THE INFLUENCE OF TONIC LABYRINTHINE STIMULATION UPON SENSORY AWARENESS AND SOLEUS MOTONEURON EXCITABILITY IN NORMAL MAN

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ABSTRACT

The objectives of this project were to examine the influence of natural labyrinthine stimulation, evoked by whole head-body displacements in the coronal plane, upon the reflex excitability of the extensor (soleus) motoneurons pool (MNP) in man and sensory awareness of static orientations in space.

Visual input was eliminated and subjects were immobilized on a modified circoelectric bed by means of partial casts for the neck and legs, a canvas corset around the torso, and straps for the upper limbs. Static lateral displacements (0-180°) from the upright vertical were applied randomly in either clockwise or anticlockwise directions and the following two series of experiments were carried out. First, the variability in the soleus MNP excitability was measured with the H-reflex technique; and second, errors in estimating the visual vertical were used to evaluate sensory awareness of head and body positions in space. 14 adolescent female subjects were tested. The ensemble responses from both experiments were analyzed separately to determine the contribution of static labyrinthine input to postural control and orientation in space. The results were also compared to shed light upon the existence of any functional correlation between conscious and unconscious postural control mechanisms.

One major and two minor response patterns emerged from the H-reflex study. In 8 out of 14 subjects, the H-reflex was progressively facilitated with increasing tilts in either an ipsi- or contralateral direction. Conversely, 3 subjects responded with bilateral inhibition, and the remaining 3 subjects with a response asymmetry characterized by ipsilateral facilitation and contralateral inhibition. These results largely coincide with the patterns obtained from unit recordings of otolithic afferents in response to static tilt (Fernandez and Goldberg, 1976a).

In the sensory awareness study, 8 out of 14 subjects responded to clockwise and anticlockwise rotation in the coronal plane with symmetrical errors in estimating the location of the upright vertical. The response was characterized by low errors of estimation for tilts in the range of 0-30°, and progressively increasing errors of estimation with greater angles of tilt. Comparison between the sensory and motor data gathered appears to provide preliminary evidence for functional correlations between motor and sensory functions.

In conclusion, tonic vestibular input has been shown to maintain a significant influence upon both conscious sensory awareness of head-body orientation in space and reflexive motor control of lower limb extensors in man.

RESUME

Ce projet a eu pour objectifs l'étude de l'influence d'une stimulation labyrinthique naturelle suscitée par des déplacements - sur le plan frontal - de tout le corps et de la tête sur l'excitabilité du groupe de motoneurons du réflexe d'extension (soléaire) (MNP) chez l'homme, ainsi que sur la perception sensorielle de l'orientation statique spatiale.

Le champ visuel a été bloqué et les sujets ont été immobilisés sur un lit circoélectrique par des plâtres partiels placés autour du cou et sur les jambes, ainsi que par un corset de toile placé autour du torse et par des courroies sur les membres supérieures. Les sujets ont été soumis à des déplacements latéraux statiques (0°-180°), à partir d'une position verticale, vers la droite ou vers la gauche selon les lois du hasard et les expériences suivantes ont alors été effectuées. Premièrement, la variabilité de l'excitabilité du groupe de motoneurons du soléaire a été mesurée grâce à la technique de Hoffmann, et deuxièmement, les erreurs des sujets dans l'évaluation des axes visuels verticaux ont servi à évaluer la perception sensorielle des positions de la tête et du corps dans l'espace. 14 sujets adolescents de sexe féminin ont été testés et les réponses des deux expériences ont été analysées séparément afin de déterminer la contribution de la puissance labyrinthique statique sur les rendements moteurs et sensoriels. Les deux groupes de réponses ont alors été comparés afin d'expliquer la corrélation fonctionnelle existant entre les mécanismes conscients et inconscients du contrôle postural.

Trois modèles de réponses ont émergés de l'étude du réflexe de Hoffman, l'un d'ordre majeur et deux d'ordre mineur. Pour 8 des 14 sujets testés, le réflexe de Hoffmann a été progressivement facilité grâce à une amplification des inclinaisons ipsi- et contralatérales. Réciproquement, 3 sujets ont répondu par une inhibition bilatérale et les 3 derniers sujets par une asymétrie caractérisée par une facilitation ipsilatérale et une inhibition contralatérale. Ces résultats coincident en grande partie avec les tracés obtenus des enregistrements des afférents otolithiques sous l'effet d'inclinaisons statiques (Fernandez et Goldberg, 1976).

