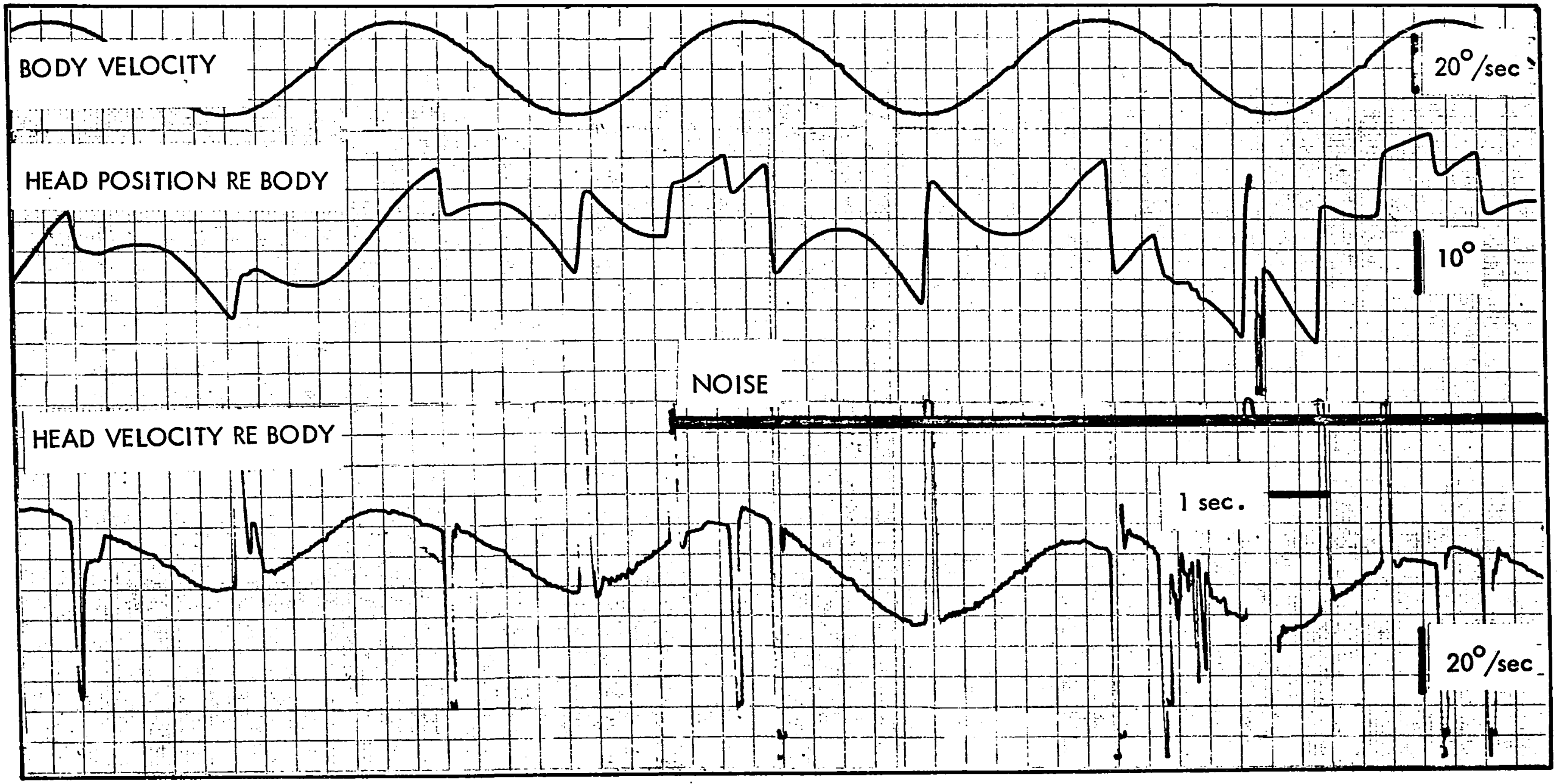


Fig. 10-4 a EFFECT OF ACOUSTICAL NOISE (CLAPPING) ON THE VESTIBULO-COLLIC RESPONSE OF PIGEON
Noise lasted for the duration of the solid bar on the record.

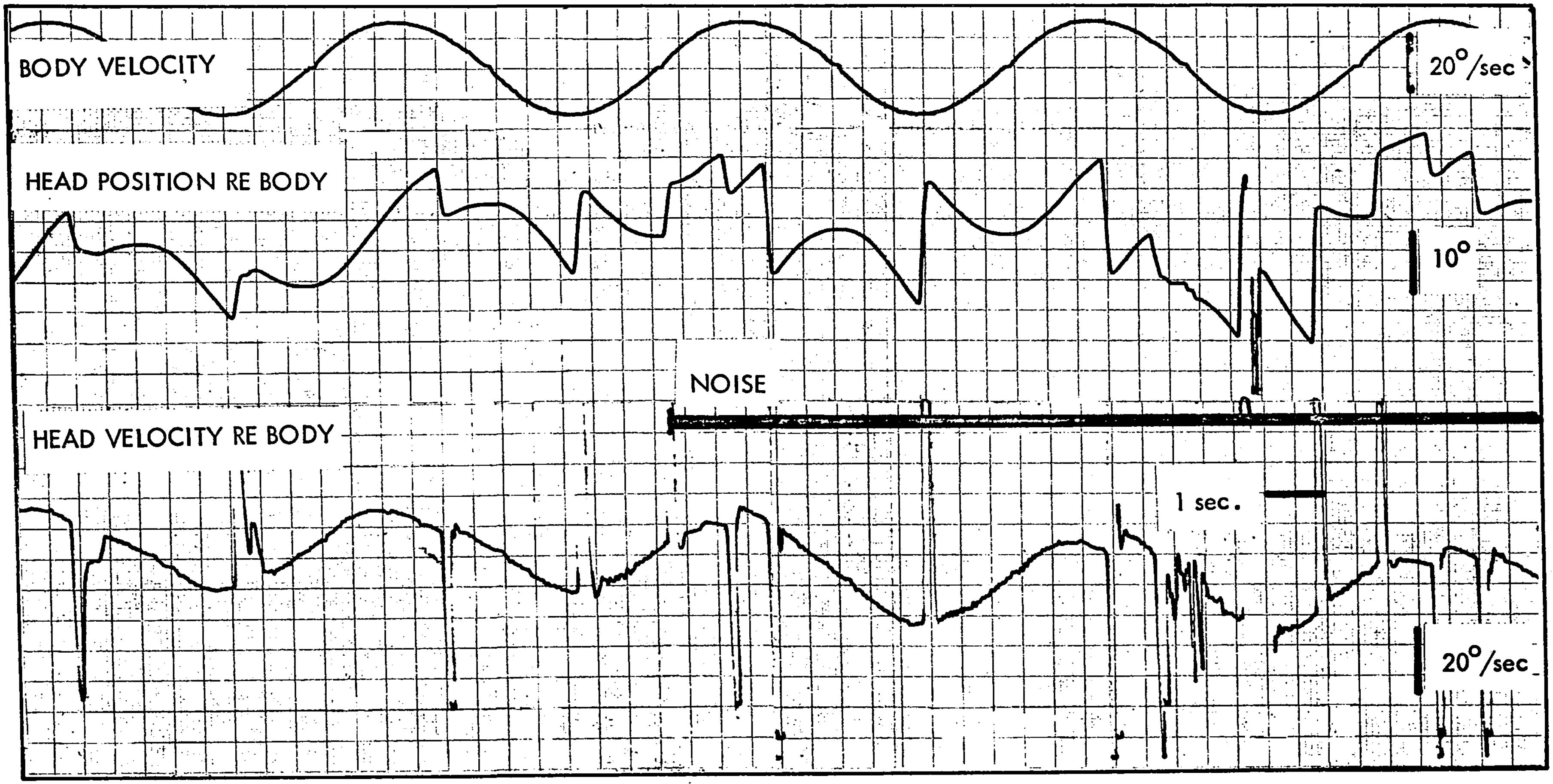


Fig. 10-4 a. EFFECT OF ACOUSTICAL NOISE (CLAPPING) ON THE VESTIBULO-COLLIC RESPONSE OF PIGEON

Noise lasted for the duration of the solid bar on the record.

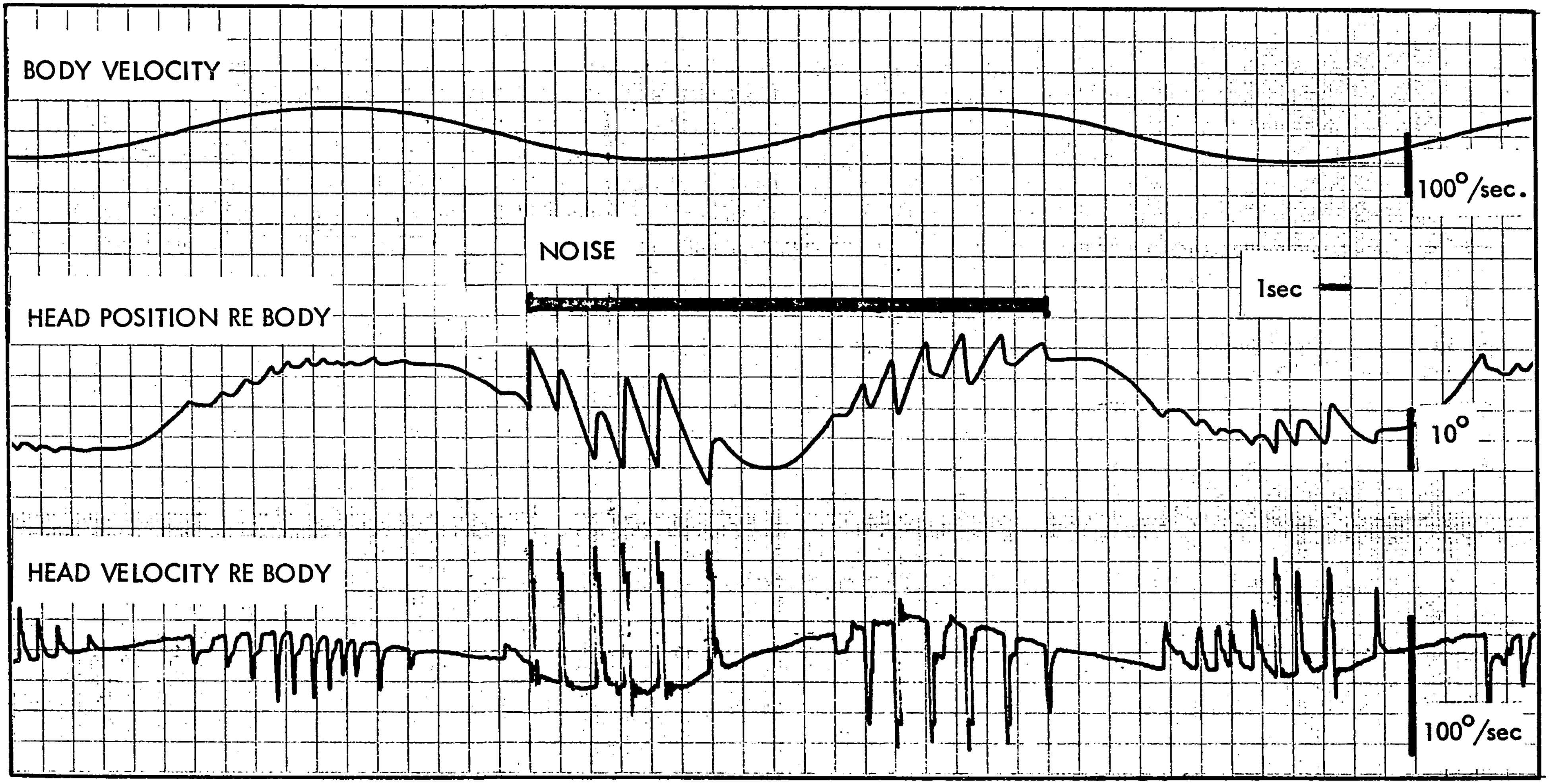


Fig. 10-4 b EFFECT OF ACOUSTICAL NOISE ON THE VESTIBULO-COLLIC RESPONSE OF PIGEON

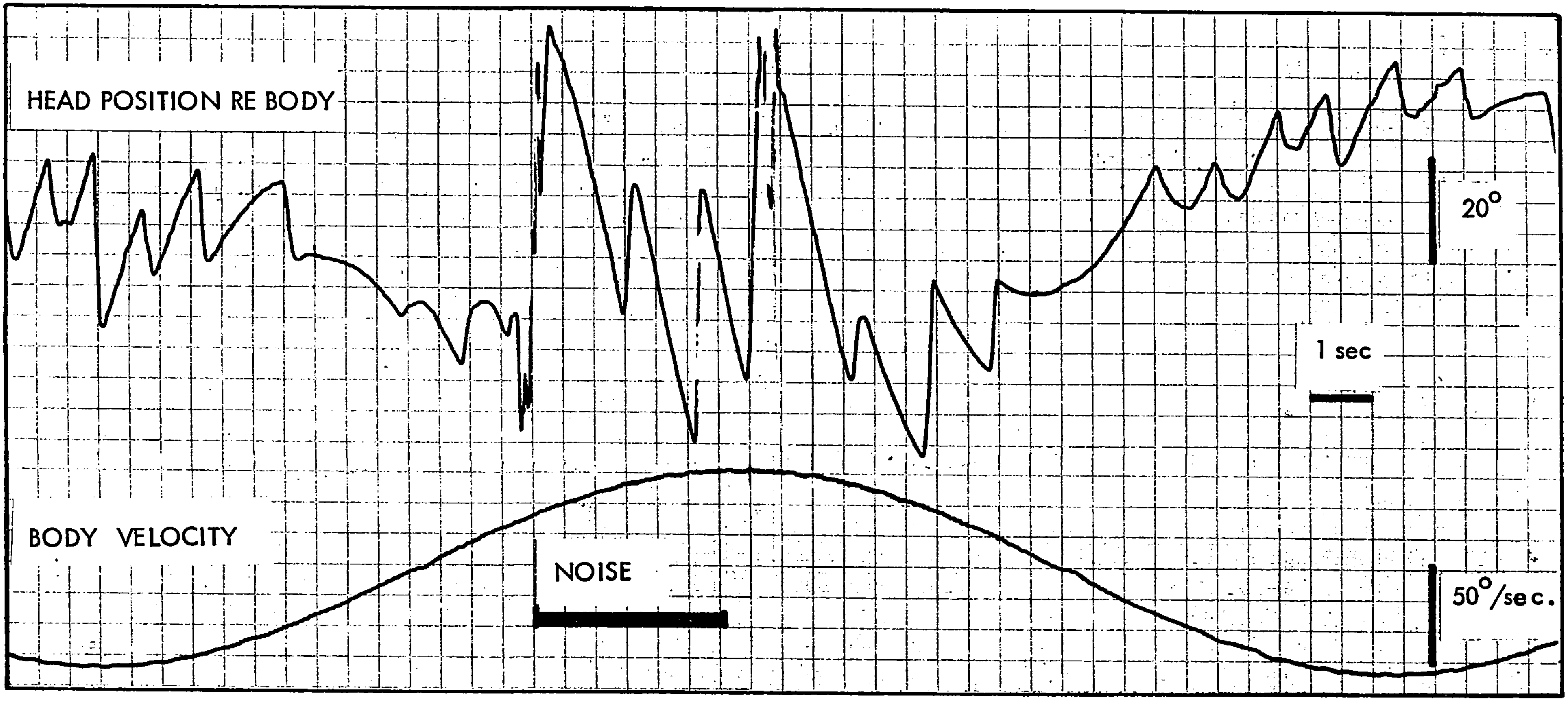


Fig. 10-4 c EFFECT OF ACOUSTICAL NOISE ON THE VESTIBULO-COLLIC RESPONSE OF PIGEON

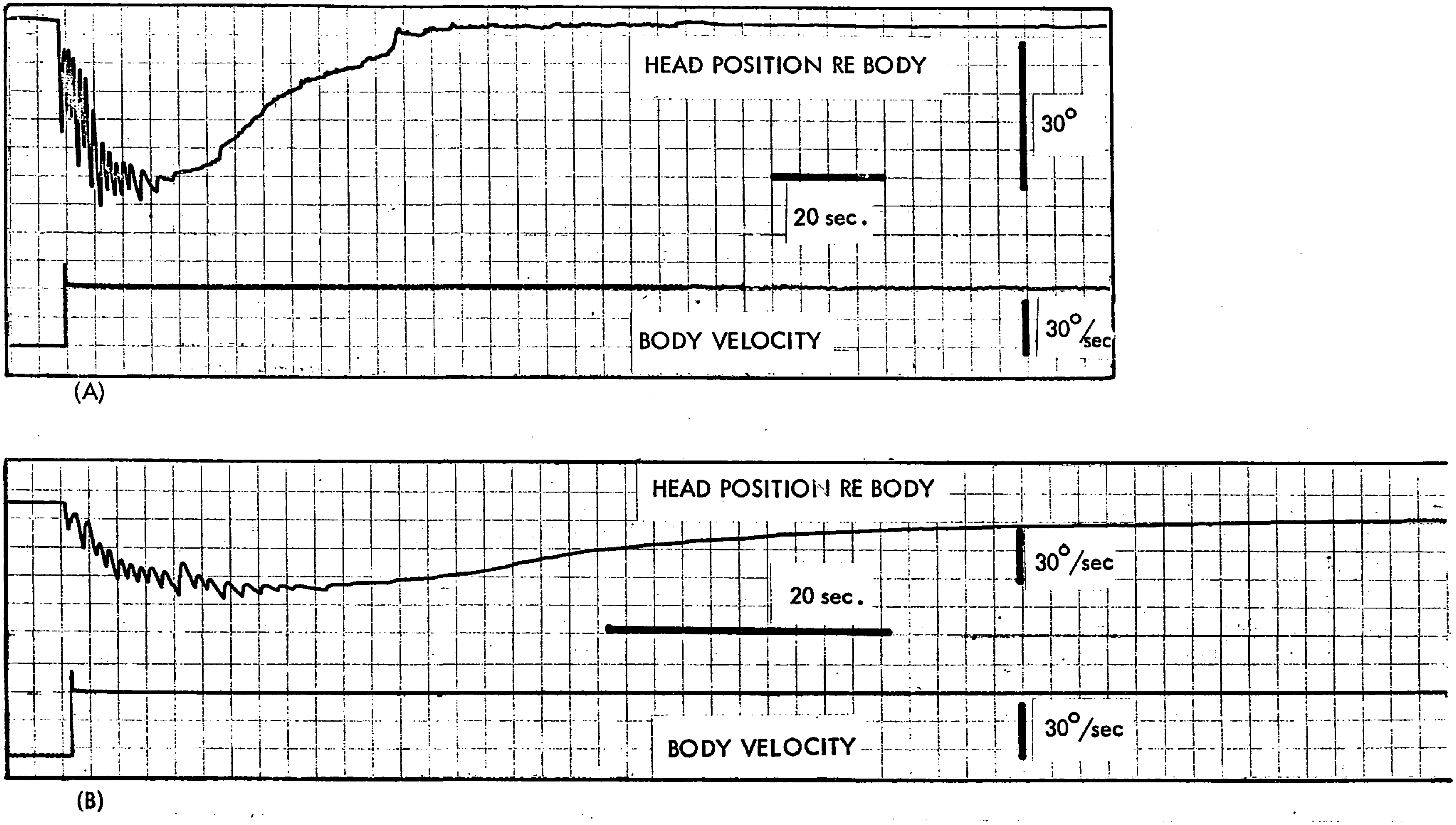


Fig. 10-5a,b VESTIBULO-COLLIC REFLEX RESPONSES TO STEP CHANGES IN BODY ANGULAR VELOCITY IN UNDISTURBED CONSCIOUS PIGEONS WITH EYES SHUT.

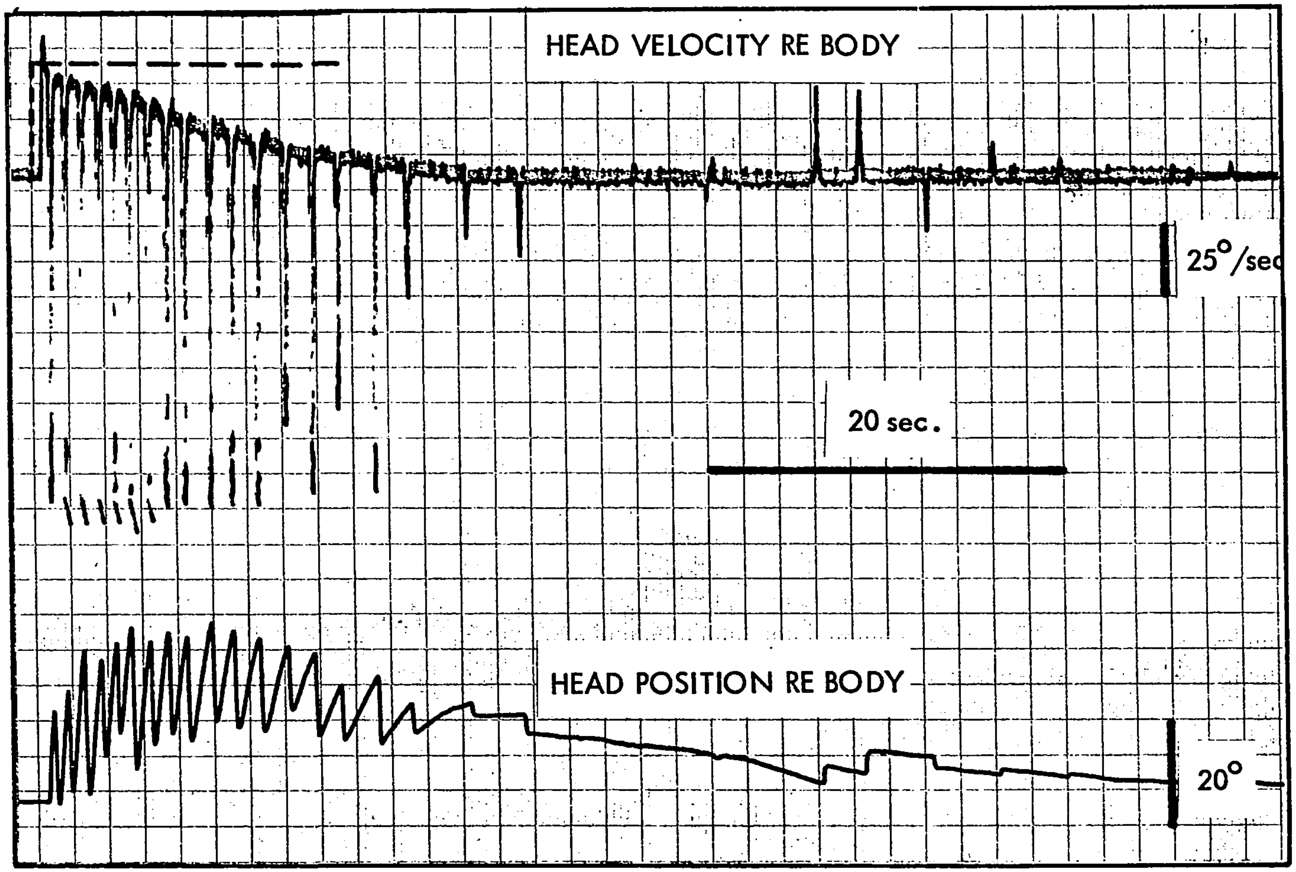


Fig. 10-5 c VESTIBULO-COLLIC REFLEX RESPONSE TO STEP CHANGE IN BODY ANGULAR VELOCITY IN UNDISTURBED CONSCIOUS PIGEON (EYES SHUT)

The dashed line in the upper record indicates the magnitude of the velocity step.

saccades and often none at all. The time course of slow phase head velocity during the slow return phase appears to be variable, but owing to the lack of recording resolution in these experiments, it was not possible to assess this return phase with great accuracy. In Fig. 10-5C head velocity relative to the table is shown in addition to head position. The decaying time course of slow-phase head velocity thus illustrated is very similar in its general form to the time course of slow-phase eye velocity following a step change in head angular velocity. However as noted earlier, head nystagmus always occurs in the lagging quadrant whereas the corresponding eye nystagmus in the vestibulo-ocular response occurs in the leading quadrant.