Dans l'étude de la perception sensorielle, 8 des 14 sujets ont répondu à des rotations vers la droite et vers la gauche, sur le plan frontal, par des erreurs de symétrie en estimant la location de la position verticale. Les réponses ont été caractérisées par des erreurs de jugement minimes lors d'inclinaisons allant de 0 - 30° et le taux d'erreur a progressivement augmenté lorsque les sujets ont été soumis à des inclinaisons plus amples.

Une comparaison des données sensorielles et motrices ont permi de conclure préliminairement à des corrélations fonctionnelles entre ces deux groupes de résultats.

Pour conclure, il a été démontré que la puissance vestibulaire tonique joue un rôle important autant dans la perception sensorielle consciente que pour le contrôle moteur réflectif d'extension des membres inférieurs chez l'homme. Des études plus poussées permettront peut-être de développer un outil d'évaluation clinique permettant de distinguer les contributions relatives des diverses sources d'afférence dans le maintien de la position verticale chez l'homme.

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subject was displaced 60° forward or backward from the vertical, and a minimal amplitude of the H-reflex in the vertical position. These findings were contrary to those found in cats with neck reflexes eliminated in that nose up tilt (dorsiflexion) of the head produced shortening of the medial triceps (Roberts, 1967; Roberts, 1968; Lindsay et al., 1976). However, they concurred with results obtained from unit recordings in decerebrate cats (Ehrhardt and Wagner, 1970) as well as those evoked by dynamic inputs to the otolith (Watt, 1976). However, macular sensitivity to tilt is more pronounced in the coronal plane (Fernandez et al., 1976b), and interest in the response patterns associated with lateral tilt away from the vertical has begun to emerge.

Therefore, the primary objective of the present study is to monitor the pattern of excitability of the human soleus motoneuron pool in response to whole head-body rotations in the coronal plane, and to determine the extent to which the reflexive response patterns differ from those seen in quadrupeds. In addition, we took the opportunity to record each subject's conscious awareness of head-body displacements in space in order to compare both motor and sensory data in the same subject. Errors in estimation of the vertical in relation to random whole head-body displacements, over a range of 0-180° in the coronal plane, were recorded from each subject on three different days in an effort to gather comprehensive psychophysical data for tonic labyrinthine inputs due to static changes in whole head-body positions.

In light of recent findings implicating abnormal labyrinthine control mechanisms in adolescents with idiopathic scoliosis (Sahlstrand *et al.*, 1978; Sahlstrand and Petruson, 1979), the experimental population consisted of 14 normal healthy female adolescents with no history of neurological or muscular disease. Utilization of this selective population permits the data to be used in the future as a baseline for comparison with adolescents diagnosed as having idiopathic scoliosis. However, before proceeding with methodological details, *Chapter Two* will review the literature concerning the role of vestibular receptors in transducing spatial information, and the pathways via which the latter is transmitted to the *lumbar cord* to effect postural adjustments. In addition, literature concerned with the transmission of sensory information to the *cortex* to provide the organism with a precise perception of head and body positions in space will be reviewed.

CHAPTER TWO

OTOLITHIC MECHANISMS INVOLVED IN MOTOR CONTROL OF POSTURE AND SENSORY AWARENESS

1. Information transduced by Otolithic Receptors

The vestibular system is composed of otoliths and semicircular canal receptors. They function to activate a motor system capable of stabilizing the head and body in space and maintain the visual image during head movements (Wilson and Peterson, 1978), as well as provide sensory appreciation of head position and dynamic linear or rotational accelerations (Melville Jones and Young, 1978).

Phasic vestibulospinal and vestibulo-ocular reflexes originate from the semicircular canals in response to rotational accelerations (Precht, 1979). In contrast, the otoliths give rise to both phasic and tonic vestibulospinal reflexes during linear accelerations and maintained displacement of the head relative to gravity (Wilson and Peterson, 1978). Thus, the static head displacements to be employed in our experiment would selectively stimulate otolithic receptors, whose response characteristics will now be examined in greater detail.