10.4 ANALYSIS OF THE RESPONSES OF UNDISTURBED CONSCIOUS PIGEONS

In four pigeons the responses to sinusoidal and step changes in table velocity were examined under quiet conditions, measures being taken to minimize all noise in the experimental room and in particular to avoid any sudden sharp noises. Before each new stimulus a period of 1-2 minutes was allowed to permit the pigeon to recover from the effects of the inevitable slight noises associated with changing the experimental conditions.

Sinusoidal rotation stimuli used were in the frequency range 0.0065-1.9 Hz. with amplitudes varying from 10 - 100°/sec. peak. Examples of the recorded responses have been shown in Fig. 10-1. In order to obtain a quantitative description of the functional efficiency of the response at different frequencies, the records were analyzed to find the frequency response of slow-phase head velocity in a manner analagous to that customarily used in analysis of the vestibulo-ocular response, the objective being to characterize the response in terms of the phase and, where possible, the amplitude of the sinusoid yielding the best fit to the sequence of slow-phase velocity segments. In three of the four experiments, in which head velocity was not recorded on-line, phase alone was measured, and this was computed from measurements of the distance between the points of zero table velocity and the points of zero head velocity. The results of these experiments are shown in

Fig. 10-6 in curves A, B, C, and CC, the two latter being obtained from the same animal. In the fourth experiment (Curves D and DD) head velocity relative to the table was obtained by on-line differentiation and recorded at the time of the experiment. In this case, a number of cycles of the response to each stimulus frequency were analyzed for amplitude as well as phase shift by cyclic averaging of the slow-phase portions of the head velocity record. The averaging was done graphically, and a sinusoid was fitted to this average by linear regression. The phase data from this experiment, shown as curves D and DD in Fig. 10-6, are replotted in Fig. 10-7 along with the corresponding estimates of the amplitude ratio , that is, the ratio of the amplitudes of slow-phase head velocity relative to table and table velocity.

Despite considerable variability, the phase data of Fig. 10-6 show a distinct tendency to cluster, and may be fitted approximately to the phase characteristic of the transfer function

$$\frac{\dot{\theta}_H - \dot{\theta}_B}{\dot{\theta}_B}(s) = \frac{181.8\ Ks^2}{(9.0s + 1)\ (20.2s + 1)} \qquad \text{............Eq. 10.1}$$

where K is an unknown constant and 181.8 is the product of the two time constants. The corresponding phase frequency characteristic is shown as a dashed line in the figure. This transfer function was obtained by iterative adjustment of the time constants to minimize the square error, and provides a rough fit, intended only as a crude means of quantitating the general trend of the data. It should be noted that the significance of the long time constant (20.2 sec.) so obtained is questionable because of the paucity of low-frequency data. However the inclusion of this term in the model is necessary because phase shift in excess of 90° occurred at low frequencies, and this cannot be explained on the basis of a simple first-order model. The gain frequency plot corresponding to Eq. 10.1, with K equal to 0.7, is shown in asymptotic form as a dashed line in Fig. 10-7, superimposed on the amplitude data from one pigeon. The fit at low frequencies is poor, a fact which may be attributable to individual variation, although it seems likely that in subsequent studies a more complex model will be required to relate phase and amplitude data.

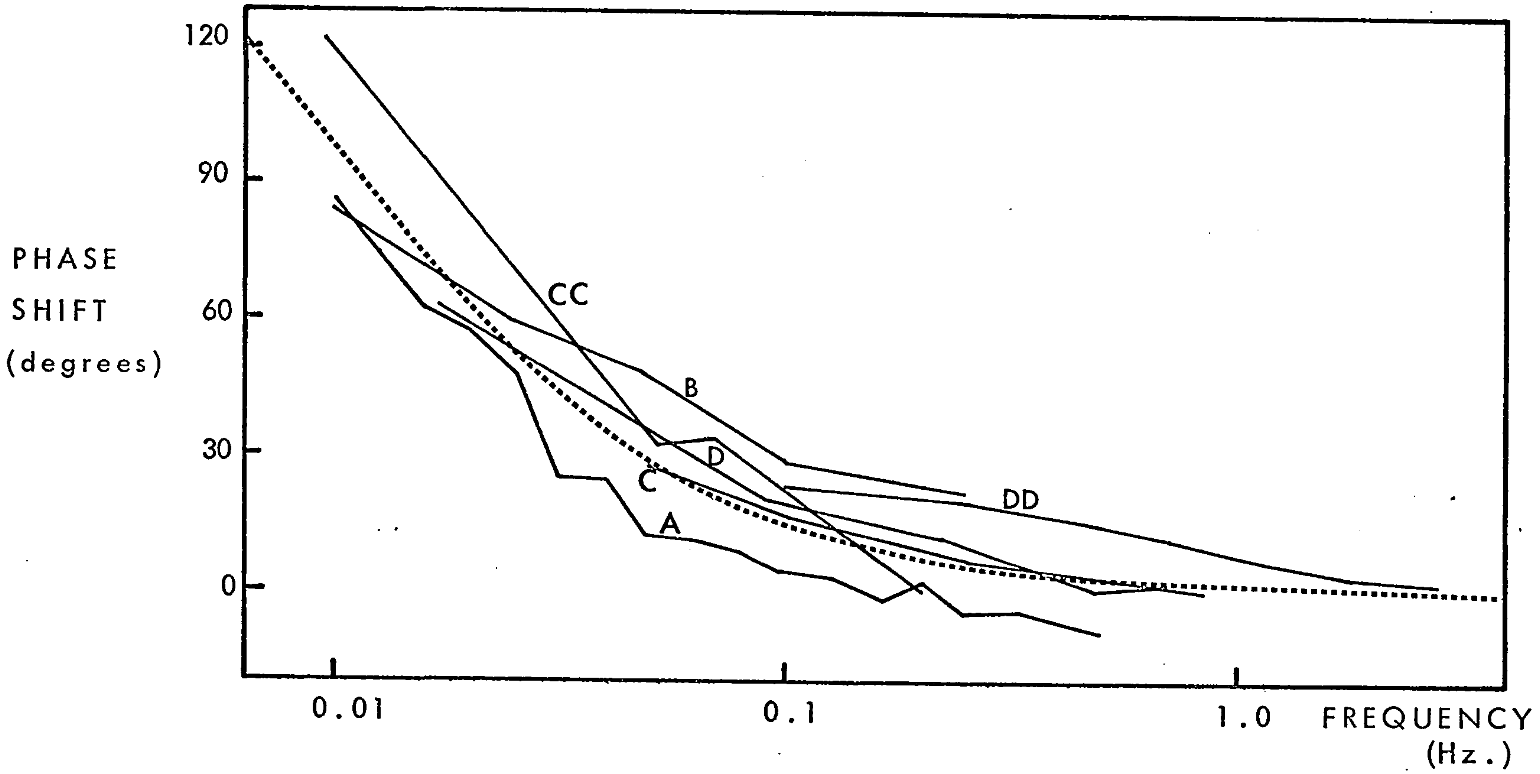


FIG. 10-6 PHASE SHIFT OF SLOW PHASE HEAD VELOCITY RELATIVE TO TABLE VELOCITY IN UNDISTURBED CONSCIOUS PIGEON, AS A FUNCTION OF SINUSOIDAL FREQUENCY. Phase shift is measured between slow-phase head velocity and table velocity. Solid lines: experimental results in four pigeons; dotted line: response of second order system having time constants of 9.0 and 20.2 seconds.

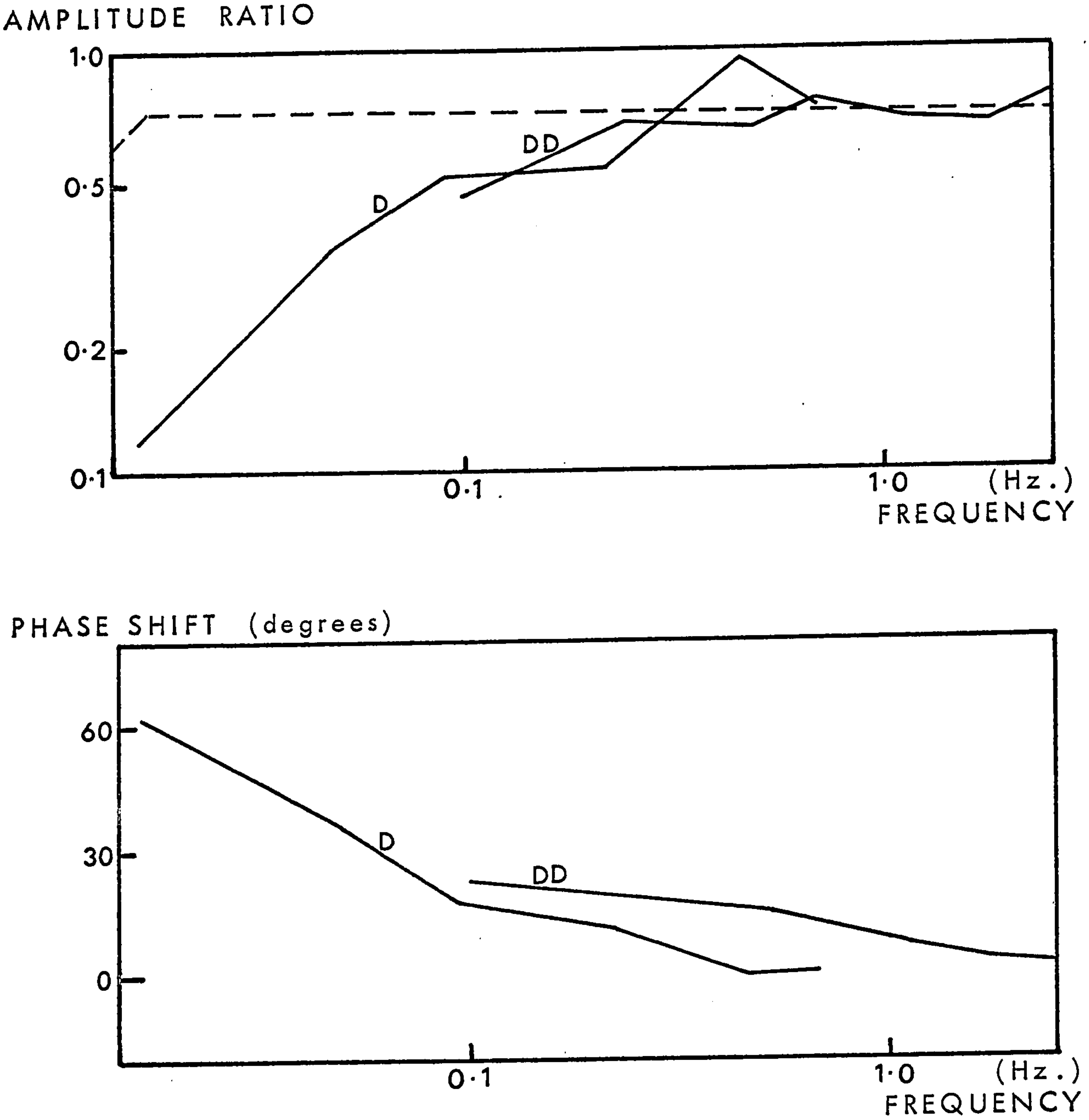


Fig. 10-7 GAIN- AND PHASE-FREQUENCY RESPONSE OF THE VESTIBULO-COLLIC SYSTEM IN ONE CONSCIOUS, UNDISTURBED PIGEON. Amplitude ratio and Phase of slow-phase head velocity $(\dot{\theta}_H - \dot{\theta}_B)$ relative to table velocity $(\dot{\theta}_B)$.

The shorter time constant of 9.0 seconds appearing in Eq. 10.1 may be accepted with less reservation as characterizing the response in most of the frequency range examined, and will serve as a rough means of comparing frequency response with transient response, and in particular of comparing vestibulo-collic and vestibulo-ocular responses in the pigeon. Note that owing to the presence of feedback in the vestibulo-collic system, the time constants of Eq. 10.1 cannot be related to open-loop time constants such as those of the semicircular canal withoutr further knowledge of components in the feedback loop.

Detailed analysis was made of the responses of two pigeons to small step changes in table angular velocity, the size of the steps varying from 28 to 56°/sec. Records of head position relative to table, obtained on a pen recorder, were analyzed by measuring the average slope during each slow-phase interval. Slow-phase velocities so calculated were normalized with respect to the magnitude of the step change in table velocity, to obtain for each individual step response a curve similar to Fig. 10-8. Each horizontal segment in this curve corresponds to a single slow-phase interval. Three such curves, corresponding to three step responses, were obtained for each pigeon, and were ensemble averaged using a time interval of one second. The resultant data are shown in Fig. 10-9 (dots) and are labelled A and B to indicate that they were obtained from the pigeons whose phase data are correspondingly labelled in Fig. 10-6. The averaged step-response data were fitted to dual-exponential functions by the iterative least-squares method of Hazelrig, Ackerman and Roseyear (1961) and the results are shown in Table 10-1, and as solid curves in Fig. 10-9.

The phase frequency characteristics corresponding to the transfer functions fitted to the observed transient responses are shown in Fig. 10-10, superimposed upon the observed phase data, and the step response corresponding to the transfer function fitted to the observed phase data is plotted in Fig. 10-11, superimposed upon the observed averaged step responses. In each case the agreement is fairly good in the portion of the respective graph which is dominated by the short time constant, i.e., in the mid-frequency range (0.6 - 1.0 Hz.) in Fig. 10-10 and in the low-time range in Fig. 10-11. The failure in the low-frequency (long-time) range is to be expected since insufficiently low frequencies of sinusoidal

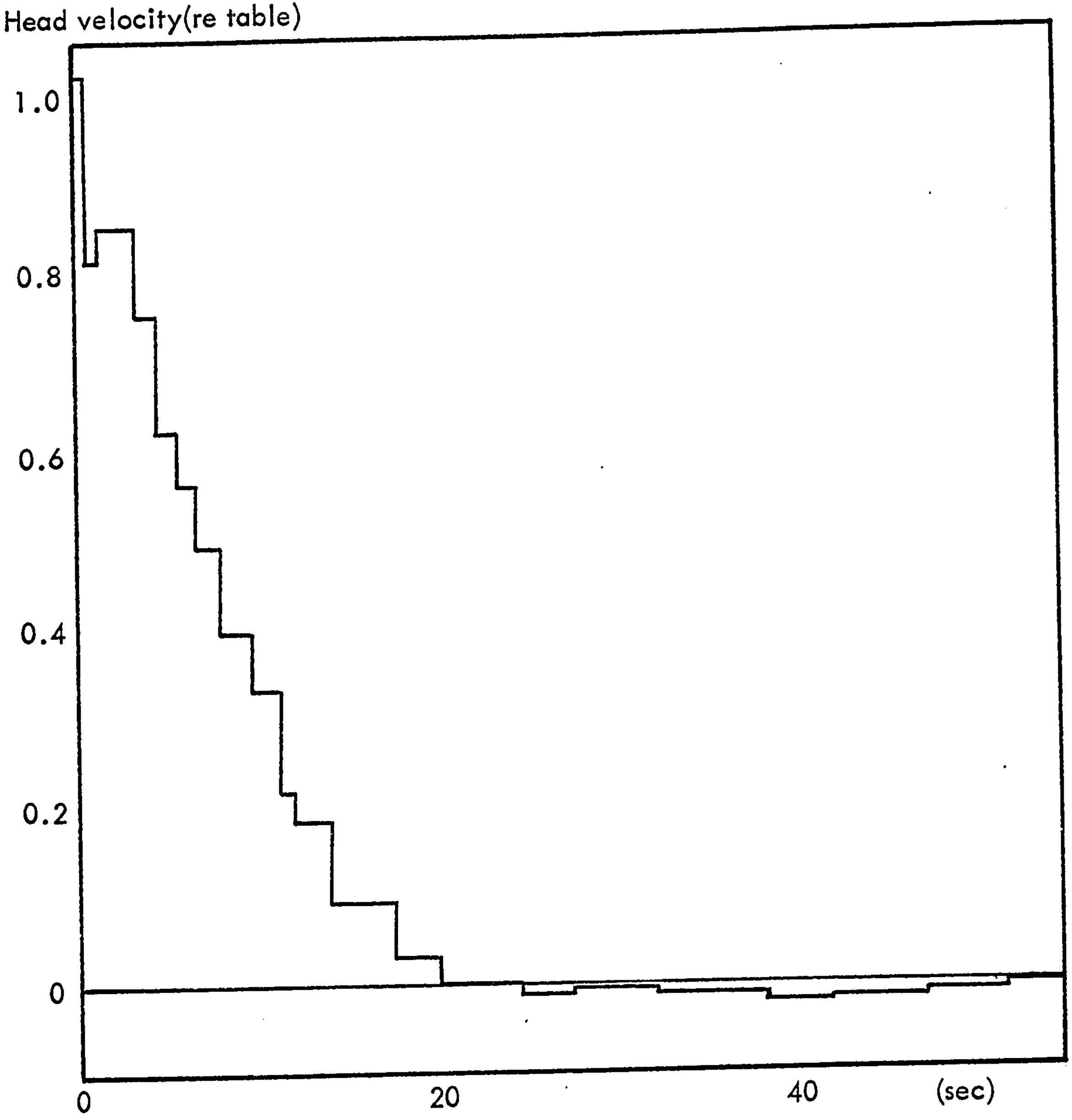


Fig. 10-8 NORMALIZED VELOCITY STEP RESPONSE OF PIGEON VESTIBULO-COLLIC SYSTEM - An example of data obtained by measuring slow-phase slopes and normalizing with respect to the magnitude of the table velocity step (30.7 °/sec in this case). Each horizontal segment corresponds in time to a single slow-phase interval.

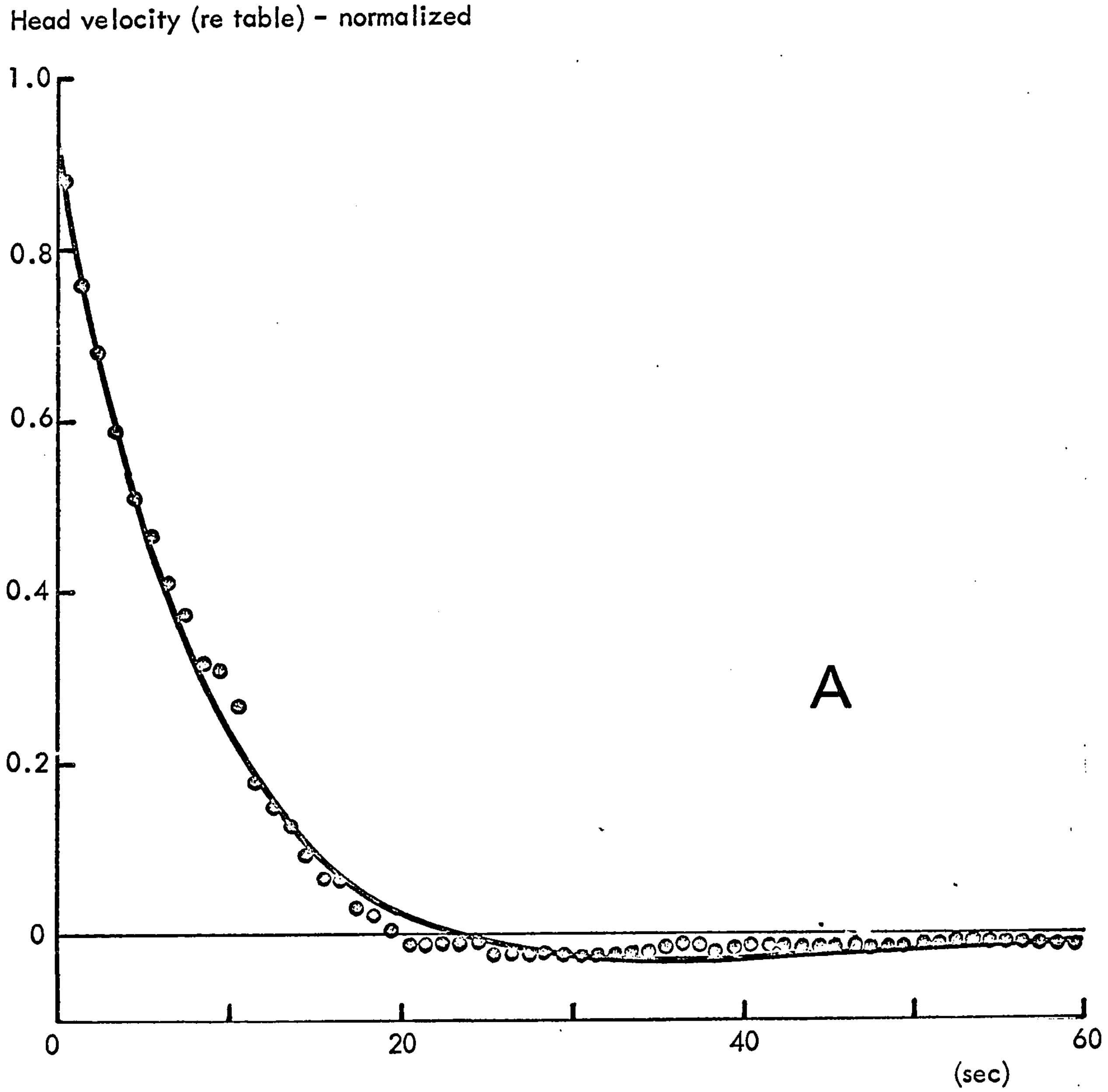


Fig. 10-9 (a) PIGEON VESTIBULO-COLLIC STEP RESPONSE - AVERAGED

Dots - values obtained by averaging, over one second intervals, the slow-phase head velocity data from three step responses in one pigeon. (original data as in Fig. 10-8); Solid Lines - fitted curve, $\dot{\theta}_H - \dot{\theta}_B = 1.5\, e^{-t/9.8} - 0.51\, e^{-t/17.4}$.

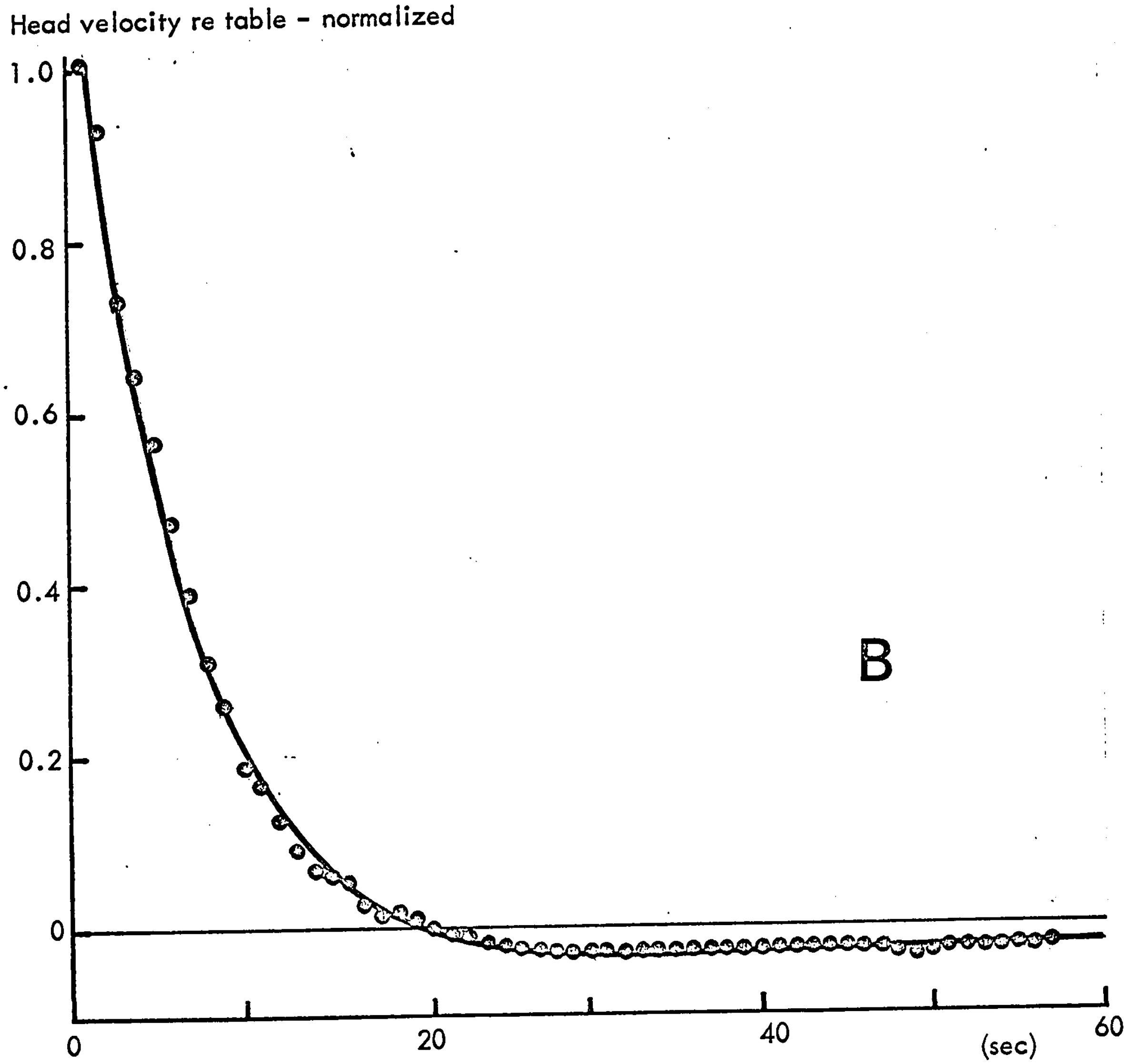


Fig. 10-9 (b) PIGEON VESTIBULO-COLLIC STEP RESPONSE - AVERAGED

Dots - averaged data from three step responses in one pigeon;

Solid Lines - fitted curve, $\dot{\theta}_H - \dot{\theta}_B = 1.6\, e^{-t/7.2} - 0.37\, e^{-t/12.9}$.

CURVE A	Step Response	$h_{-1}(t) = 1.5\,e^{-t/9.8} - 0.5\,e^{-t/17.4}$
	Transfer Function	$H(s) = \dfrac{5.3s(30.3s+1)}{(9.8s+1)(17.4s+1)}$
CURVE B	Step Response	$h_{-1}(t) = 1.6\,e^{-t/7.2} - 0.37\,e^{-t/12.9}$
	Transfer Function	$H(s) = \dfrac{7.0s(16.8s+1)}{(7.2s+1)(12.9s+1)}$

Table 10 - 1 FUNCTIONS FITTED TO THE PIGEON VESTIBULO-COLLIC STEP RESPONSE OF Fig. 10 - 9.

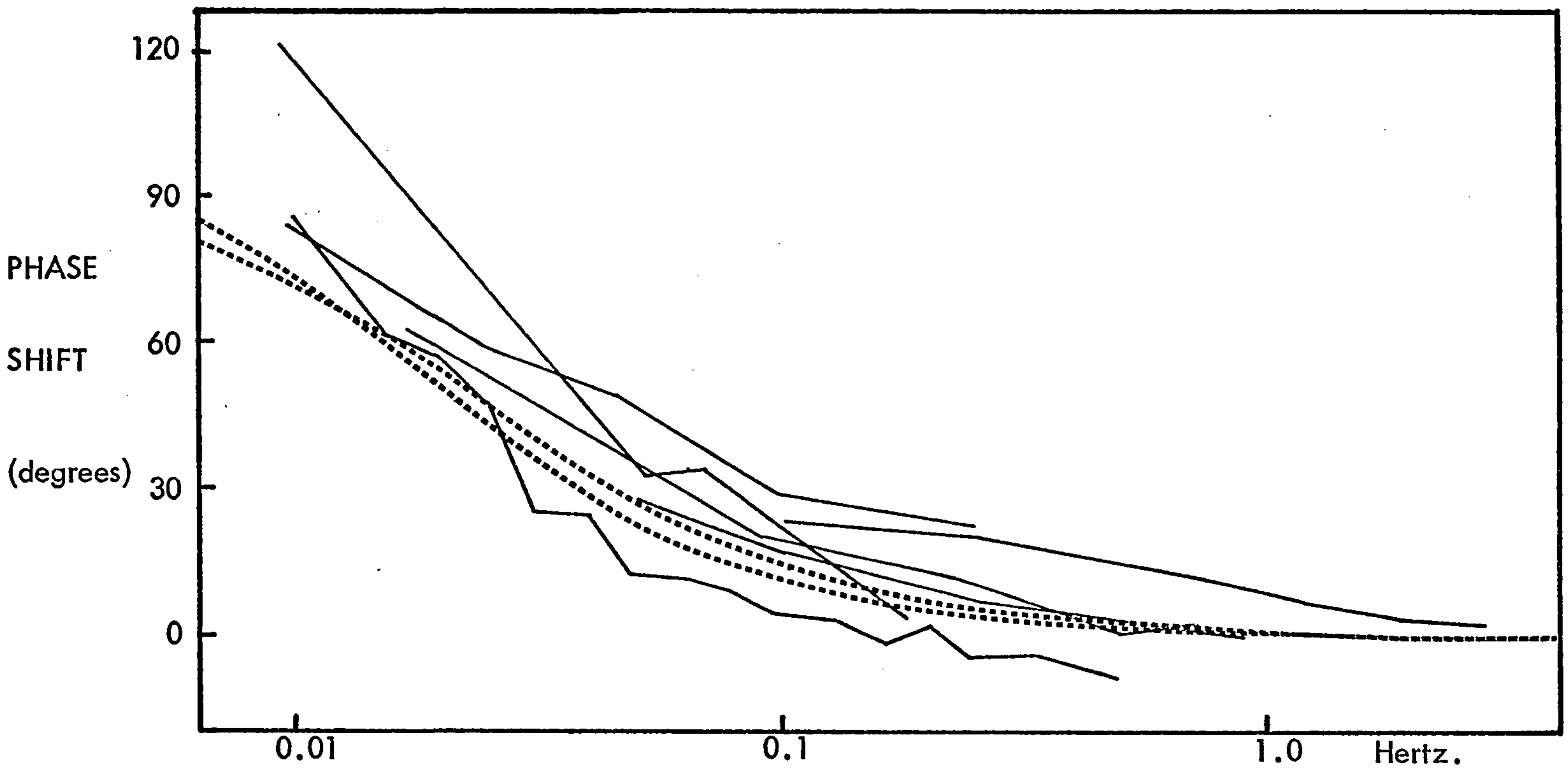


Fig. 10-10 PHASE-FREQUENCY RELATIONSHIPS IN THE PIGEON VESTIBULO-COLLIC SYSTEM
Dotted Lines - phase-frequency characteristic predicted from observed step responses;
Solid Lines - observed phase advance of slow-phase head velocity relative to table velocity.

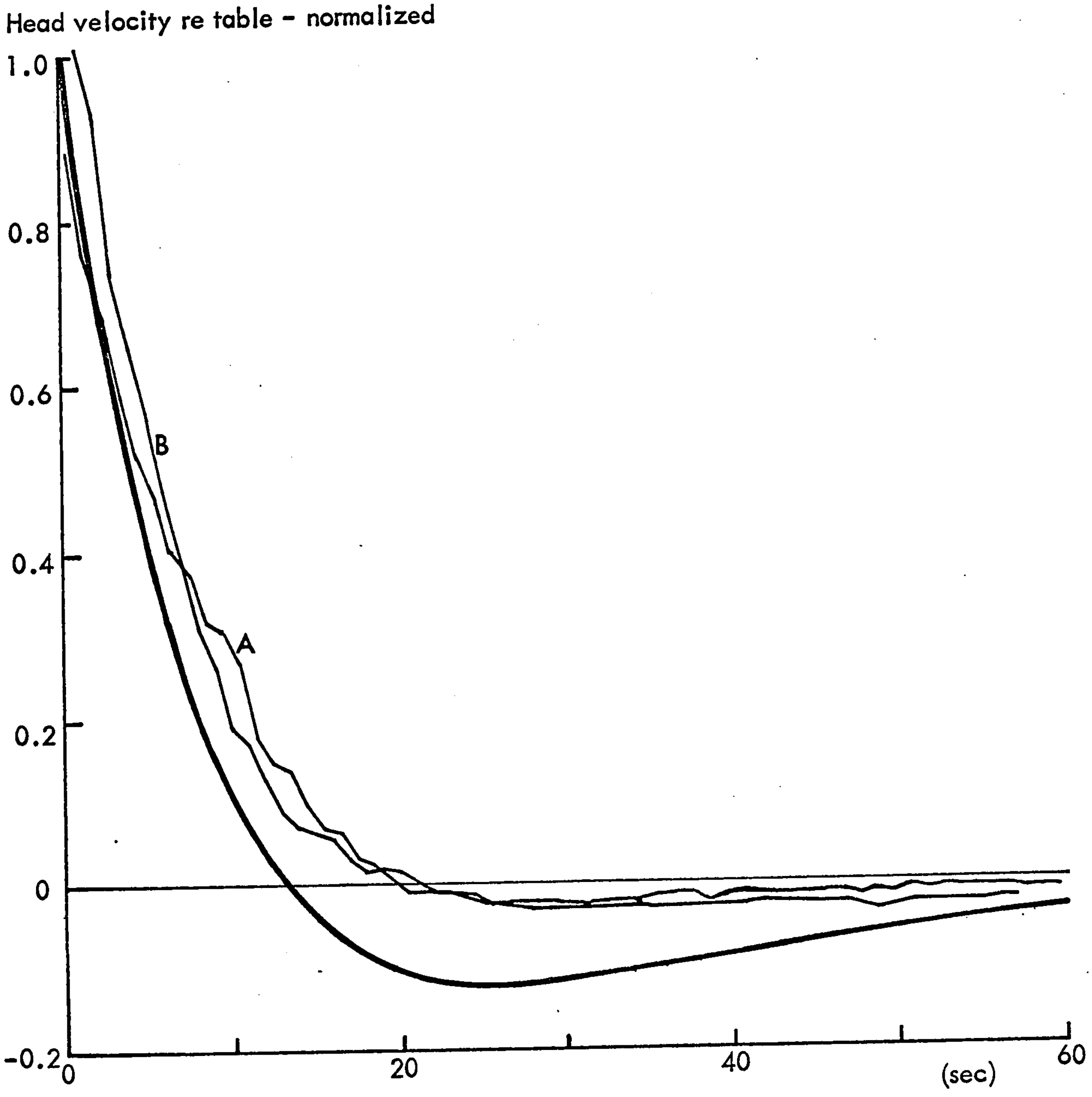


Fig. 10-11 PREDICTED vs. OBSERVED STEP RESPONSE IN THE PIGEON VESTIBULO-COLLIC SYSTEM. Smooth Curve - Step response predicted from observed sinusoidal frequency response; Irregular curves - averaged step response data from two pigeons.

stimulation were applied.

The analysis thus suggests that, under the conditions of these experiments, the relationship between slow-phase head velocity (relative to table) and table velocity in the vestibulo-collic system of the pigeon may be modelled approximately by a linear dynamic system whose mid-frequency behaviour is dominated by a time constant of about 9 seconds and has a high-pass characteristic with a high frequency gain of slightly more than unity. The latter estimate derives from the functions fitted to the observed step responses and is equivalent to the zero-time intercept of the normalized step-response. It should be emphasized however that considerable variation undoubtedly exists both between individuals and between the responses of the same individual on different occasions. Such variation is exemplified in Fig. 10-6 and Fig. 10-7, and is expected on theoretical grounds to be greater in the vestibulo-collic system than in the vestibulo-ocular system because of the feedback which exists in the former.

The transient and frequency response characteristics of slow-phase head velocity in the vestibulo-collic system in pigeons are strikingly similar to the corresponding response characteristics of slow-phase eye velocity in the vestibulo-ocular system in cats and man. It therefore becomes of great interest to know the value of the long time constant of the semicircular canal in the pigeon. This question is considered in the next chapter, in which experimental evidence from studies of the pigeon's vestibulo-ocular system is presented, suggesting that the canal time constant is about two seconds in these birds. Thus in the undisturbed conscious pigeon the vestibulo-collic system response seems to be extended in the low frequency direction as compared with the response of the semi-circular canal, apparently bearing out a conjecture made on theoretical grounds in Section 7.5.

Further discussion of these and other experimental findings in the pigeon vestibulo-collic system is deffered to the end of the next chapter.

10.5 VESTIBULO-COLLIC RESPONSE IN DECEREBRATE AND DRUGGED PIGEONS

In studying the vestibulo-collic response in intact conscious pigeons two difficulties arose, namely: (1) while it was possible to obtain a fairly steady level of arousal by simply minimizing the levels of acoustical noise in the surroundings, it was not possible to examine the system at different levels of arousal; and (2) it was not possible to obtain a non-saccacadic response except with high frequency sinusoidal inputs. Examination at different levels of arousal is desirable in order to test the hypothesis made in Section 7.5 that arousal affects loop gain and hence closed-loop system performance, and examination of the non-saccadic response should considerably simplify some aspects of system identification. An investigation was therefore made of the effects of decerebration, ether anaesthesia and amphetamine administration, in order to assess the possible usefulness of these procedures. Three pigeons were used, one for each condition.

Decerebration was achieved using the methods outlined in Section 8.5, care being taken to avoid damage to the prominent optic lobes. Examination of the pigeon was begun about two hours after the operation, at which time bleeding from the operative site had apparently ceased, and the bird's condition had stabilized. The pigeon's standing posture was symmetrical with the body and wings held rather lower to the ground than usual. At rest the head was held deviated to the left about 20 degrees, a finding which persisted throughout the experiment. When dropped in an upright position from a height of about 6 inches, the pigeons landed on its feet but teetered a bit before coming to a stable position. Head compensation for hand-held rotation about three axes was apparently normal but reduced in magnitude; the pigeon vomitted after vigorous multi-axis rotation. After a period with no stimulation, horizontal rotational inputs were applied on the turntable in the usual way. Samples of the sinusoidal response obtained at this stage are shown in Fig. 10-12. The responses differed from those seen in intact, conscious pigeons in that saccadic head movements were less abrupt in onset and offset and of lower velocity than normal. Accoustical noise in the room had very little effect on the response. Response gain appeared to be stable over a period of approximately two hours, during which time two sinusoidal frequency response runs were made. The gain and phase relationships between slow-phase head velocity ($\dot{\theta}_H - \dot{\theta}_B$, recorded on-line) and table velocity were measured as described in the previous section and are shown in Fig. 10-13. The results of the two runs are similar, and are not remarkably different from the results obtained in intact, conscious pigeons, although the data are insufficient for any conclusions to be drawn on this question. A step response obtained early in the

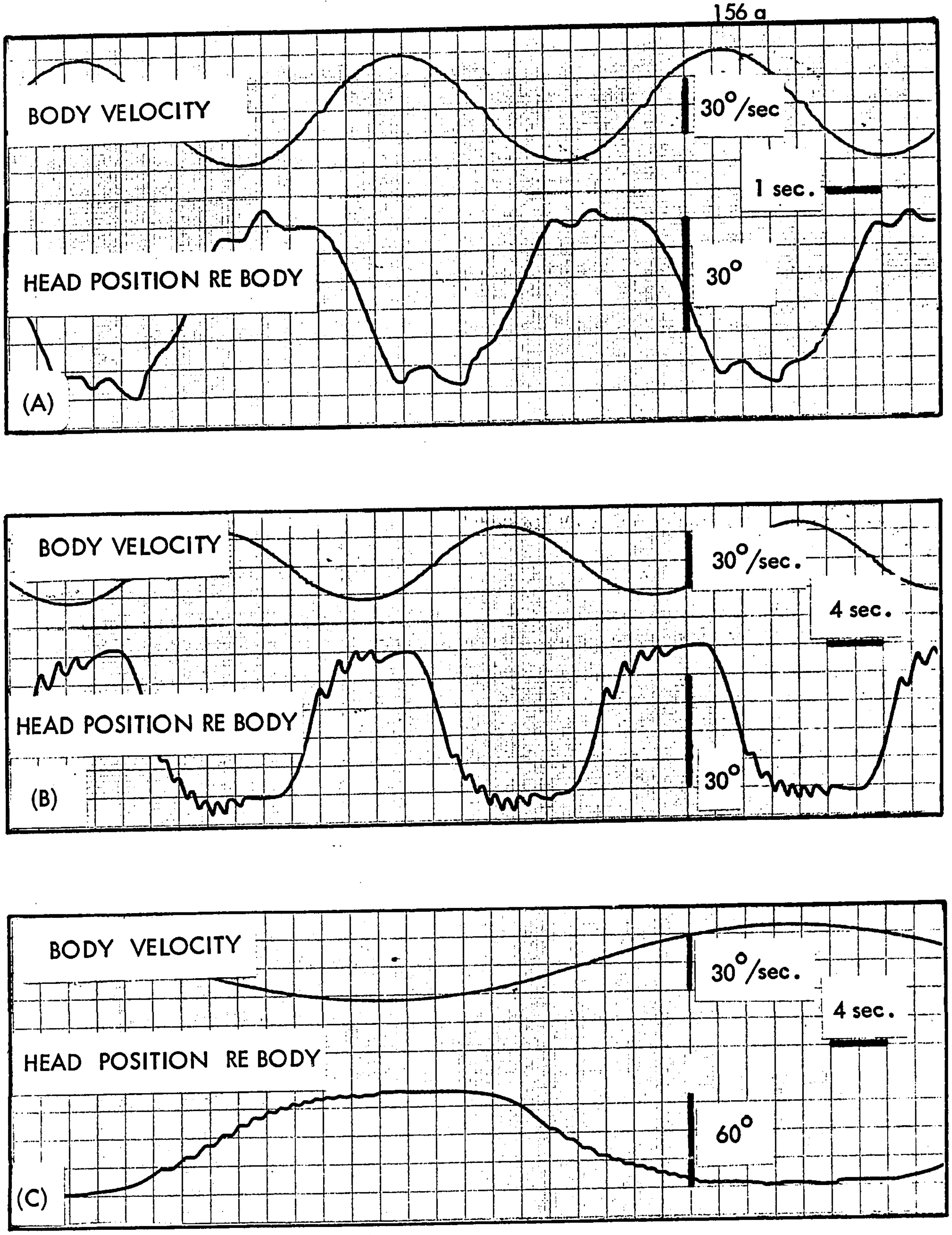


Fig. 10-12 RESPONSES OF THE VESTIBULO-COLLIC SYSTEM TO SINUSOIDAL OSCILLATION IN DECEREBRATE PIGEON.

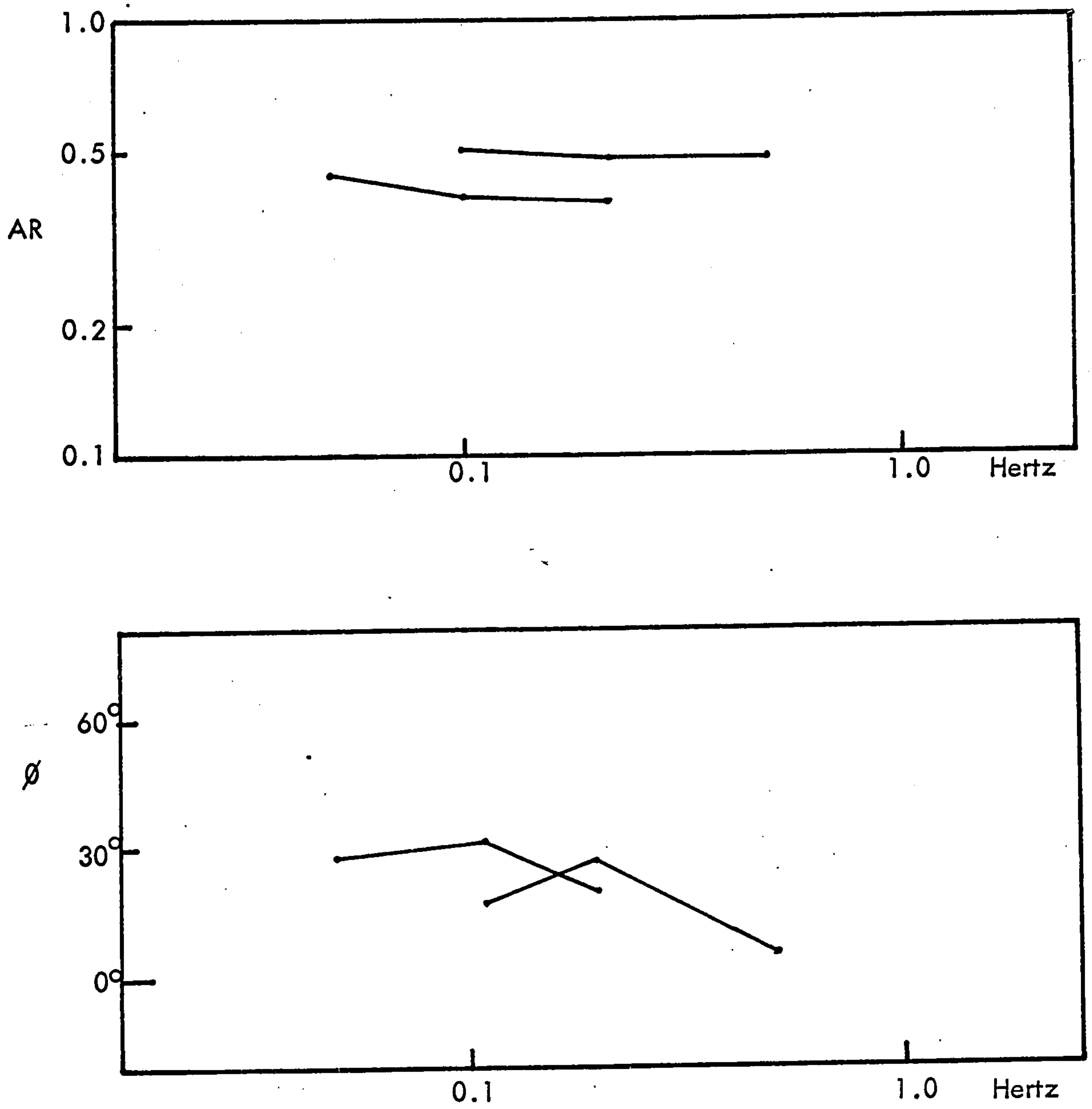


Fig. 10-13 FREQUENCY RESPONSE OF THE VESTIBULO-COLLIC SYSTEM IN A DECEREBRATE PIGEON. AR - amplitude ratio, and Ø - phase shift of the sinusoid describing slow-phase head velocity compared to sinusoidal table velocity.

experiment is shown in Fig. 10-14. Following these stimuli, vomitting was unintentionally induced during a period of high-amplitude oscillation of the turntable, and subsequently the response was even less vigorous, with very few saccades. An example of the step response during this latter interval is shown in Fig. 10-15; response is almost entirely non-saccadic, the small oscillations in head position appearing on the record being due to head movements associated with respiration. Such movements were commonly seen at low levels of arousal, when the pigeon's head was retracted and held very close to the body.