1.1 Role of the Utricle and Saccule

Morphologically, the utricle and saccule contain hair cells embedded in a sensory membrane, known as macula, superimposed upon which is a gelatinous otolith membrane containing crystals of calcium carbonate (Wilson and Peterson, 1978). As mentioned previously, the effective stimulus of these otolithic organs is generally agreed to be gravity or other inertial forces which systematically transmit traction, pressure and shearing movements to the mechanical end-organ (Trincker, 1962; Melville Jones, 1967). The maculae are capable of yielding distinctive patterns of afferent neural signals of static positions of the head relative to gravity and linear accelerations in the horizontal, vertical and sagittal planes (Fernandez _et al_., 1972; Fernandez and Goldberg, 1976a, c).

To accomplish this task, each neuron has a characteristic polarization vector which defines the axis of greatest sensitivity (Baloh and Honrubia, 1979). The utricle anatomically lies in the horizontal plane and the majority of its functional polarization vectors likewise lie in this plane. In the upright position, utricular units have a resting discharge which averages approximately 60 spikes per second and have a higher sensitivity than saccular units (Fernandez _et al_., 1972). Some 75% of these utricular units are excited by ipsilateral tilt and inhibited by contralateral tilt, whereas 25% are activated by contralateral tilt. Some response to forward and backward tilt can also be elicited because of a slight curvature in the utricle which alters the plane of its peripheral polarization vectors (Fernandez and Goldberg, 1976b). In contrast, the saccule is anatomically situated in the sagittal plane which results in the majority of its functional polarization vectors being parallel to gravity vectors. Thus, linear accelerations and small tilts away from the gravitational vertical evoke responses in the neuronal units of the saccule. Furthermore, the neuronal units of the otolithic receptors have been subdivided into several classes according to their different response characteristics. As will emerge below, a continuum of tonic, tonic-phasic and phasic response patterns, as seen generated by the cristae of the semicircular canals, have been recorded from otolithic receptors.

1.2 Otolithic Response Patterns

Distinctive "regular" and "irregular" firing patterns have been identified by several authors in various mammalian species (Goldberg and Fernandez, 1971; Macador *et al*., 1975; Anderson *et al*., 1978). "Regular" firing units maintain a constant ratio between the applied force and the response generated. Their tonic output displays little change in gain or phase over a wide range of frequencies and shows no significant adaptation to sustained input (Fernandez and Goldberg, 1976c). "Irregular" firing units not only adapt rapidly to changes in linear acceleration, show a continuous increase in gain, and have a wide frequency response range, but they also respond to the velocity of displacement (Baloh and Honrubia, 1979). These phasic units have no position sensitivity and respond only when the head and body are moving. Consequently, tonic vestibulospinal reflexes are likely mediated by "regular" firing units which have been shown to project via specific pathways through the vestibular nuclei as far as the lumbar cord (Gernandt *et al.*, 1957). The processing of information in the CNS thus begins in the vestibular nuclei of the brainstem, and the following section will shed light upon some of the complex central vestibular mechanisms which transform the raw signals generated by the peripheral receptors to both postural control and the perception of spacial orientation.

2. The Central Vestibular System

The vestibular nuclei are not simply relay stations but complex integrating centers. Anatomical and physiological studies have established connections between these nuclei and the following structures: (1) vestibular receptors, (2) reticular formation, (3) cerebellum, (4) cortex, (5) visual centers, and (6) peripheral cutaneous, joint and muscle receptors (Wilson and Peterson, 1978). Therefore, signals arising in the two labyrinths could interact with signals from other somatosensory systems in the vestibular nuclei, and the efferent output of the latter actually reflects the interaction of the various afferent systems. Thus, in outlining the anatomical connections between the labyrinthine receptors and the vestibular nuclei, and the connections between each nucleus and other sites in the CNS, a conceptual framework for understanding the functional responsibilities of each nucleus will be formulated.

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CHAPTER ONE

GENERAL INTRODUCTION

Studies focusing upon the contribution of vestibulospinal reflexes to the control of upright human posture have recently begun to emerge as a basis for understanding deficient or distorted vestibular function (Lund and Broberg, 1983; Black and Nashner, 1984; Bles et al., 1984). However, current understanding of postural control mechanisms remains predominantly based upon findings in quadrupeds as opposed to bipeds, and further research is necessary to correlate and compare animal with human studies.

To date, human experimentation has largely been restricted to dynamic rather than static stabilizing influences and/or has relied upon non-physiological forms of labyrinthine stimulation which include caloric and electrical stimulation (e.g. Delwaide and Juprelle, 1977; Lund and Broberg, 1983). The role of tonic, otolith-originating vestibulospinal reflexes in the maintenance of postural equilibrium in response to static head and body displacement in space is in need of further exploration. Thus, Chan and Kearney (1982) examined the influence of whole head-body displacements in the sagittal plane (i.e. fore-aft tilts) upon the excitability of the human soleus motoneuron pool. The amplitude of the H-reflex was mapped in relation to different degrees of angular displacement over a range of 30° to 150° while neck and visual inputs were eliminated, and exteroceptive stimulation minimized. They reported maximal increase in the amplitude of the H-reflex when the

2.1 The Vestibular Nuclei

The vestibular nuclei consist of a group of neurons located on the floor of the fourth ventricle. Four distinct anatomical groups of neurons have been described. These include the superior vestibular nucleus, the descending vestibular nucleus, the medial vestibular nucleus, and the lateral vestibular or Deiter's nucleus (Brodal, 1974). The majority of these nuclei receive primary afferent input from vestibular nerve fibers.

2.1.1 The Superior Vestibular Nucleus

The superior vestibular nucleus receives afferent projections from the cristae of the semicircular canals and a large proportion of its input from the cerebellum. From this nucleus, axons project to the medial longitudinal fascicle and innervate the motor nuclei of the extrinsic eye muscles (Gacek, 1969). It would appear that this nucleus is a major relay center for ocular reflexes mediated by the semicircular canals.

The number of neurons which project to the thalamus from the superior nucleus is relatively small and has led to speculation concerning their existence (Mergner, 1979). However, more recent anatomical and physiological studies in the cat have reaffirmed the existence of bilateral vestibulothalamic pathways which project to the ventrocaudal and ventrobasal complexes (Maciewicz *et al.*, 1982). Given the multiple modalities of sensory input to these thalamic regions, the functional significance of relays through the thalamus appears to be subcortical sensory integration.

2.1.2 The Descending Vestibular Nucleus

The descending vestibular nucleus is anatomically not as well circumscribed as the other vestibular nuclei, but nonetheless appears to play an important role in integrating signals from both labyrinths with information from the cerebellum and the reticular formation. It receives primary afferent projections from the utricles and saccules as well as a small contribution from the semicircular canals. In addition, cerebellar afferents seem to be scattered throughout the nucleus (Gacek, 1969).

Efferent pathways project to the cerebellum, the reticular formation, the contralateral vestibular nuclei, and the thalamus by running parallel to the classical auditory pathway through the brainstem (Abraham *et al.*, 1977). They thereby facilitate communications between both sides, and hypothetically allow the cerebellum to exert fine control over visual and postural adjustments to the input mediated by otolithic receptors.

2.1.3 The Medial Vestibular Nucleus

The superior part of the nucleus receives input from the cristae of the semicircular canals and from the floccule and fastigial nucleus of the cerebellum. The ventral and caudal portions of the nucleus receive contralateral input from the cerebellum and some fibers from the reticular formation (Brodal, 1974).

The medial vestibulospinal tract which descends bilaterally to the muscles of the cervical and thoracic spine, originates in part from this nucleus (Nyberg-Hansen, 1965) as well as the descending (Wilson _et al_., 1967b) and lateral (Rapoport _et al_., 1977) vestibular nuclei. Once again, there are efferent projections to the cerebellum, reticular formation, the contralateral vestibular nuclei, and the contralateral thalamus. Moreover, a projection to the cerebral cortex of the cat has been found in the region of the anterior suprasylvian sulcus (ASSS) and the anterior ectosylvian gyri (Abraham _et al_., 1977; Becker _et al_., 1979). Thus, the medial nucleus becomes a center for coordinating eye, head, and neck movements and probably contributes to sensory appreciation of these movements in space.

2.1.4 The Lateral Vestibular (Deiter's) Nucleus

The lateral vestibular nucleus is an important locus of control for vestibulospinal reflexes. It receives primary vestibular afferents from the utricular macula and its output is projected to both the spinal cord (Gacek, 1980), and via the ascending tract of Deiter's to the ipsilateral thalamus and the sensorimotor cortex (Maciewicz _et al_., 1982). Given the natural physiological stimulus of head and body tilt in the longitudinal, vertical or transverse planes, signals are relayed through the lateral vestibular nucleus to the ipsilateral muscles at all levels of the neuraxis via the lateral vestibulospinal tract (Abzug et al., 1974). In addition, responses recorded from the region of the anterior suprasylvian gyrus to static tilts in the sagittal and coronal planes showed that cortical neurons are likewise stimulated by off-vertical rotations, and the patterns of response are comparable to those recorded directly from the lateral vestibular nucleus (Becker et al., 1979). The lateral vestibular nucleus is in turn strongly influenced by the sensorimotor cortex as well as peripheral sensory and proprioceptive stimuli (Azzena et al., 1983). Thus, this nucleus is considered to be an important locus of motor control and contributes directly to sensory awareness of orientations in space (see section 4.1).