The effects of ether were studied in an intact pigeon by administering the anaesthetic by nose cone until the head just began to sag, following which the response to turntable rotation was examined and compared with the pre-anaesthetic response. Segments from a record of the sinusoidal response before and during the recovery from anaesthesia are shown in Fig. 10-16, and velocity step responses before and after ether are shown in Fig. 10-17. Immediately after ether (Fig. 10-16) saccades were almost entirely absent, and the response magnitude was low. Saccades reappeared gradually in a "blunted" form and became progressively larger and sharper as the effect of ether wore off. The changes are reminiscent of the response variations which occur in the vestibulo-ocular system with different levels of ether anaesthesia (Sugie & Jones, 1966).

In a third pigeon Metamphetamine (1 mg.) was administered intraperitoneally after a control recording of the response to sinusoidal rotation at various frequencies. Following the injection there was no apparent change in the response of the undisturbed bird to sinusoidal oscillation, but it became very irritable, so that slight noises in the room would evoke violent head-shaking behaviour, apparently in an attempt to dislodge the pick-up coil mounted on the head. Such head-shaking occurred occasionally in normal pigeons, but only after considerable provocation. Thus amphetamine appeared to result in wider fluctuations in arousal than were displayed by normal animals, suggesting that the drug is unsuitable for achieving a sustained high-level of arousal in pigeons. However the drug has been used successfully for this purpose in cats (Crampton, 1962), and the possibility of its use in birds should not be discarded without further study.

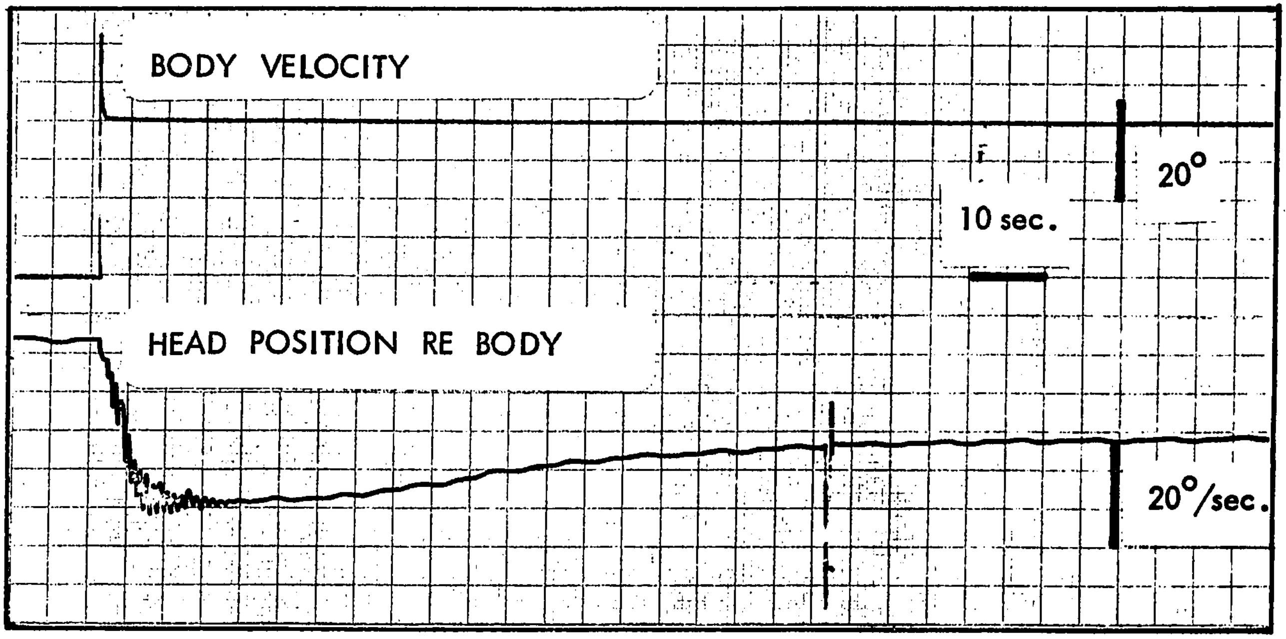
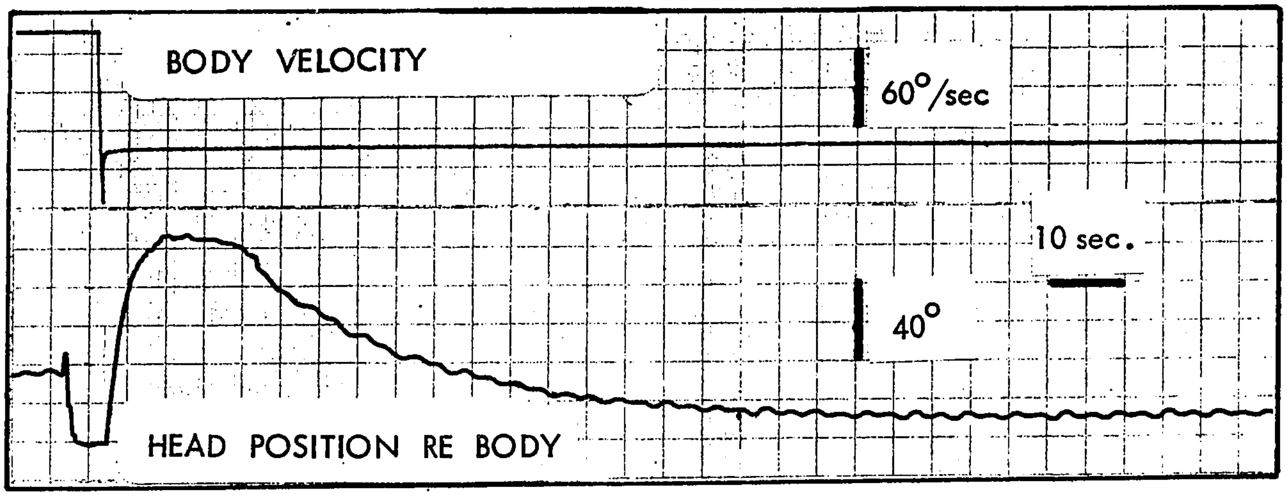


Fig. 10-14 SACCADIC RESPONSE OF THE VESTIBULO-COLLIC SYSTEM IN A DECEREBRATE PIGEON TO A STEP CHANGE IN BODY ANGULAR VELOCITY.



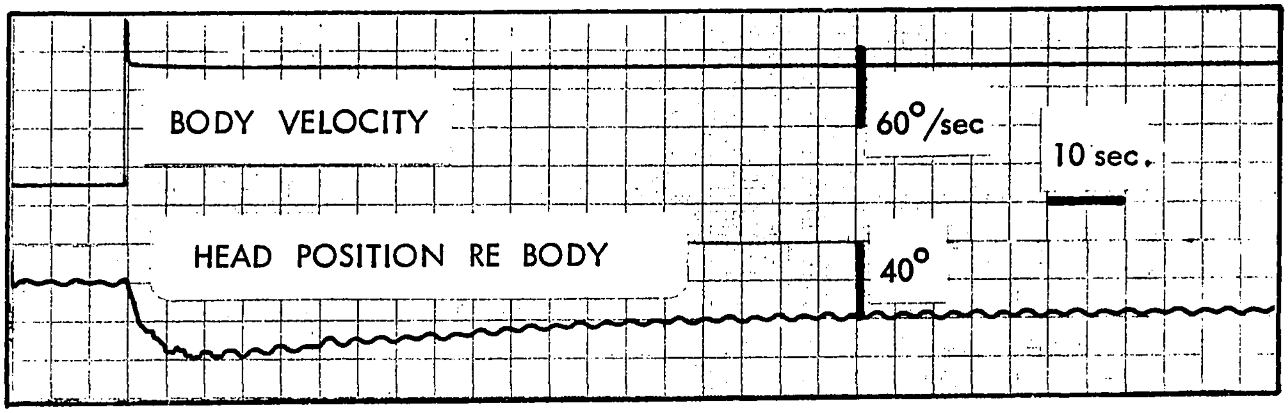
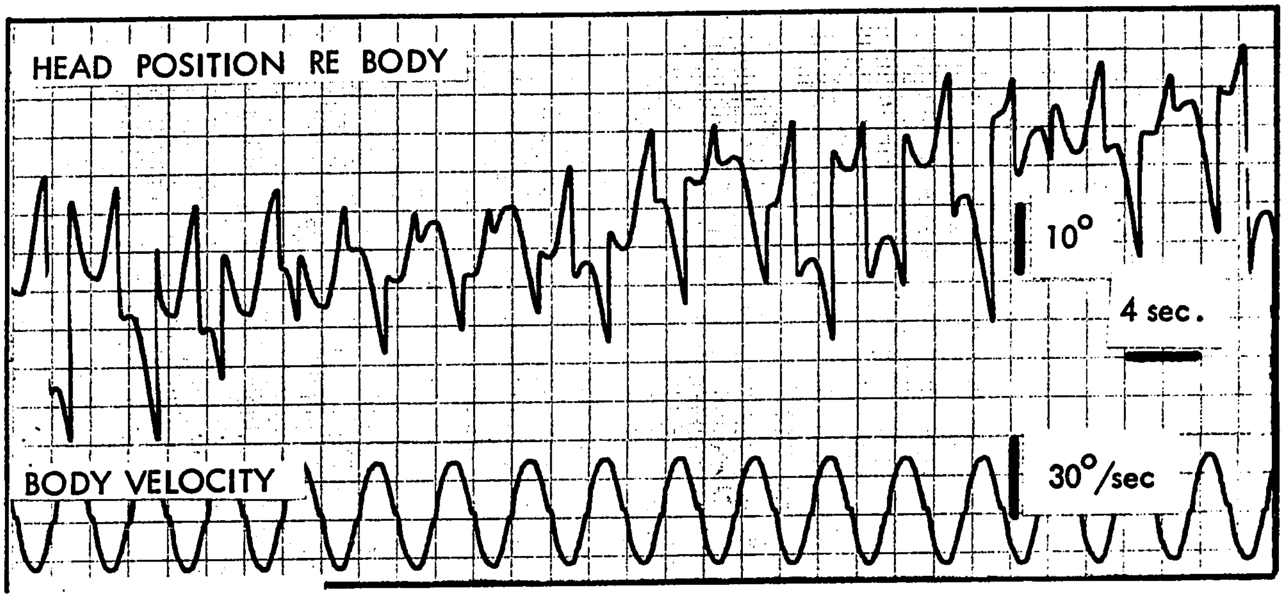
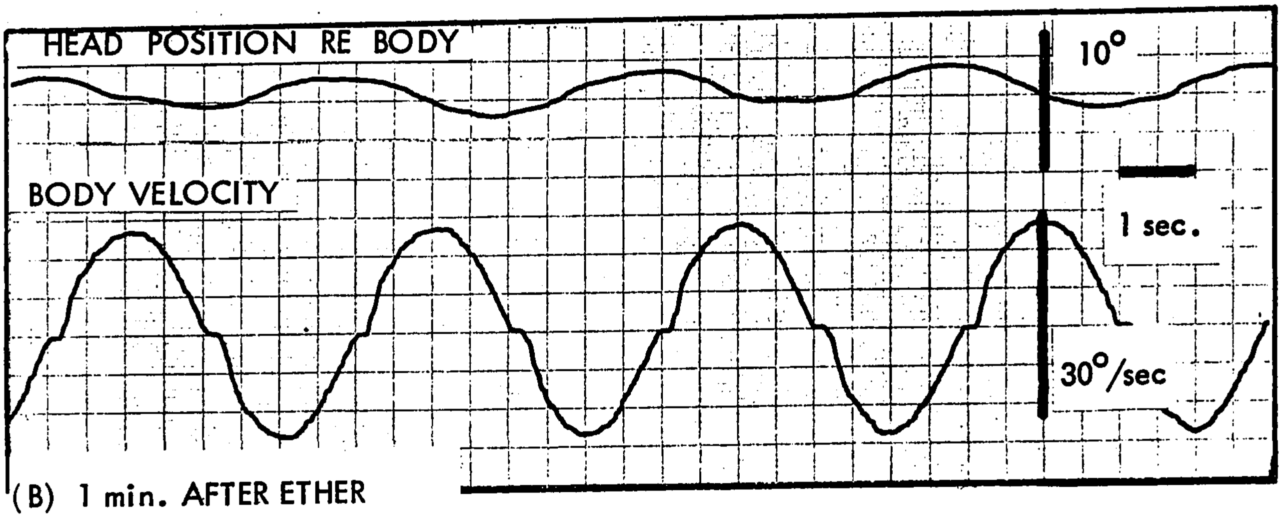


Fig. 10-15 NON-SACCADIC RESPONSES OF THE VESTIBULO-COLLIC SYSTEM IN A DECEREBRATE PIGEON.

The persistent, low-amplitude, oscillatory head movements were associated with respiratory movements.

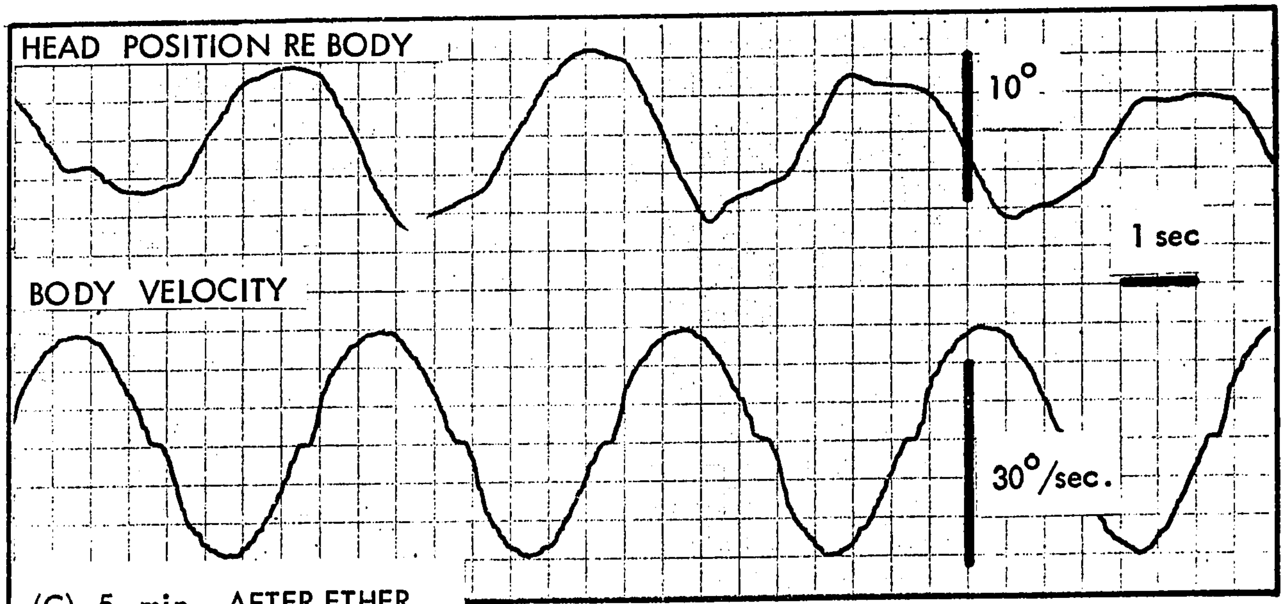


(A) BEFORE ETHER

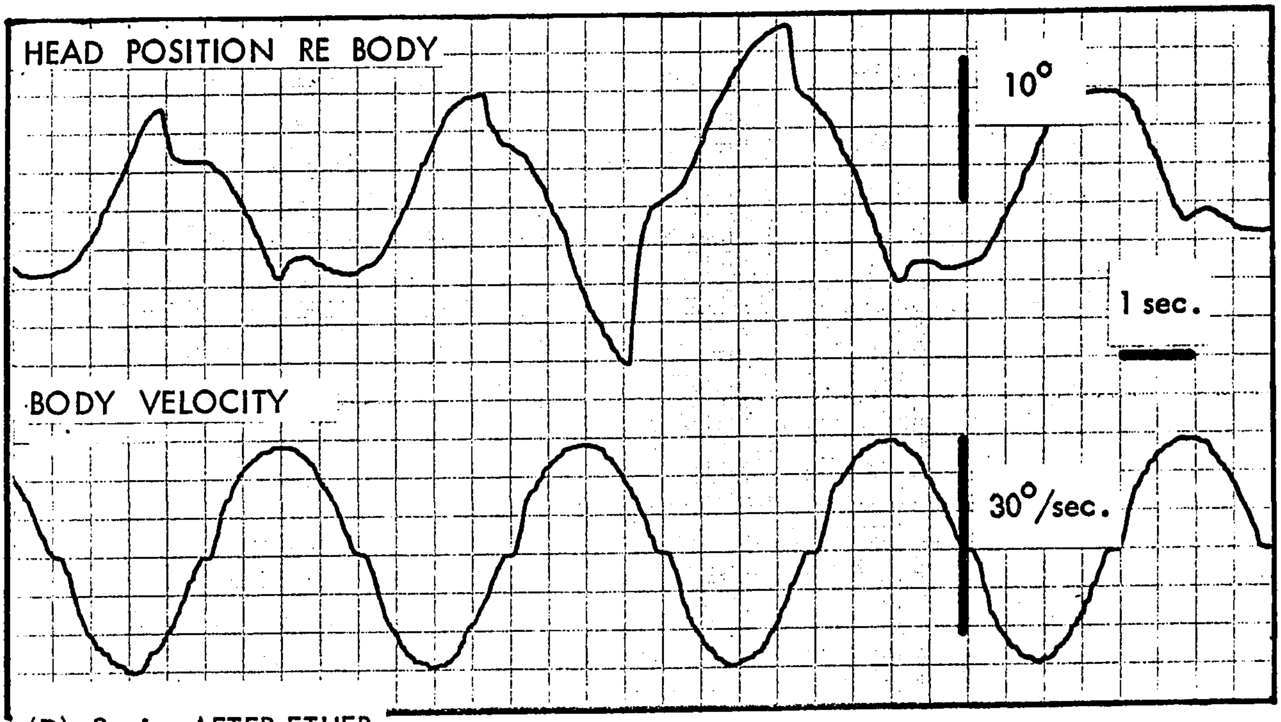


(B) 1 min. AFTER ETHER

Fig. 10-16 EFFECT OF ETHER ON VESTIBULO-COLLIC RESPONSE OF BLINDFOLDED PIGEON. A - before ether; B-D - records made 1, 5 and 9 seconds after ether administration, showing disappearance and reappearance of saccades.

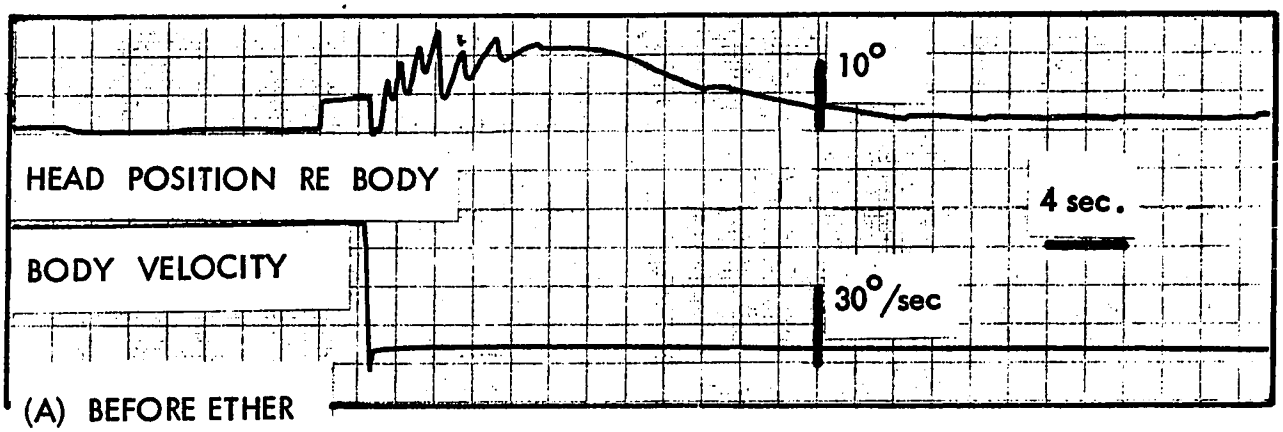


(C) 5. min. AFTER ETHER

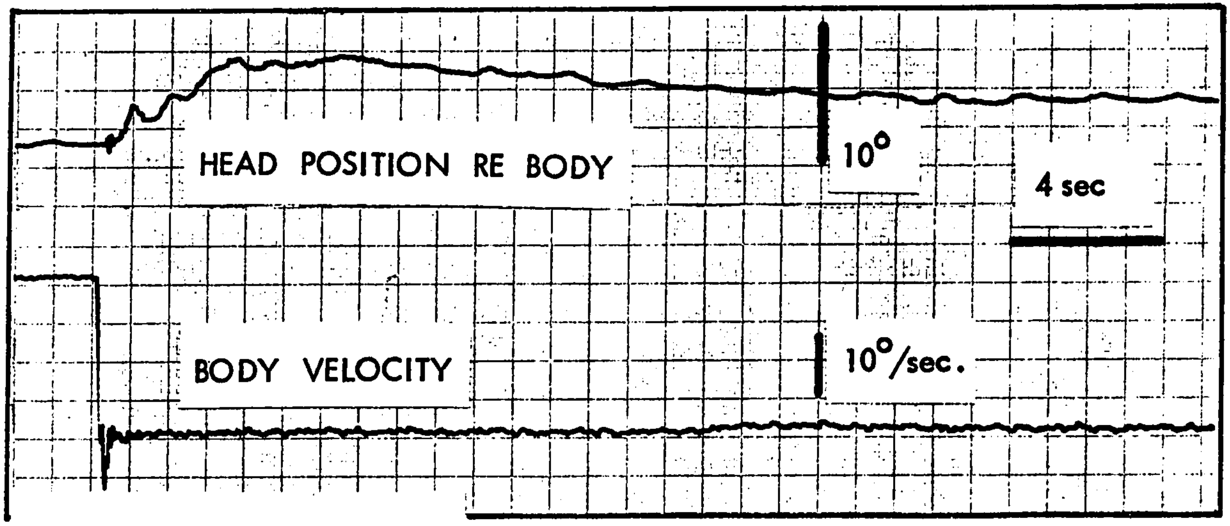


(D) 9 min AFTER ETHER

Fig. 10-16 (continued) VESTIBULO-COLLIC RESPONSE IN PIGEON -- EFFECT OF ETHER.



(A) BEFORE ETHER



(B) 5 min. AFTER ETHER

Fig. 10-17 EFFECT OF ETHER ON THE RESPONSE OF THE VESTIBULO-COLLIC SYSTEM IN A BLINDFOLDED PIGEON TO A STEP CHANGE IN BODY ANGULAR VELOCITY.

The small residual oscillations in the latter portion of the head position record in (B) were persistent, and appeared to be related to respiratory movements.

The results with ether anaesthesia and decerebration are more encouraging, and it seems clear from the experiments described that these procedures will be useful in future studies. Both anaesthesia and decerebration appear to result in reduced system gain and reduced saccade amplitude . Of the two, decerebration is perhaps the most promising since it yields a more stable preparation.

CHAPTER II

PIGEON VESTIBULO-OCULAR RESPONSE AND THE ESTIMATION OF SEMICIRCULAR CANAL PARAMETERS

11.1 INTRODUCTION

It is evident from the experimental and theoretical studies described above that in order to understand the operation of the vestibulo-collic system and to appreciate its functional role, it is essential to have reliable knowledge of the dynamic response characteristics of the semicircular canals in the species under study, in this case the pigeon. At the present stage it is particularly important to know the long time constant (of cupular restoration) of the pigeon's horizontal canal. Two previous estimates, by Mayne (1950) and Schierbeck (1953), are to be found in the literature, but these must be rejected on theoretical grounds. An experimental study has therefore been made of the vestibulo-ocular response in the pigeon, yielding a new and more realistic estimate of the desired parameter.

Schierbeck (1953) attempted to estimate the long time constant of the pigeon horizontal canal using the method of cupulometry (see Section 3.4.3) applied to observations of head nystagmus. He measured the duration of post-rotational head nystagmus in a hooded pigeon in response to step changes in turntable velocity of various magnitudes, and plotted the logarithm of the step magnitude as a function of the duration of nystagmus. The results were somewhat irregular and he does not quote an average value for the "time constant" so obtained. As pointed out in the theoretical discussion of Section 7.5, the time constant of the canal cannot be obtained in this way from a system such as the vestibulo-collic reflex in which the canal operates in a feedback path.

The estimate of Mayne (1950) is based on analysis of observations made by Mowrer (1935) who recorded the latency of onset of head movements in pigeons exposed to step changes in angular acceleration. Mayne assumed that there was a threshold cupula deviation below which no reflex response would occur, and argued that the onset of head movements in Mowrer's experiments could therefore be interpreted as indicating the time when the cupula reached this threshold deviation. From the torsion pendulum model he derived an equation relating the latency to the magnitude of the acceleration step and fitted this to Mowrer's data, obtaining a value of 8.3 seconds for the long time constant.

The validity of the analysis depends on the nature of the threshold effect. If, as Mayne assumed, there is a true threshold in the mechanical-to-neural transduction then his analysis is quite valid. However since the majority of primary vestibular neurones appear to have a resting discharge (Groen, Lowenstein & Vendrik, 1952) it is hard to see how a true threshold effect can exist, there being little to distinguish zero cupula deflection from any other position. It seems likely that what appears to be a threshold effect is really due to the problem of resolving signal from "noise" (See Chapter 4). If this is true Mayne's analysis must be rejected since the latency measured by Mowrer must then be regarded as reflecting dynamic characteristics of the vestibulo-collic system as a whole. Here again, since the canal exists in a feedback path in this sytem, the dominant time constant of the overall system cannot be equated with the canal time constant. In fact, Mayne's estimate, and estimates made in the manner of Schierbeck, are more properly regarded as estimates of the dominant time constant of the closed-loop vestibulo-collic system. The fact that Mayne's time constant (8.3 sec) is so similar to the 9.0 second time constant of Eq. 10.1 is thus easily explained.

As discussed in Chapter 3 the short time constant of the semicircular canal is probably so short in most animals that its value cannot be estimated by ordinary experimental methods in live animals, but only by calculation from physical dimensions and properties. This appears to be the case in the pigeon as well. A recent estimate is that of Money, Sokoloff and Weaver (1966) who made careful measurements of canal dimensions and endolymph properties, and found the ratio of the effective moment of inertia of the endolymph to the coefficient of viscous retardation to be 1/360 sec. for the horizontal semicircular canal of the pigeon. According to the conventional model of the canal (Chapter 3) this ratio is almost exactly equal to the short time constant. The result implies that a one degree per second step change in head angular velocity would result in a peak relative displacement of the endolymph of one second of arc.

In the experiments to be described below, eye movements were recorded in blindfolded pigeons exposed to sinusoidal and step changes in head angular velocity.

An estimate of the long time constant of the semicircular canal was obtained by analysis of the relationship between slow-phase eye velocity and head velocity, in what has become a fairly conventional manner. However, it might well be argued, especially in view of the theoretical analysis of Chapter 5, that slow-phase eye velocity is not necessarily as closely related to the canal signal in the bird as it appears to be in the cat, and that such an estimate cannot be accepted without corroboration. Hence, in addition, pigeon vestibulo-ocular response has been carefully examined from the standpoint of the Sugie-Jones model discussed in Chapter 5, and a new method of analyzing vestibulo-ocular response has been developed to provide an independent check on the results of the conventional analysis.

This chapter contains in addition a brief account of experiments in which eye movements, and the electical activity in neck muscles, were recorded simultaneously in pigeons during rotation showing a close relationship between vestibulo-ocular and vestibulo-collic systems.

11.2 METHODS

Eye movements were recorded in four pigeons during sinusoidal rotational oscillation and in response to step changes in rotational velocity in the horizontal plane. Pigeons were anaesthetized with ether, tracheotomized, and placed in a head holder (David Kopf Instruments, Type 1404 Stereotaxic Instrument) with the head over the axis of rotation. The eye-lids were closed with adhesive tape, and the head was held in the normal resting position, with the beak tilted slightly downwards. Light ether anaesthesia was maintained throughout the experiments. Eye movements were recorded by D.C. electro-oculography using special electrodes. Details of electrode and anaesthetic techniques are described in Chapter 9. Precise calibration of eye movement recordings was not attempted, but rough visual estimation indicated that eye excursions were of the order of 10-15° peak. Records of table velocity, and of eye position relative to the head were obtained on a pen recorder (Bandwidth DC to 20 Hz) after suitable amplification.

11.3 GENERAL FEATURES OF THE RESPONSE

The form of recorded eye movements was variable, a fact presumably due in part to the varying level of anaesthesia. A number of records illustrating the observed variability are to be found in Fig. 11-1, which shows velocity step responses, and in Fig. 11-2, showing sinusoidal responses. The smooth curves in each case represent head velocity, and the irregular nystagmoid curves indicate eye position relative to the head. All eye-movement records are to some extent contaminated by electrical interference, attributable principally to the fact that the small E.O.G. potentials were taken through sliprings before amplification.

Variations in frequency and amplitude of the saccadic flicks of eye position were noticeable in all records, as in those illustrated. The variation was particularly prominent in records of the velocity step response, there being a tendency for the amplitude and frequency of saccades to decrease with time following the step input. A similar decline is commonly observed in the responses of human subjects and cats (Sugie & Jones, 1966).

It is interesting to note in the response of one pigeon (Fig. 11-1, A) the occurence of very rapid saccades, (about 10 per second) with high slow-phase velocities, appearing in the initial portion of the response to a large step change in head velocity. As these rapid, large saccades occur it will be seen that there is in these two records a tendency for the overall position of the eye to deviate in the anti-compensatory direction. Such anticompensatory deviation of overall eye position is a usual finding in man, during many forms of vestibular stimulation (Fenn & Hursch, 1937; Jones, 1964; Mayne, 1965; Mishkin & Jones, 1966). However in records of pigeon vestibulo-ocular response recorded to date the opposite tendency seems to be the general rule, i.e. the eyes tend to show either no overall deviation or deviation in the compensatory direction.

11.4 CONVENTIONAL ANALYSIS OF PIGEON VESTIBULO-OCULAR RESPONSES

Records of the sinusoidal response of the vestibulo-ocular system were obtained in four pigeons. Typical response patterns during horizontal-plane rotational

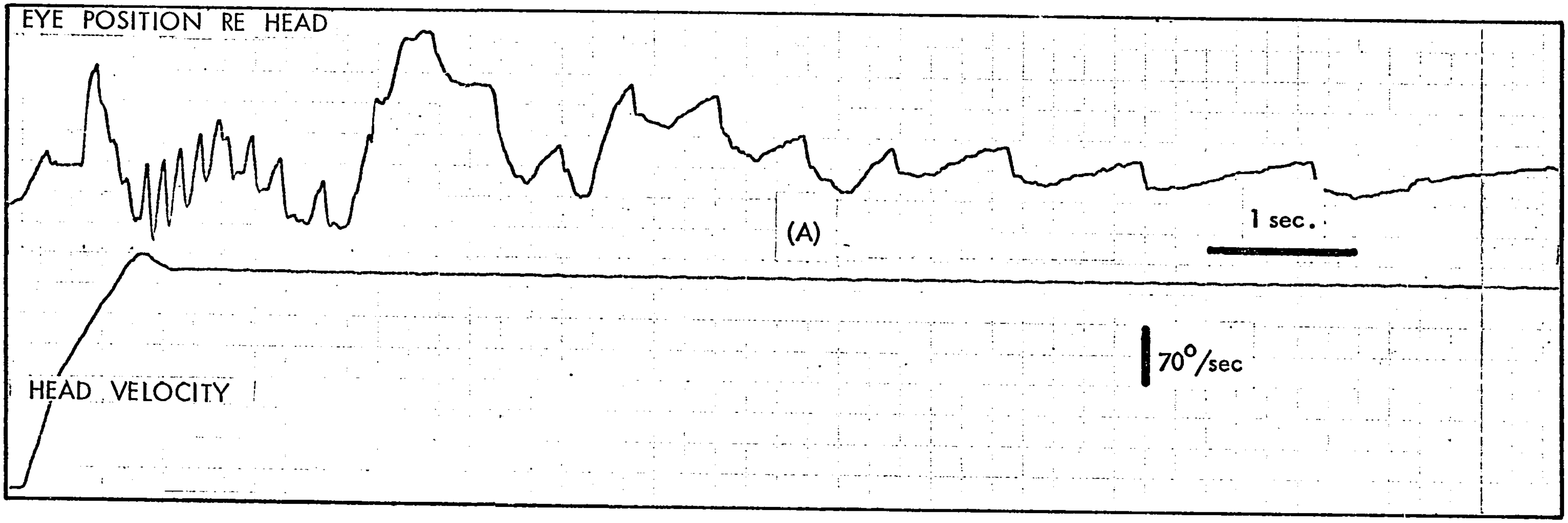


Fig. 11-1 RESPONSES OF THE VESTIBULO-OCULAR SYSTEM IN BLINDFOLDED PIGEONS TO STEP CHANGES IN HEAD ANGULAR VELOCITY.

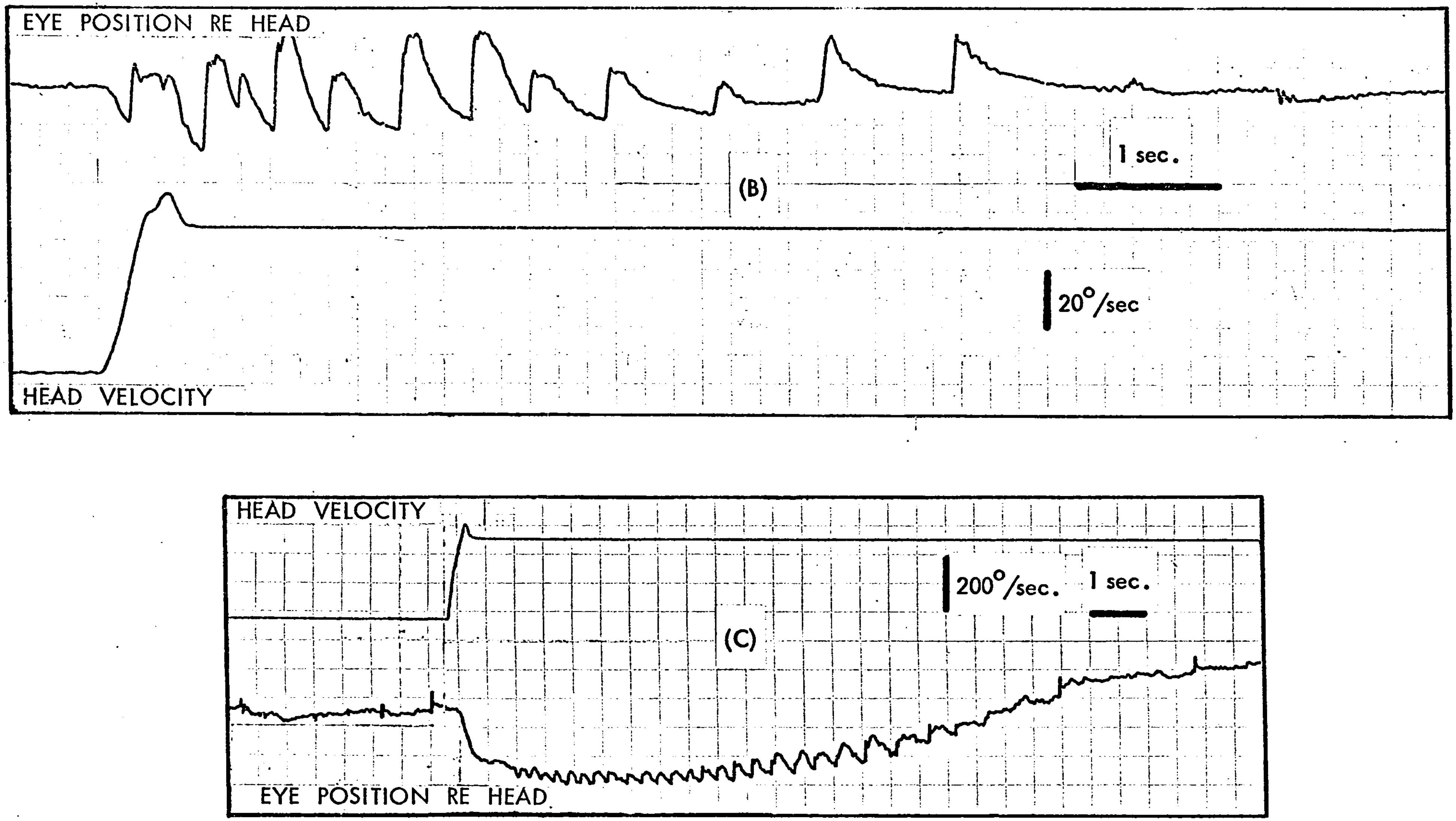
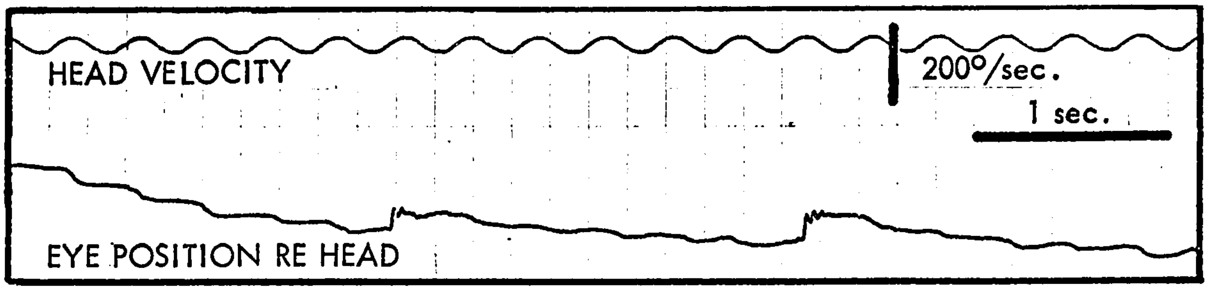
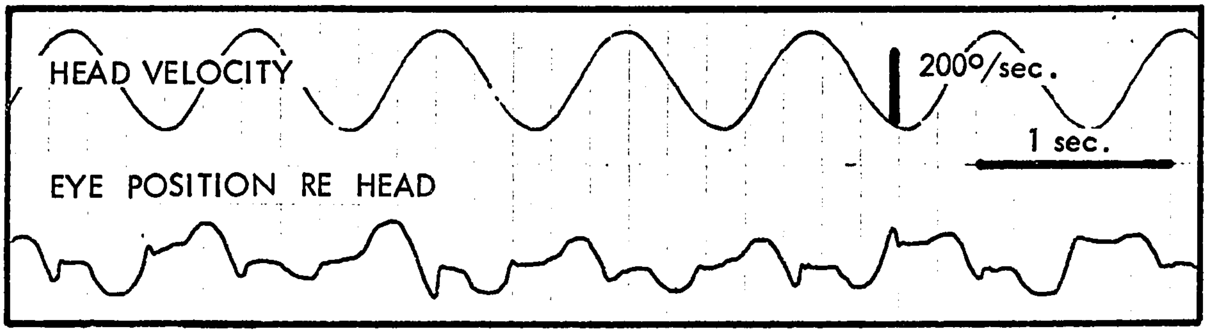


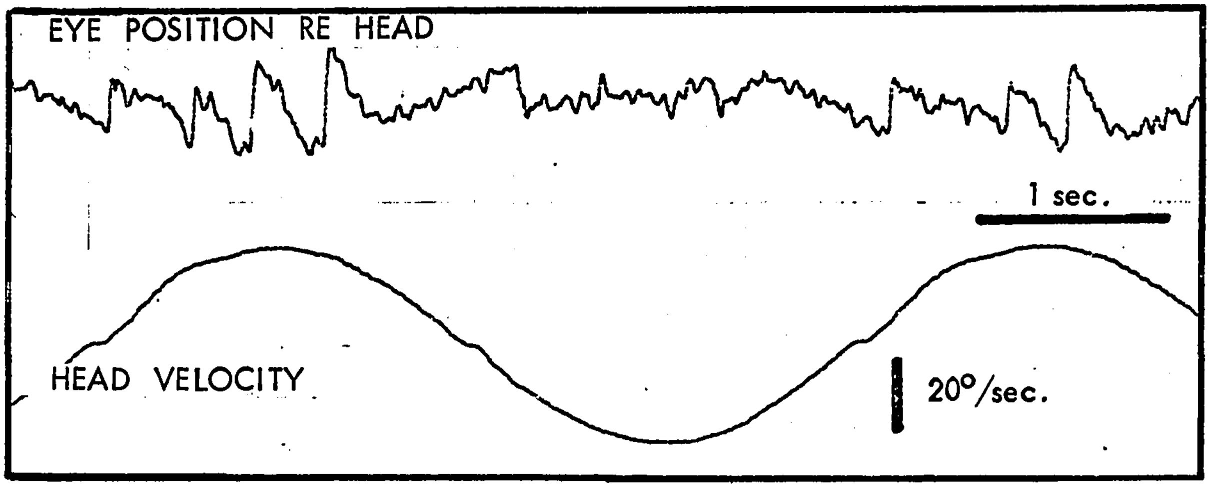
Fig. 11-1 (cont.) PIGEON VESTIBULO-OCULAR RESPONSES TO VELOCITY STEP INPUTS.



(A) 3.0 Hz.

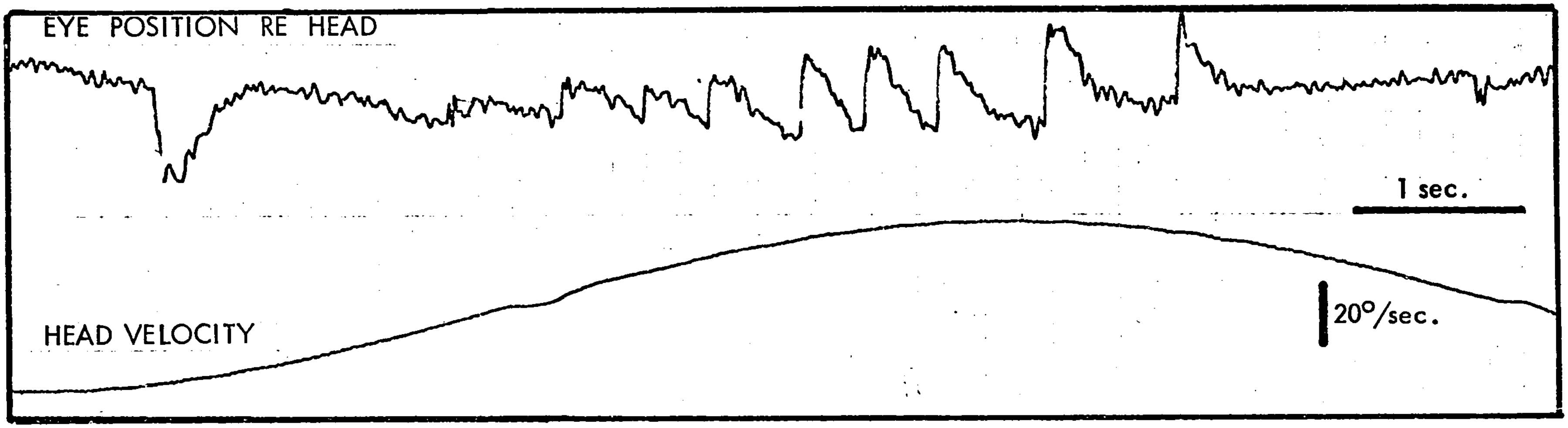


(B) 1.04 Hz.

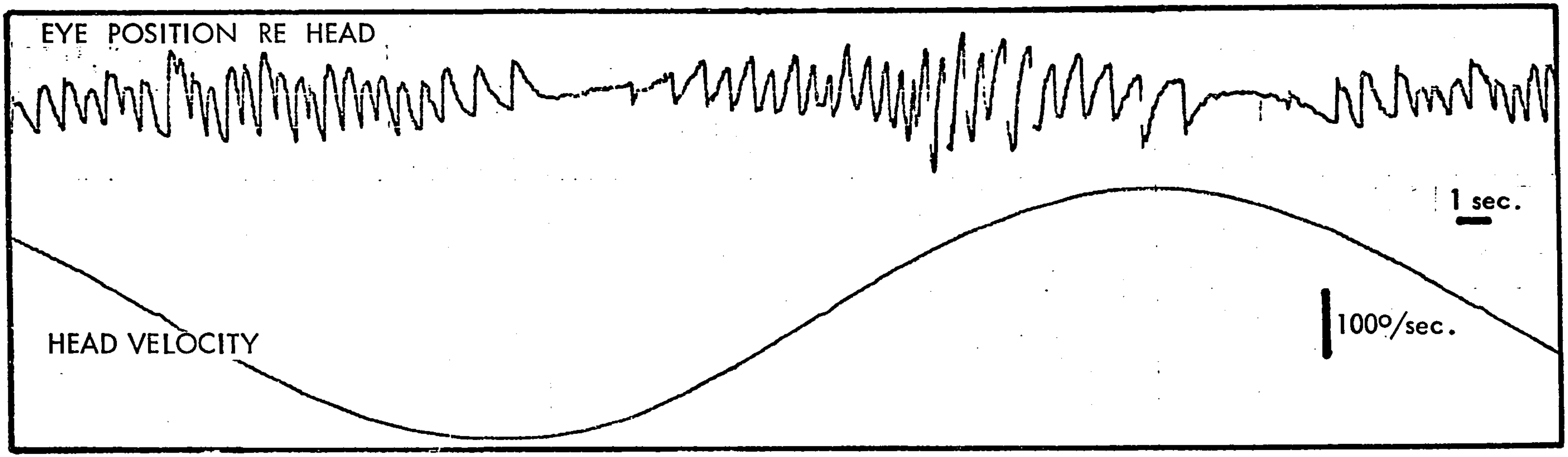


(C) 0.25 Hz.