This tract and others (cf. section 2.2) which mediate vestibulospinal information to the lumbosacral cord are most relevant to the present study, by virtue of the fact that our primary objectives are to investigate the role of tonic labyrinthine influences upon soleus motoneuron excitability and its contribution to conscious experience of static head-body displacements in space (see section 4.1). Hence, having globally examined the contribution of the vestibular nuclei to integration of sensory inputs and their role in the motor control of ocular and postural reflexes, it is now important to consider in more detail the specific pathways which project to the spinal cord.

2.2 Vestibulospinal Tracts and Their Influence on Spinal Motoneurons

It has been shown that vestibular activity is relayed to the spinal cord through the vestibular nuclei in the medulla and the pons by three main tracts: the medial vestibulospinal (MVST), the lateral vestibulospinal (LVST) and the reticulospinal tracts (RST) (*cf*. Wilson and Melville Jones, 1979).

2.2.1 The Medial Vestibulospinal Tract

Briefly, the MVST originates in the medial (Nyberg-Hansen, 1965), descending (Wilson *et al*., 1967b) and lateral (Rapoport *et al*., 1977) vestibular nuclei. It projects bilaterally to the level of the *cervical* region of the spinal cord, and functions to transmit excitatory and inhibitory information to upper axial and *neck* muscles (Nyberg-Hansen, 1965; Pompeiano, 1975; Wilson and Melville Jones, 1979), in response to predominantly *rotatory* stimuli (Wilson and Maeda, 1974). Thus, input to this tract is primarily from the semicircular canals and there are no known MVST connections with lower limb motoneurons. Its functions is therefore of little relevance to the present study.

2.2.2 The Lateral Vestibulospinal Tract

As mentioned previously (section 2.1.4), the LVST is presently thought to originate solely from the lateral vestibular or Deiter's nucleus (Nyberg-Hansen and Mascitti, 1964; Akaike, 1983) and projects ipsilaterally to all levels of the spinal cord. Antidromic stimulation of fibers in the lateral vestibular nucleus has demonstrated that (a) otolithic receptors are its primary source of input (Stein and Carpenter, 1967), and (b) it is somatotopically organized according to spinal segments (Ito *et al.*, 1964; Wilson *et al.*, 1967a; Akaike, 1983). Hence, functionally this tract is capable of influencing the tone of both axial and limb musculature, and indeed, lateral tilt has been found to excite identified LVST neurons projecting to the lumbar level (Peterson, 1970; Orlovsky and Pavlova, 1972).

More specifically, electrophysiological studies have revealed that these descending impulses facilitate extensor and inhibit flexor alpha and gamma motoneurons of the fore- and hind-limbs via mono-, di-, and poly-synaptic pathways (Wilson and Yoshida, 1969; Grillner *et al.*, 1970; Kato and Tanji, 1971). It should be noted that the interneurons involved in these circuits also mediate spinal segmental reflexes (Hultborn *et al.*, 1976), and may therefore be biased by somatosensory input.

2.2.3 The Reticulospinal Tract

The reticulospinal tract (RST) arises from four reticular nuclei which receive input from both semicircular canals and otolithic receptors (Spyer *et al*., 1974). The bulk of this tract reaches the lumbar cord bilaterally (Nyberg-Hansen, 1965), and evokes monosynaptic excitatory (Grillner and Lund, 1968) as well as disynaptic excitatory and inhibitory influences on lumbar motoneurons (Akaike *et al*., 1973). The pattern of influences is generally reciprocal to that of the LVST (Grillner and Lund, 1968; Wilson and Yoshida, 1969).