Fig. 11 - 2 VESTIBULO-OCULAR REFLEX RESPONSE TO SINUSOIDAL TABLE OSCILLATION IN PIGEONS (EYES SHUT, HEAD FIXED TO TABLE)



(D) 0.083 Hz.



(E) 0.025 Hz.

Fig. 11 - 2 (cont) VESTIBULO-OCULAR REFLEX RESPONSE TO SINUSOIDAL TABLE OSCILLATION IN PIGEON

oscillation of head and body appear in Fig. 11-2. Records obtained at stimulus frequencies ranging from 0.008 to 2.9 Hz were analyzed for the phase shift of compensatory eye velocity relative to head velocity. Owing to the irregularity observed in many records, measurements of slow- phase eye velocity did not lead to useful results except in a few cases, and hence it was not possible to obtain adequate data on the variation of input-output amplitude ratio with frequency. However, the points of zero slow-phase eye velocity could be identified with reasonable accuracy in almost every cycle of the recorded responses. In a given cycle the time interval between this point and the point of zero table velocity provides a measure of phase shift, which has been used previously (Niven & Hixson, 1961; Sugie & Jones, 1966) and is discussed theoretically in Chapter 5.

The results of such phase measurements are shown in Fig. 11-3, in which phase shift (degrees) is plotted against the logarithm of stimulus frequency (cycles per second). Phase angles shown represent the phase shift between actual slow-phase eye velocity and the required eye velocity, the latter being taken as equal to head velocity but of opposite sign. The four solid curves in the figure summarize the experimental findings in four pigeons, each point being the average of measurements from between 5 and 50 cycles. The experimentally determined phase-frequency relationships are reasonably consistent, and show phase advance of slow-phase eye velocity relative to head velocity at low frequencies, with decreasing phase shift at higher frequencies.

In two pigeons, phase advance in excess of 90° was observed at low frequencies, a finding consistent with the adaptation model of the vestibulo -~~collic~~ ocular system proposed independently by Young (1968) and by Malcolm and Jones (1969). The data were therefore fitted to such a model by the iterative least-squares technique described in the previous chapter. The result is shown as a smooth curve in Fig. 11-3, and corresponds to the transfer function,

$$G(s) = \frac{Ks^2}{(2.5s + 1)(71s + 1)}$$

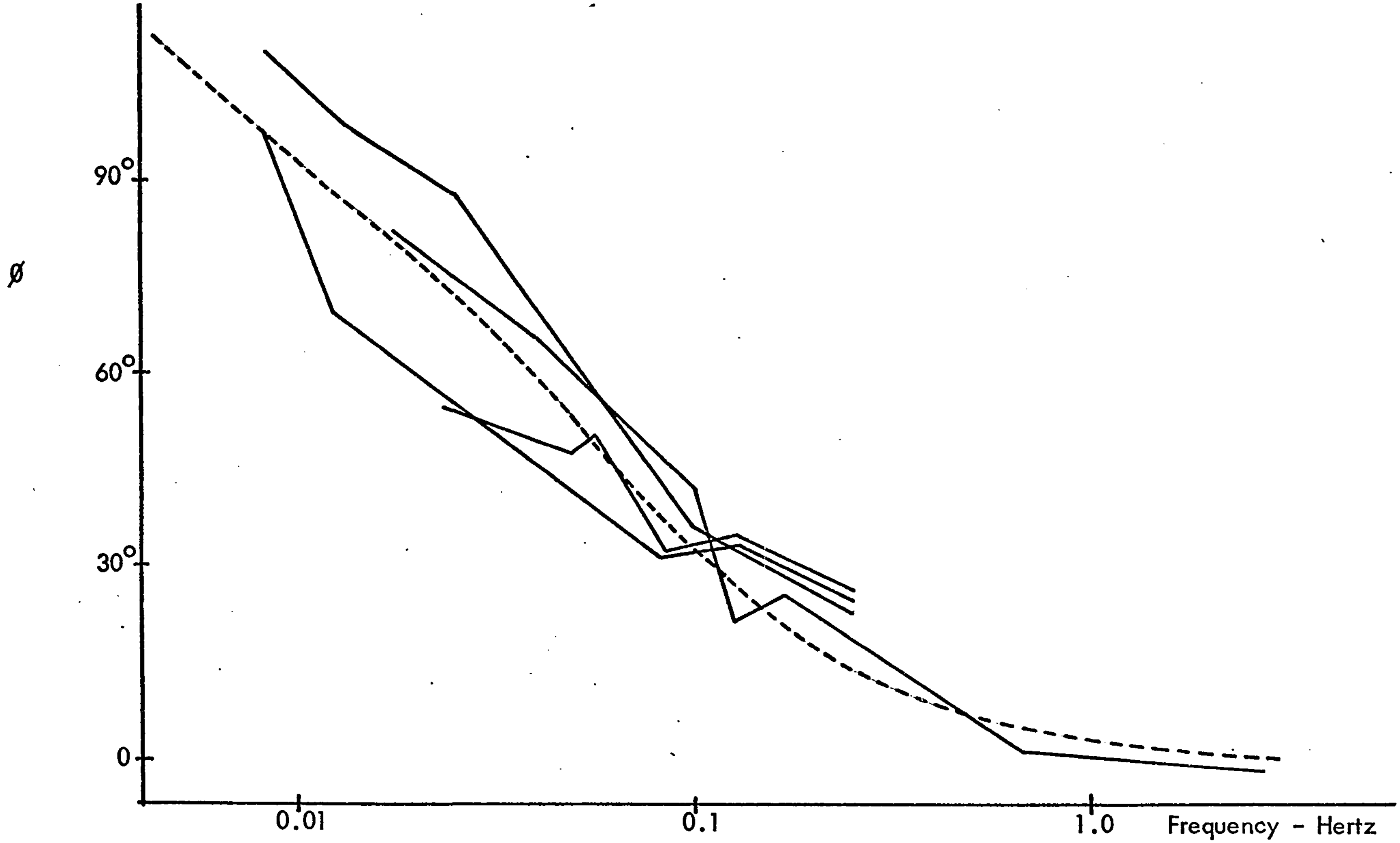


Fig. 11 - 3 PHASE-FREQUENCY RESPONSE OF PIGEON VESTIBULO-OCULAR SYSTEM
ø - phase shift between slow-phase eye velocity and applied sinusoidal head velocity; Solid Lines join experimentally determined points from four pigeons; Dotted Line - fitted curve.

The long time constant so obtained (71 seconds) is an approximate estimate only, owing to the paucity of low-frequency data, but one may have reasonable confidence in the estimated value of the short time constant (2.5 seconds) which corresponds in Young's model to the long time constant of the canal.

The ocular response to step changes in the angular velocity of the head was examined in three pigeons, and the graphical records were analyzed by measuring the mean slope during each slow-phase interval. For each pigeon, values so obtained from two consecutive step responses (one in each direction) were averaged in the manner previously described (Section 10.4), and the averaged data were fitted to exponential functions by the method of Hazelrig et al. (1961). The raw data and the corresponding fitted curves are shown in Fig. 11-4 A,B and C, the letters indicating in each case the response of a pigeon whose phase-frequency data are similarly designated in Fig. 11-3. In cases A and C, since the duration of recording following the respective step inputs was short (23 and 13 seconds respectively) and there was little overshoot, the data were fitted to single-exponential functions. The fitted time constant was 2.5 sec. in case A, and 1.9 sec. in case C. In case B recording was continued for 60 seconds, and a dual exponential function was fitted, having time constants of 2.0 and 11.0 seconds.

Inadequacy of data in the low frequency range is a problem in interpreting the results of both sinusoidal-response testing and transient-response testing. Nevertheless the results from both forms of stimulation suggest that the system response in the frequency range from 0.05 to 2.0 Hz. may be explained as resulting from a dominant time constant of about two seconds duration. According to classical concepts of the vestibulo-ocular system it therefore seems reasonable to propose that the long time constant of the pigeon semicircular canal has a value of approximately two seconds, and not eight seconds as estimated by Mayne (1950).

The next section of this chapter is devoted to an examination of the Sugie-Jones model as it applies to the pigeon vestibulo-ocular system. The results support for the case of the pigeon the classical method of estimating the canal time constant from observations of slow-phase eye velocity , so that the value of two

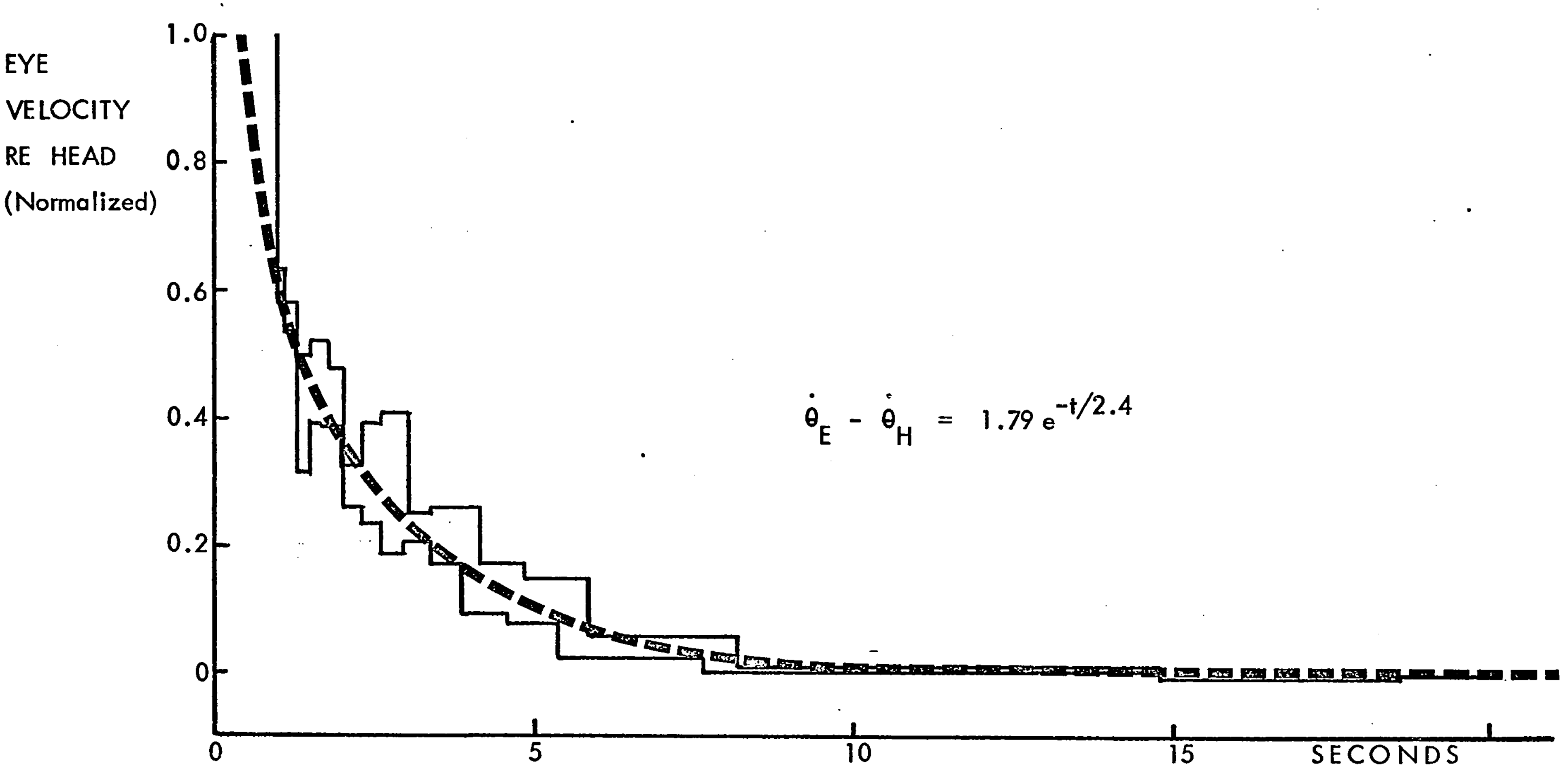


Fig. 11 - 4 (a) NORMALIZED STEP RESPONSE OF PIGEON VESTIBULO-OCULAR SYSTEM
Solid Lines - Slow-phase eye velocity relative to head in response to two step changes in head angular velocity in one pigeon (each horizontal segment = one slow-phase interval); Dotted Line - fitted curve.

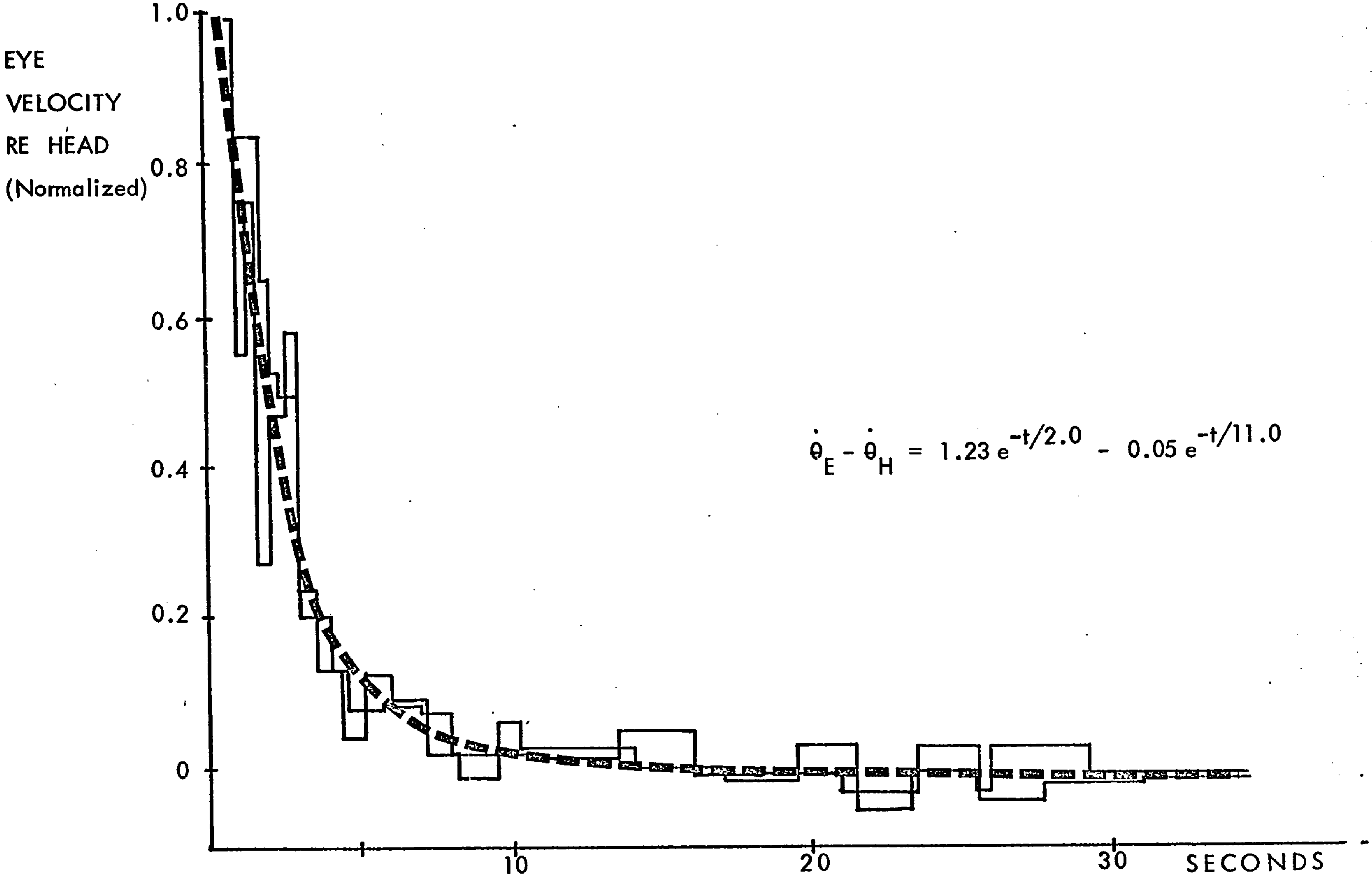


Fig. 11 - 4 (b) NORMALIZED STEP RESPONSE OF PIGEON VESTIBULO-OCULAR SYSTEM
See legend Fig. 11-4 (a)

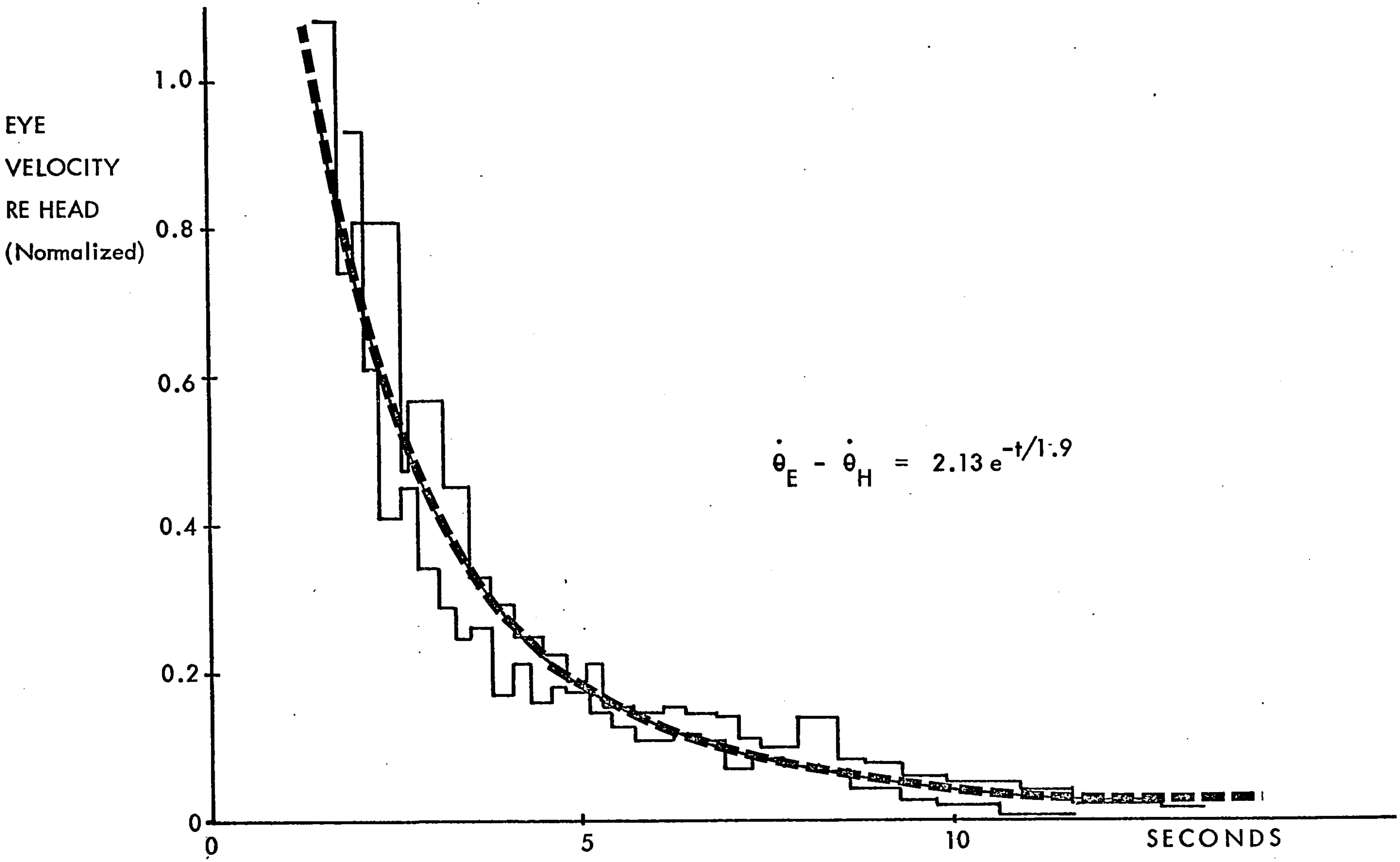


Fig. 11 - 4 (c) NORMALIZED STEP RESPONSE OF PIGEON VESTIBULO-OCULAR SYSTEM
See Legend Fig. 11-4 (a)

seconds obtained in this section emerges as a confident estimate of the canal time constant in this animal.

11.5 PIGEON VESTIBULO-OCULAR RESPONSE AND THE SUGIE-JONES MODEL

The Sugie-Jones model of the vestibulo-ocular system has been discussed at length in Chapters 5 and 6 and the reader is referred to that Chapter and especially to Figs. 5-1 and 6-1 for details of the model. The basic feature proposed by Sugie and Jones (1966) is that the vestibulo-ocular system may be regarded as containing a low-pass filter (called the "eye-centering filter" in Chapter 5), whose output is eye position and which receives as input a continuous signal proportional to cupula deflection, and also a train of pulses, each pulse being responsible for the occurrence of a single saccade. Sugie and Jones found that in the cat the filter could be approximated as a linear first order system with a time constant of one second. After making certain assumptions as to saccadic pulse frequency and amplitude, these authors showed that under certain conditions the pattern of eye movement in the cat could be such as to yield a proportional relationship between slow-phase eye velocity and canal signal over a wide range of input conditions. This relationship has commonly been taken for granted, and the Sugie-Jones model gives qualified support to the assumption, for the case of the cat. The analysis of Chapter 5 however indicates that considerable divergence from this relationship could readily occur even in the cat, and suggests that in other animals it is unwise, in the absence of supporting evidence, to make inferences as to semicircular canal behaviour from vestibulo-ocular response characteristics without studying the nature of the vestibulo-ocular system. To this end the pigeon vestibulo-ocular response has been examined from the point of view of the Sugie-Jones model, the characteristics of the low-pass "eye-centering" filter in the pigeon have been identified, and a method has been developed to compute both the filter time constant and the phase and relative amplitude of the semicircular canal signal from a record of the vestibulo-ocular response to a sinusoidal input.

The simplest and most direct way of measuring the filter time constant of the Sugie-Jones model is to examine the time course of eye movement following a spontaneous saccade (Sugie & Jones, 1966). Only a few such saccades were observed in the present experiments and these are shown in Fig. 11-5. The relevant portions of these curves were fitted graphically and found to be adequately explained as single exponential decays. Time constants so obtained ranged from 0.20 to 0.46 seconds (Fig. 11-5)

Sugie and Jones (1966) also estimated the filter time constant by analysis of responses to rotational stimulation when saccadic activity was completely suppressed by ether anaesthesia. Such investigation was not feasible in the pigeon since complete saccadic suppression could only be achieved by using lethal or near-lethal dosage of the anaesthetic.

It was therefore necessary to devise a new method for determining the time constant of the eye centering mechanism, a computational method being chosen because of the nature of the data available. The method as it presently exists is implemented on a digital computer, and is suitable for determining in a least squares sense the coefficients and exponents in an expression of the form

$$y = C_o + C_1 e^{-a_1 t} + C_2 e^{-a_2 t} + \ldots\ldots + C_n e^{-a_n t}$$

$$+ D_1 \cos \omega t + D_2 \sin \omega t$$

in which the frequency ω of the sine and cosine terms is known . The fitting procedure is based on Prony's method (Hildebrand, 1956) and is applicable to data spaced equally in time. The data are first fitted to a form of difference equation to determine the exponents $\{a_i\}$, and the coefficients are subsequently obtained by linear regression. A complete description of the method is lengthy and is deferred to an Appendix.

A most important feature of the method lies in the fact that the exponents $\{a_i\}$ are determined first, independently of the coefficients $\{C_i\}$ so that it

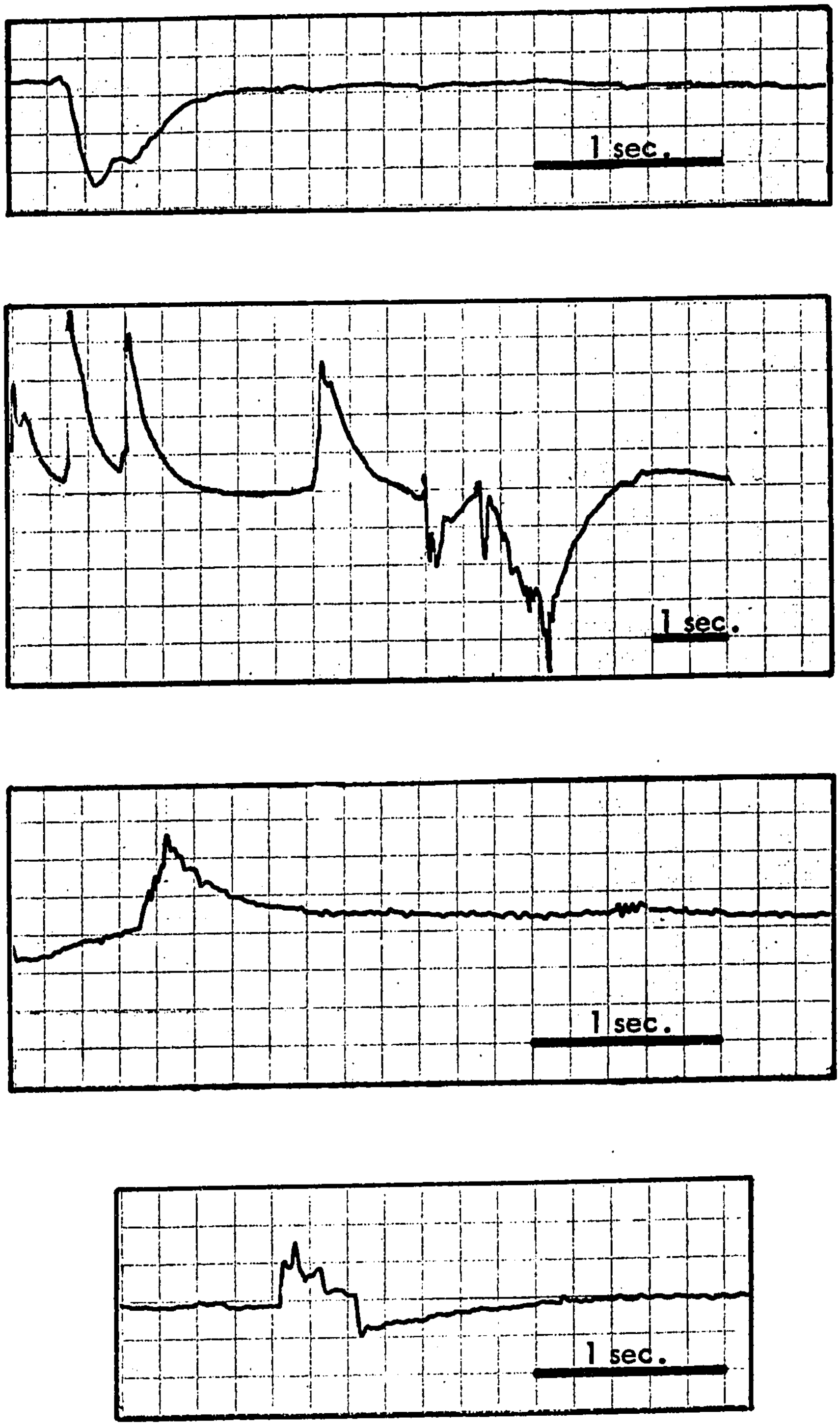


Fig. 11-5 SPONTANEOUS OCULAR SACCADES IN BLINDFOLDED PIGEONS. Light ether anaesthesia; electro-oculographic recording.

is possible to evaluate the exponents even when there exist jump discontinuities in the magnitudes of the exponential coefficients or when these coefficients are undefined for short intervals. The coefficients must however remain constant between the discontinuities, and the time at which these changes occur must be known. The reader will recognize from the discussion of Chapter 5 that the sinusoidal response of the Sugie-Jones model fulfills all these requirements. During each slow-phase interval the response is of the form

$$\theta_E(t) = A_1 e^{-at} + D_1 \cos \omega t + D_2 \sin \omega t \qquad \text{Eq. 11-1}$$

Each saccade results in a sudden change in the value of A_1, but the other parameters a_1, D_1 and D_2 remain constant. For the purpose of fitting to actual data, the coefficient A_1 is regarded as undefined for the duration of the quick phase movement.

Three segments from the sinusoidal response of one pigeon were analysed in this way. Each segment contained one or more cycles of the response, and was manually converted to digital form from a graphical record at intervals of 0.1 to 0.2 sec. The results are shown in Fig. 11-6. In each record the fitted curves are indicated by solid lines, and the original digitized data by dots. The fit obtained is excellent in some slow phase intervals, but rather poor in others. The inconsistency may result in part because of the crude method of digitizing the records. The time constant of the eye-centering filter mechanism ($T_3 = 1/a_1$) obtained from these records varies from 0.21 to 0.71 sec., thus confirming the estimate obtained above from analysis of spontaneous saccades.

Other information of considerable interest is available from these results. The sine and cosine terms in Eq. 11-1 define a single sinusoid which according to the Sugie-Jones model (Chapter 5) should be equal to the position output of the continuous pathway, i.e.

$$\begin{aligned} y_1(t) &= D_1 \cos \omega t + D_2 \sin \omega t \\ &= A_1 \sin (\omega t + \alpha_1) \end{aligned}$$

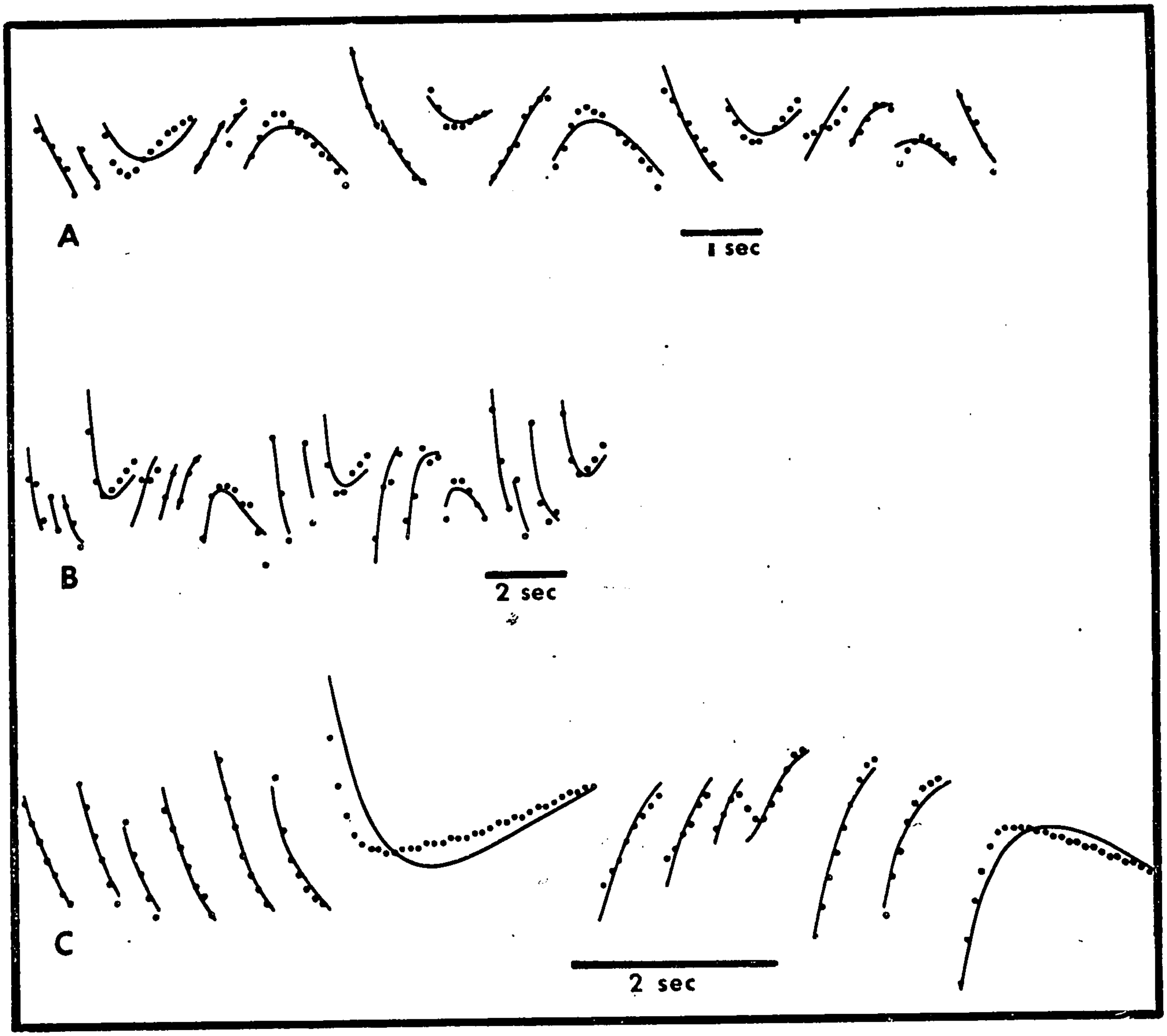


Fig. 11 - 6 RESULTS OF CURVE-FITTING TO RECORDS OF PIGEON VESTIBULO-OCULAR RESPONSE. Dots - values read from records of head position re body during sinusoidal rotation of the body (eyes shut) at 0.26 Hz.(A), 0.17 Hz.(B), 0.083 Hz.(C). Solid lines - curves fitted by the method of Section 11.5 .

where

$$A_1 = (D_1^2 + D_2^2)^{1/2}$$

is the amplitude ration $y_1/\dot{\theta}_H$, and

$$\alpha_1 = \tan^{-1}(D_1/D_2)$$

is the phase shift of continuous-pathway position output relative to head velocity. The contribution of the eye-centering filter mechanism to this amplitude ratio and phase angle may be calculated, and by appropriate manipulation one directly obtains values for the amplitude-ratio and phase shift of the canal signal relative to head velocity. The amplitude ratio so calculated will contain as a multiplicative factor the continuous pathway gain K_1, which remains unknown, but this will not affect the usefulness of the amplitude-frequency relationship for determining dynamic parameters of the canal.

In the present analysis the frequency range investigated is insufficient for the amplitude data so calculated to be very meaningful. The calculated phase shifts may however be compared to the phase data presented in Section 11.4. This comparison is made in Fig. 11-7, in which the lines indicate the phase data of Fig. 11-3, obtained in the manner of Niven and Hixson (1961) and the closed circles represent phase shifts computed from segments of the records from one pigeon. The agreement is quite good, although it must be emphasized that complete agreement would be surprising from a theoretical stand point. Even if the pigeon vestibulo-ocular system did conform to the critical assumptions regarding saccade frequency and amplitude which are the basis for the detailed frequency response calculations of Chapter 5, the observed phase shift of mean slow-phase eye velocity as assessed in Section 11.4. would only be identical to the phase shift of the canal signal for a single critical value of the gain ratio K_1/K_2 of the Sugie-Jones model.

The fitting procedure discussed in this section offers the possibility of estimating the time course of the canal signal from records of saccadic vestibulo-ocular response without the necessity of making any assumptions regarding the amplitude and frequency of saccades. The method can easily be generalized to

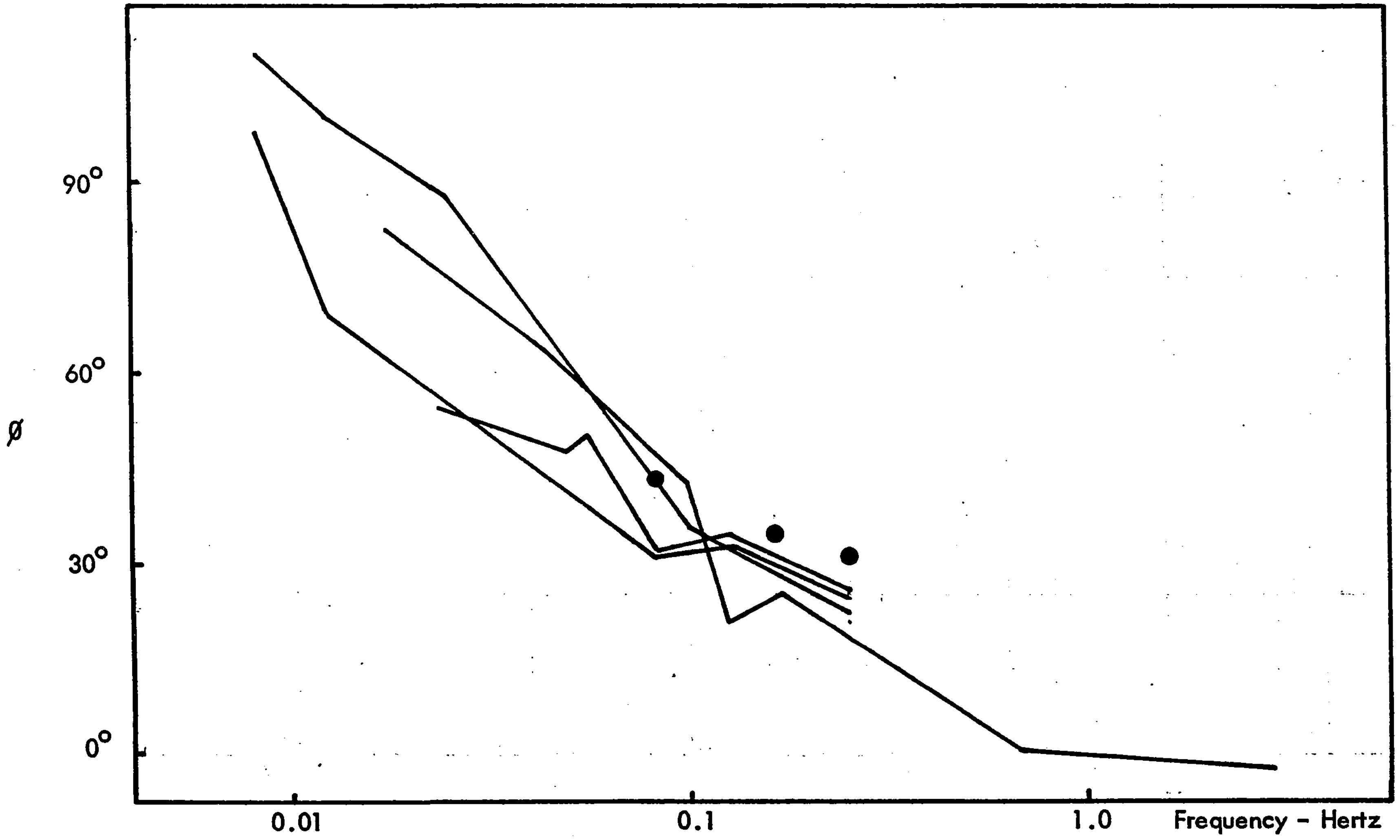


Fig. 11 - 7 CALCULATED PHASE SHIFT OF CANAL SIGNAL (DOTS) vs. OBSERVED PHASE SHIFT OF SLOW-PHASE EYE VELOCITY (POINTS JOINED BY LINES) RELATIVE TO HEAD VELOCITY IN PIGEONS.

deal with inputs which are not sinusoidal, or to more complex filter mechanisms, provided measurement and recording accuracy and resolution are adequate. Moreover the analysis of records of nystagmus by this method could fairly easily be completely automated provided saccades are reasonably abrupt. For this purpose it would only be necessary to detect the occurrence of each saccade, and using some suitable criterion cause data points corresponding to the quick phase intervals to be disregarded in the computation. Such complete automation however would result only in a relatively trivial further increase in the speed of analysing the records. Far more important is the potential increase in the amount of information which could be gained from the records. It will be evident to the reader that the method has not yet been fully exploited.

11.6 SYNCHRONY OF PIGEON EYE MOVEMENT WITH NECK MUSCLE ACTIVITY

During investigation of the vestibulo-ocular system, in which pigeons were exposed to rotational stimulation with head fixed to the turntable, it was noted that there were muscular movements of the neck whose occurrence was related in time to that of the ocular saccades. To record this phenomenon objectively, neck-muscle activity was registered electromyographically in three pigeons while simultaneously recording eye movement in the manner described above. One such record is shown in Fig. 11-8, the traces shown representing eye position, table velocity and neck EMG respectively, from top to bottom. The recorded EMG was of the multiple-unit type, obtained using a concentric electrode placed in the left Rectus Capitis Anterior Minor. This muscle originates on the anterior surfaces of the upper cervical vertebrae, and inserts near the occipital ridge, so that activity in the muscle is associated with a torque causing head rotation to the right when viewed from above. It will be seen from the record that neck muscle activity is synchronized with eye movement towards the right during both quick and slow phases.

The precise time relation between EMG activity and eye motion differed slightly with changes in electrode position, and when activity in neighbouring muscles was examined. Such differences are to be expected as a result of differing

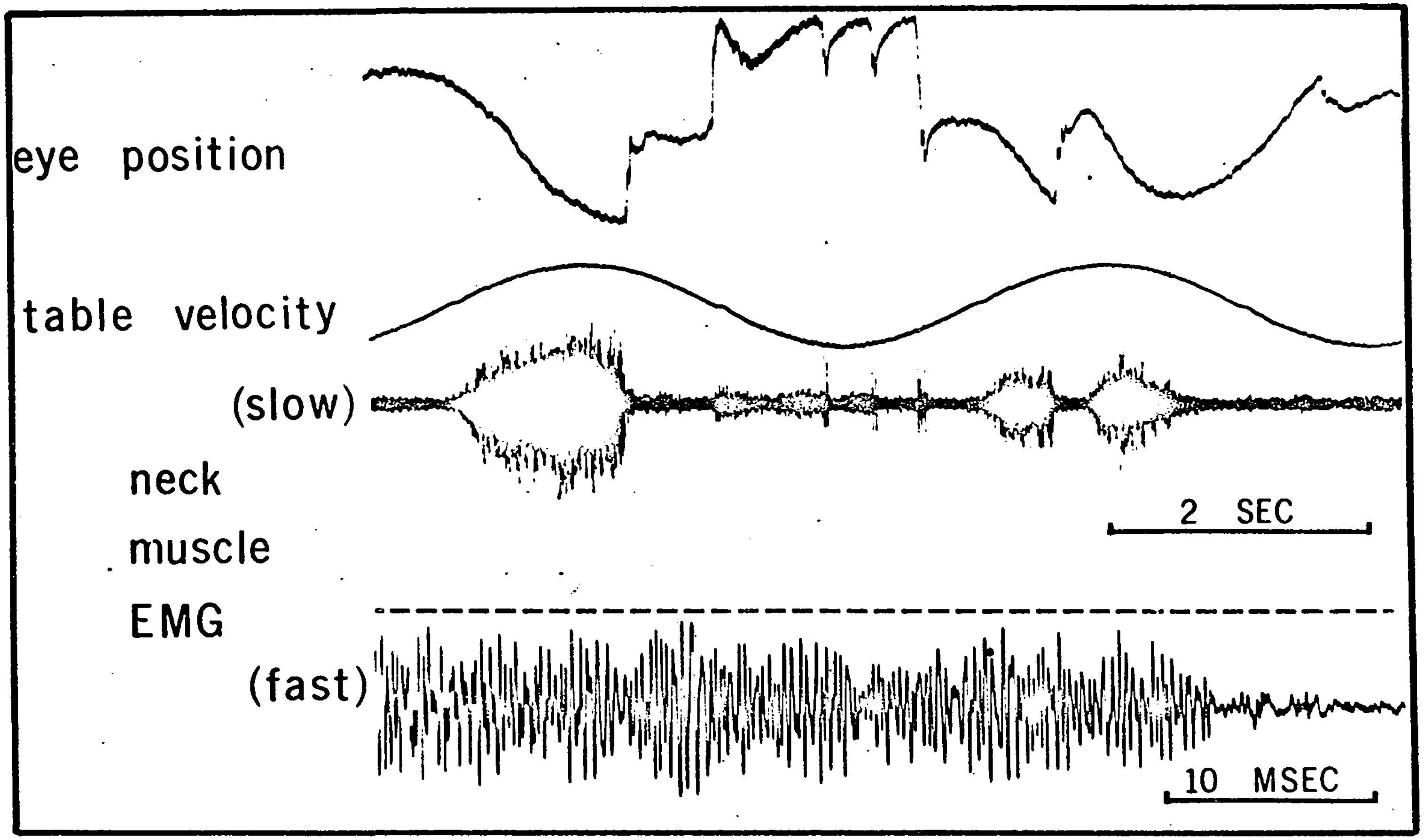


Fig. 11-8 SYNCHRONY OF SACCADIC AND SLOW-PHASE ACTIVITY IN THE VESTIBULO-OCULAR AND VESTIBULO-COLLIC SYSTEMS IN THE PIGEON . Records of eye position re head (top), and neck electromyogram(two lowest traces) in blindfolded pigeon with head fixed to the turntable, under light ether anaesthesia. EMG was recorded in the Left Rectus Capitis Anterior Minor, which when active pulls the head to the right; muscle activity is synchronous with slow- and quick-phase eye movement to the right.

muscle geometry and are not of particular concern here. The point to be emphasized is that in all cases examined the burstsof neck muscle activity were always consistently related to the cycles of saccadic and slow-phase motion of the eye. This strongly suggests that vestibularly-controlled eye and head saccades are generated by closely related mechanisms, if not by the same mechanism.

This conclusion is hardly surprising, as pointed out in Section 9.2.1 in connection with the simultaneously recorded eye and head movements in human subjects, since uncoordinated saccadic movements of head and eyes would be detrimental to visual image stabilization. It will be noted however that while in the pigeons examined there was a one-to-one relationship between eye saccades in one direction and the burstsof neck muscle activity, in man (Fig. 9-3) there were rather more eye saccades than head saccades. This may be due to the fact that the quick phases of head movement in man were of rather long duration, since usually slow-phase head movements in the human case were not interupted by eye saccades. On the other hand it must be noted than in these pigeon experiments, the vestibulo-collic system was operating in an open-loop mode, since no head movement relative to the table could occur as a result of the recorded muscle activity. It is not yet clear what effect such restriction of head movement has on the timing of saccadic neck muscle activity.

Thus it has beendemonstrated that in the pigeon, with head-on-body movement prevented, there is synchronous saccadic activity in the vestibulo-ocular and vestibulo-collic systems, a finding which has considerable significance both from a functional point of view and also from the point of view of future studies of saccade generating mechanisms. In addition, the fact that active contraction of neck muscles during vestibular stimulation continues to occur when head motion is totally restricted means that it should be possible, by recording isometric neck-muscle torque, to study the vestibulo-collic system quantitatively in this open-loop mode. Such studies will probably be valuable in attempts to identify the system's dynamics, although it will of course be necessary to take into account the altered proprioceptive feedback from neck muscles which will result from the restriction of head movement.

11.7 DISCUSSION OF EXPERIMENTAL RESULTS IN PIGEONS

Detail analysis of experimental data from the pigeon vestibulo-ocular system yields a fairly consistent picture of the function of this system, and values for some of the important dynamic parameters may be stated with confidence. Conventional analysis of the response, that is, by evaluating the relationship between slow-phase eye velocity in the responses to sinusoidal and step changes in the latter suggest that the long time constant of the pigeon's horizontal semicircular canal is about two seconds. In order to check the validity of this method of analysis, pigeon vestibulo-ocular response has been examined from the standpoint of the Sugie-Jones model. It seems highly probable that the basic features of this model exist in the pigeon as in the cat, with a filter time constant of about 0.5 sec. in the pigeon. The ratio of the canal time constant to the "eye centering" filter time constant is thus about the same in the pigeon (2.0/0.5) as in the cat (4.0/1.0), and it appears likely on this basis alone that slow-phase eye velocity in the pigeon is closely related to the canal signal, at least for input frequency components of up to about one cycle per sec. The new computational method described above for the analysis of vestibulo-ocular responses offers the possibility of evaluating this relationship in greater detail. There is no evidence from these experiments for a significant contribution by the short time constant of the semicircular canal in the frequency range investigated. This time constant is therefore taken to be 1/360 sec. as calculated from canal dimensions (Section 11.1). Adaptation type phenomena are proposed to explain the large phase advance of slow phase eye velocity at very low sinusoidal input frequencies and the overshoot in the step response, but the exact nature of adaptation dynamics remains unclear. These findings and postulates are summarized in Fig. 11.9 in a block diagram of the pigeon vestibulo-ocular system. It should be noted that Young's model for adaptation dynamics has been used implicitly in curve fitting to the experimental data and is included in the model for this reason,

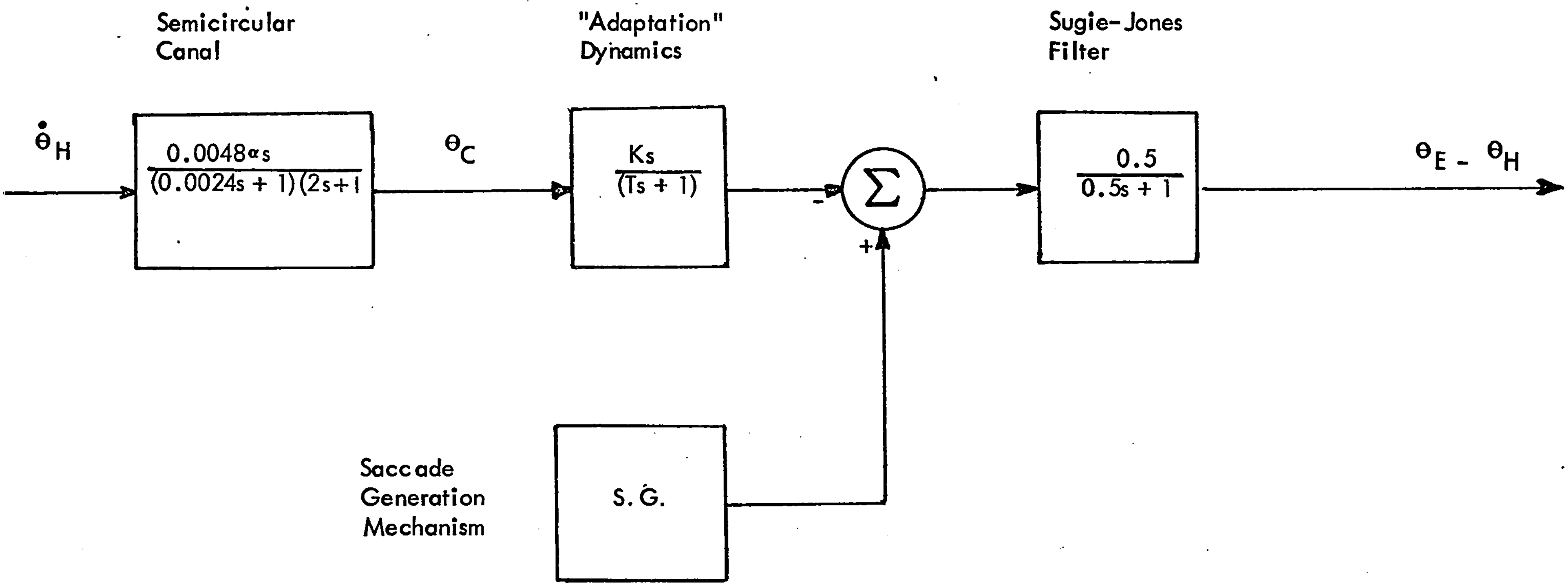


Fig. 11-9 PROPOSED MODEL OF PIGEON VESTIBULO-OCULAR SYSTEM

although it seems unlikely that this will prove to supply a full explanation of these effects.

In undisturbed conscious pigeons, it has been shown (Chapter 10) that there is an approximately linear dynamic relationship between slow-phase head velocity and the rotational velocity of the body in the horizontal plane. In the frequency range examined (0.01 to 2.0 Hz) this relationship may be described approximately by a second-order low-pass model, having time constants of approximately 9.0 sec. and 20 sec., the former being dominant in this frequency range. It has been pointed out that, owing to the complexity of the closed loop vestibulo-collic system, it is not possible to make any functional interpretation of these time constants in terms of, for example, the relationship of one or other to the long time constant of the semicircular canal. However this simple model makes possible a direct quantitative comparison of the functional characteristics of the vestibulo-collic and vestibulo-ocular systems in the frequency range examined. The relationship between slow-phase response velocity and input velocity is very similar in its general form, showing, in the frequency domain, a low-pass characteristic in both cases. The dominant time constant is two seconds in the case of the vestibulo-ocular system and eight to nine seconds in the case of the vestibulo-collic system, a difference which from the functional point of view is considerable. Thus the input sinusoid which yields a just-tolerable phase advance (say 5°) in the vestibulo-collic response, would have four times the periodic time of the sinusoid producing similar error in the vestibulo-ocular response. Moreover it should be remembered that quantitative investigation of the vestibulo-collic system was made under conditions of rather low arousal. There remains a distinct possibility, suggested by the observed effects of noise on system response, that under conditions of increased arousal the low frequency response of the vestibulo-collic system might be even further extended as a result of increased loop gain. Such an extension might be of considerable survival value in birds when flying in turbulent air with poor visibility, since the inertial head stabilization capability offered by the vestibulo-collic system might then be usefully employed for short term inertial guidance.

The possible effect of arousal variation on the response of the vestibulo-collic system has been examined both theoretically and experimentally, and emerges a most interesting topic for future investigation. From a theoretical standpoint it has been pointed out that variations in the level of arousal must almost certainly result in changes in the loop gain of the system, and may thus be expected to cause changes in the dynamic parameters (e.g. time constants) of the closed loop response. Experimentally, the vestibulo-collic response in the pigeon has been found to be very susceptible to the level of environmental noise, although it has not been possible to achieve a sustained increase in the level of arousal by this means. Of the operative and pharmacological methods tested as means of obtaining steady increase or decrease in the level of arousal, the method of decerebration appears to be the most promising, particularly because it appears possible to maintain such preparations for several days or weeks. However ether anaesthesia appears attractive for another purpose, namely that of obtaining a completely non-saccadic response from the vestibulo-collic system. A difficulty in this case is to maintain a steady level of anaesthesia, but if this problem can be overcome the technique may be very useful in providing data with which to test a non-saccadic model of the system. Such a model would be relatively simple to develop since the mathematical difficulties resulting from the introduction of saccades within a closed loop would be eliminated. This would considerably simplify analysis of some relatively inaccessible components of the feedback loop such as neural and neuromuscular elements.

The question of saccade generation is of great interest in the vestibulo-collic system, as in other systems involved in stabilization of the visual image. Saccadic mechanisms in the vestibulo-collic and vestibulo-ocular systems in the pigeon have been shown to be very closely related (Section 11.6) and a similar observation has been made in man (Chapter 9) although in the latter case the relationship is not so clear, perhaps because of the relatively slow time course of head saccades in man. It seems reasonable to expect that saccadic mechanisms in the visual tracking system are also closely related, since incoordinate saccade generation in the vestibulo-ocular and visual tracking systems would result in highly inefficient performance. To date, quantitative studies of saccade-generation mechanisms have largely been confined to the visual tracking system, in the studies of Young and others (Young, 1962; Young, Forster & van Houtre, 1968). Young has been particularly concerned with stochastic and other variations on the regular sampling theme, although schemes such as these seem less plausible from a biological point of view than adaptive sampling schemes, such as that proposed by Sugie (1968), in which the amplitude of saccades and/or the interval between them is somehow dependent on relevant system variables, such as the tracking error. The theoretical studies of optimal saccade placement and timing in the vestibulo-ocular system, described in Chapter 6, are particularly emphatic in suggesting that variations in these saccade characteristics are far from being random, but rather are strategically-varied so as to optimize system response. Intensive study of saccade-generation mechanisms in the three systems mentioned is necessary before it will be possible to understand how they function cooperatively in normal life. At the present time it seems most profitable to study these mechanisms in the isolated systems, and a useful approach, at least in the vestibulo-ocular and visual tracking systems in which mathematical models are available, would appear to be through simulation of a number of plausible saccade-generation schemes to find which one or ones most nearly duplicate the observed pattern of response for a wide variety of input waveforms. However a study of the isolated systems must eventually lead to a study of combined system operation and it seems advisable to think in terms of defining ultimately a single saccade-generation mechanism involved in the operation of all three systems.

CHAPTER 12

SUMMARY

(i) Current knowledge and understanding of the vestibular sensory pathway has been reviewed with emphasis on the nature and transmission of semicircular canal information, and the potential for information processing at various levels.

(ii) On the basis of existing neurophysiological data (Shimazu & Precht, 1966) it has been proposed that a mechanism for selective attenuation of high-frequency components in the semicircular canal signal exists in certain neural elements in the vestibular nuclear region.

(iii) A mathematical model of the vestibulo-ocular system, proposed by Sugie and Jones (1966) and incorporating two pathways ('saccadic' and 'continuous'), has been examined theoretically, with the following results:

> For a certain 'ideal' ratio of the gains in the saccadic and continuous pathways of the model, for which it has previously been shown that the error between predicted slow-phase eye velocity and canal signal is minimized, it has here been shown that the extent to which the eye deviates from its central position during vestibular stimulation is also minimized, a desirable feature physiologically.
>
> For values of the gain ratio slightly different from the 'ideal' value the model may offer an explanation of some previously unexplained phenomena. However,
>
> Model perfomance, judged in terms of the degree to which velocity error and maximum eye deviation are minimized, deteriorates rapidly when the gain ratio is varied from its 'ideal' value.

(iv) A theoretical study has been made (in collaboration with U. Wettstein) of the optimal amplitudes and occurrence times of saccadic flicks of eye position in the vestibulo-ocular system, in an attempt to uncover an explanation for the apparently erratic variations in these parameters which are observed experimentally. Working from the axiom that evolutionary development of a system is equivalent to optimization of functional performance, and postulating a plausible performance criterion, a modified version of the Sugie-Jones model has been used in a digital computer study to obtain simulated optimum responses of the system. The results closely mimic observed responses in adult cats, and strongly suggest that physiological variations in saccade amplitude and intersaccadic interval are strategically determined in some input-dependent or error-dependent fashion, so as to optimize system response. It is suggested that this finding has implications for studies of saccade-generation mechanisms in other visual stabilization systems.

(v) The vestibular control of head rotation during body rotation in the horizontal plane (vestibulo-collic reflex) has been considered from the standpoint of control systems theory, with emphasis on possible functional characteristics of the system which may be predicted from the fact that the semicircular canal appears as a feedback transducer in this system, rather than as an open-loop component as in the vestibulo-ocular system. Functional components of the feedback loop have been evaluated in terms of their possible contribution to system performance, and possible experimental approaches, aimed at characterizing these components, have been proposed. Specific hypotheses concerning features of the closed-loop response have been made on theoretical grounds, i.e.:

> That dynamic parameters of the response, such as time constants, will vary with loop gain, and therefore depend on the level of arousal;
>
> That the system may have significantly greater bandwidth than the vestibulo-ocular system (which uses the same rotation sensor), the region of accurate head stabilization being extended in the low-frequency range because of the presence of significant feedback, and in the high-frequency range

both for this reason and because of the stabilizing effect of head inertia;

That in contrast to the situation pertaining in the vestibulo-ocular system, the time constants governing vestibulo-collic response will all be different from those of the semicircular canal (and of other loop components), except perhaps at certain specific values of the loop gain.

(vi) Rotational head movements have been examined in normal human subjects with eyes shut during step-wise and sinusoidal changes in body angular velocity in the horizontal plane. The following results show that vestibularly-driven nystagmoid head movements may occur in man, and that the human vestibulo-collic reflex is capable of contributing significantly to visual stabilization.

During sinusoidal stimulation at 0.01 Hz., five of eleven subjects produced nystagmoid head movements. Quantitative analysis of records from the two most responsive subjects showed that phase advance of slow-phase head velocity relative to table (body) velocity was 26° - 31°, which was almost double the phase advancement (46° 64°) observed in the vestibulo-ocular response under similar conditions but with head fixed to table.

Three of seven subjects exposed to step changes in table angular velocity showed maintained head nystagmus having characteristics similar to that observed in pigeons.

In one subject, in whom head and eye movements were recorded, slow-phase head velocity during the first few seconds of the post-rotational response was consistently greater than or equal to slow-phase eye velocity.

(vii) Responses of the vestibulo-collic system to body rotation in the horizontal plane have been examined in blindfolded pigeons, head deviation being recorded by an electromagnetic method with minimal restriction of head motion. Major findings were:

> Nystagmoid head response, although similar in many respects, was notably different from vestibulo-ocular responses in man and cats, in that head position tended to lag body position, whereas eye position tends to lead head position in most cases.
>
> For sinusoidal inputs at frequencies exceeding 0.5 Hz., the accuracy of head stabilization relative to space was remarkable, especially in aroused pigeons.
>
> The general form and amplitude of the response was extremely susceptible to changes in arousal induced by sudden loud noises, so that to obtain repeatable responses in conscious, normal pigeons it was necessary to reduce room noise to a minimum.
>
> Ether anaesthesia, decerebration and amphetamine administration were tested as possible means of obtaining maintained but different levels of arousal. It was found that ether anaesthesia and decerebration were feasible, but that after amphetamine susceptibility to noise was much increased.
>
> In conscious, normal pigeons under quiet conditions, variations in slow-phase head velocity during sinusoidal (0.0065-1.9 Hz.) and step changes in body angular velocity could be described by a linear second order differential equation with a low-pass characteristic, having time constants of 8-9 sec. and approximately 20 sec., and a gain of 0.8-1.0 in the pass band (high frequencies).

(viii) Vestibulo-ocular response was examined in blindfolded pigeons with head fixed to the turntable, using sinusoidal (0.002-2.85 Hz.) and step-inputs of head velocity. Eye movements were recorded electro-oculographically using subcutaneous Ag-AgCl electrodes. It was found that:

The relationship between slow-phase eye velocity and head velocity could be approximately described by a linear second-order differential equation with a low-pass characteristic, having a dominant time constant of 2.0 to 2.5 seconds and a second time constant of 11 to 70 seconds. The latter was difficult to estimate exactly, but was necessary to explain phase advance exceeding 90° at low frequencies, and overshoot in the velocity step response (secondary post-rotational nystagmus).

Spontaneous saccades occurred occasionally and were followed by an approximately exponential decay of eye position towards zero, with a time constant of 0.2 to 0.46 seconds.

Responses of one pigeon to sinusoidal inputs were analyzed by a new method (see below) and by this means the time constant of the eye-centering filter of the vestibulo-ocular system was estimated to be 0.2 to 0.7 seconds, and the calculated phase advance of the canal signal relative to head velocity was found to be similar to the phase advance of slow-phase eye velocity.

It is concluded from these results that:

The long time constant of the pigeon's horizontal semicircular canal has a value of 2.0 to 2.5 seconds;
"Adaptation"-type effects occur in the pigeon vestibulo-ocular system as in man and may be modelled in the manner of Young (1968), with however a time constant which is relatively much larger in the pigeon than in man;

The Sugie-Jones model of the vestibulo-ocular system is valid for the pigeon as for the cat, the "eye centering" filter having a time constant of 0.2 to 0.5 seconds in the pigeon;

Slow-phase eye velocity in the pigeon vestibulo-ocular response is closely related to the semicircular canal signal.

(ix) A modified version of the Sugie-Jones model of the vestibulo-ocular system, including only its essential dynamic elements, has been used as the basis of a new, curve fitting method of analysis of vestibulo-ocular responses to sinusoidal stimulation. The method, which may in principal be extended to apply to non-sinusoidal inputs and to more complex dynamics, accepts as input a multi-saccade segment of the response and yields an estimate of the time constant of the eye centering filter mechanism and also an estimate of the amplitude and phase of the cupular signal.

(x) Eye movement and electromyographic activity in neck muscles were simultaneously recorded during rotation in three ether-anaesthetized pigeons with eyes closed and head fixed to table. Slow-phase eye movements in one direction where associated with slowly varying EMG activity, and quick-phase eye movements in the same direction were associated with sharp bursts on the electromyographic record. Complete synchrony of saccadic activity in vestibulo-ocular and vestibulo-collic systems was thus demonstrated in this situation.

APPENDIX

Method of fitting to records of the saccadic vestibulo-ocular response

Hildebrand (1956) and Parsons (1968) consider the case in which, given a set of data points $y(kT)$, $k=0, 1, 2, \ldots, N-1$, spaced T seconds apart, it is required to find an approximation of the form

$$y_k = y(kT) = D_1 e^{a_1 kT} + D_2 e^{a_2 kT} + \ldots\ldots + D_n e^{a_n kT}$$

or equivalently, setting $x_i = e^{a_i T}$,

$$y_k \cong D_1 x_1^k + D_2 x_2^k + \ldots\ldots + D_n x_n^k . \qquad \text{Eq. A.1}$$

It is shown by these authors that if the approximation (A.1) were an equality then each sequence of N successive values of y_k would satisfy a linear difference equation of the form

$$y_k - b_1 y_{k-1} - b_2 y_{k-2} - \ldots\ldots - b_n y_{k-n} = 0 \qquad \text{Eq. A.2}$$

whose coefficients were the coefficients of a polynomial

$$x^n - b_1 x^{n-1} - b_2 x^{n-2} - \ldots\ldots - b_n = 0 \qquad \text{Eq. A.3}$$

whose roots were the $\{x_i\}$ of Equation A.1. If N is at least twice as large as n, then at least n equations of the form of Eq. A.2 may be written, and solved for the $\{b_i\}$ either directly, if $N = 2n$, or by linear regression if $N > 2n$. The $\{x_i\}$ may then be found as roots of Eq. A.3 and the exponents found from the relation

$$a_i = \frac{1}{T} \log_e (x_i) \qquad \text{Eq. A.4}$$

With the $\{x_i\}$ known, Eq. A.1 becomes a linear expression in the $\{D_i\}$ only, and these coefficients may be found by linear regression.

It will be noted that since the exponents $\{a_i\}$ are found in the first step, independently of the coefficients $\{D_i\}$, the method may readily be applied to fit a set of data in which it is known that there are jump changes in some or all of the $\{D_i\}$

at certain known instants. It is only necessary that there be at least n data points between these discontinuities.

In the case of fitting to the vestibulo-ocular response the situation is complicated by the fact that the observed variable, here called f(kT), is to be fitted to an expression of the form

$$f(kT) \cong \sum_{i-1}^{n} D_i e^{a_i kT} + A_0 + A_1 \sin(\omega kT) + A_2 \cos(\omega kT) \qquad \text{Eq. A.5}$$

where the frequency of the sine and cosine terms is known. In fact there is only one exponential term in the Sugie-Jones model, but it is useful to consider this more general case. Fitting to this expression involves only a slight modification of the procedure outlined above. After rearrangement Eq. A.5 may be re-written as

$$y_k \cong f_k - A_0 - A_1 S_k - A_2 C_k$$

$$= \sum_{i=1}^{n} D_i x_i^{k} \qquad \text{Eq. A.6}$$

where the abbreviations y_k, f_k, S_k, C_k, are used to represent y(kT), f(kT), sin(ωkT) and cos(ωkT) respectively, and x_i is equal to $e^{a_i T}$ as before. Now y_k in Eq. A.6 must satisfy Eq. A.2, and hence by substitution it is found that

$$f_k - A_0 - A_1 S_k - A_2 C_k = \sum_{i=1}^{n} (f_{k-i} - A_0 - A_1 S_{k-i} - A_2 C_{k-i}) b_i$$

and therefore

$$f_k = \sum_i b_i f_{k-i} + A_0(1 - \sum_i b_i) + A_1(S_k - \sum_i b_i S_{k-i}) + A_2(C_k - \sum_i b_i C_{k-i}),$$

$$i = 1, 2, \ldots\ldots n. \qquad \text{Eq. A.7}$$

The last two terms on the right hand side of this expression may be readily simplified using well known trigonmetric identities, yielding,

$$f_k = \sum_i b_i f_{k-i} + A_0(1 - \sum_i b_i) + A_1(S_k(1 - \sum_i b_i C_i) + C_k \sum_i b_i S_i)$$

$$+ A_2(C_k(1 - \sum_i b_i C_i) - S_k \sum_i b_i S_i),$$

$$= b_1 f_{k-1} + b_2 f_{k-2} + \ldots\ldots + b_n f_{k-n} + G_0 + G_1 S_k + G_2 C_k,$$

$$i = 1, 2, \ldots\ldots, n. \qquad \text{Eq. A.7a}$$

where

$$G_0 = A_0(1 - \sum_i b_i)$$

$$G_1 = A_1(1 - \sum_i b_i C_i) - A_2 \sum_i b_i S_i$$

$$G_2 = A_2(1 - \sum_i b_i C_i) + A_1 \sum_i b_i S_i .$$

Implementation of this fitting procedure is straightforward if the $\{D_i\}$ are constant throughout the time interval $0 \leq t \leq (N-1)T$ for which the data are provided. However in fitting to the vestibulo-ocular response this is not the case, and some explanation of the procedure used is necessary. Consider an arbitrary segment of the sinusoidal vestibulo-ocular response, containing several saccades in the time interval $0 \leq t \leq (N-1)T$. It is assumed on the basis of the Sugie-Jones model that during each slow-phase interval the response may be fitted to a sampled funtion having the same form as Eq. A.5, with $i = 1$, but that the magnitude D of the exponential term, while constant during each single slow-phase interval, will differ in successive slow-phase intervals owing to the occurrence of saccades. Thus during the m^{th} slow-phase interval, the output could be represented as

$$f(kT) = D_m e^{akT} + A_0 + A_1 \sin(kT) + A_2 \cos(kT),$$

in which the subscript on D now refers to the interval number. Now Eq. A.7a, from which the parameters b, G_0, G_1 and G_2 are to be determined by regression, is independent of D and hence data from several slow-phase intervals, each having a different value for D_m, may be used in the regression provided only that the D_m are constant during each interval. Thus in the digital-computer implementation of this method, the sampled values $f(kT)$, $K=0, 1, 2, \ldots$ $\ldots, (N-1)$, of the eye position records are inputted to the program, along with a list of the times at which the slow-phase intervals begin and end. In performing the regression on Eq. A.7a, the program accepts those values which lie within the slow-phase intervals and ignores data points corresponding to the quick phases. It must be emphasized that data from all the slow phase intervals are included in this first regression (on Eq. A.7A) which yields the parameters b, G_0, G_1 and G_2. These parameter values are used to calculate a, A_0, A_1, and A_2, and then each D_m is computed separately using the data from the m^{th} interval.

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