Summarizing, it is clear that there are extensive vestibular pathways which exert their influence on spinal motoneurons either *directly* via monosynaptic excitation of alpha and gamma motoneurons, or *indirectly* by altering the bias of interneurons. In addition, some of these interneurons subserve somatosensory reflexes. In the context of this project, the interaction between somatosensory inputs and vestibulospinal reflex pathways are most relevant. Somatosensory inputs not only contribute greatly to ensuring that functionally meaningful reflex responses occur, but also provide greater subjective cues for awareness of orientations in space. Moreover, it appears that inputs from the peripheral receptors of spinal and limb muscles and articulations are largely funneled through the cerebellum for fine-tuning before transmission to the vestibulospinal tracts. In light of their functional importance, therefore, somatosensory, proprioceptive, cerebellar, and central inputs to the vestibulospinal tracts will now be considered.

2.3 Inputs to the Vestibulospinal Tracts

It appears that both peripheral and central inputs converge upon neurons of the vestibular nuclei (Azzena *et al.*, 1983). Stimulation of peripheral nerves which activate a variety of receptors, can directly produce long-lasting facilitation of spinally projecting neurons of Deiter's nucleus (Wilson *et al.*, 1966; Pompeiano, 1972; Rubin *et al.*, 1977). More importantly, 81% of the neurons in Deiter's nucleus are influenced by *both* labyrinthine stimulation and body movements (Frederickson and Schwarz, 1971), providing firm evidence for functional interaction between somatosensory and labyrinthine inputs. Furthermore, single cells of the lateral vestibular nucleus reponded to cortical sensorimotor stimulation as well as ipsilateral sciatic or radial nerve stimulation (Deecke *et al.*, 1979; Azzena *et al.*, 1983). These findings reinforce the concept of integration of convergent inputs to control the output of Deiter's nucleus.

2.3.1 Somatosensory and Proprioceptive Inputs

Wilson *et al.* (1966) reported that cutaneous and muscle afferents, with the possible exclusion of spindle afferents and those arising from tendon organs, mediate facilitatory influences on neurons of the lateral vestibulospinal tract in decerebellated cats. Further evidence supporting the role of somatosensory and vestibular interactions in the maintenance of both static and dynamic postural equilibrium has been provided by studies on vestibular compensation for distortions or deficiencies of labyrinthine input. Compensation occurs rapidly provided that afferent input from the cortex, cerebellum, and peripheral receptors are adequate (cf. Schaefer and Meyer, 1974; Pfaltz, 1983; Bles et al., 1984; Igarishi, 1984). Exercises which reinforce spinal ascending systems, including work on inclined planes or subject centrifugalization, accelerate compensation significantly (Pflatz, 1983; Igarishi, 1984). However, damage to the spinal cord or changes in somatosensory afferent activity can delay or prevent the compensation of lesions in the vestibular system (Schaefer and Meyer, 1973; Pfaltz, 1983).

Proprioceptive inputs have likewise been found to play an important role in maintaining postural equilibrium. It has been shown that nerve endings in the ligaments and capsules of the upper three cervical articulations contribute highly to the maintenance of normal cervico-ocular and tonic neck reflexes (Hikosaka and Maeda, 1973). More recently, Mauritz and Dietz (1980) evaluated the significance of proprioceptive input to the control of upright stance in man by ischaemic blocking of leg afferents and found that body sway increased and was characterized by an oscillation frequency (of about 1 Hz) which was observed in patients with tabes dorsalis.[1]

Thus, joint, cutaneous, and muscle receptors of both the trunk and the extremities appear to interact with vestibular input to provide an important integration of messages concerning head and body localizations in space and contribute to the control of an upright stance.

2.3.2 Cerebellar Inputs

Anatomically, it has been demonstrated that primary and secondary vestibular fibers project to the flocculo-nodular lobe of the cerebellar cortex, as well as parts of the uvula and the fatigial and dentate nuclei (Brodal et al., 1962). The flocculus receives input from vestibular, visual, and proprioceptive sources to Purkinje cells which in turn project to second-order vestibular neurons involved in the vestibulo-ocular reflex arc (Ito et al., 1974; Takemori and Cohen, 1974; Precht, 1979). Functionally, it is thought to provide constant feedback from the eye to the labyrinths to aid in stabilization of the retinal image (Precht, 1979). Moreover, the flocculus is likely responsible for the plasticity of the vestibulo-ocular reflex demonstrated by Gonshor and Melville Jones (1971, 1976).

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[1] A condition in which proprioceptive afferents are lesioned.

The nodulus also receives input from vestibular, visual, and proprioceptive inputs but efferently projects to sites involved in postural control rather than oculomotor control (Igarishi et al., 1973). In addition, the anterior and posterior lobes of the cerebellum as well as the vermis receive multisensory spinal inputs and appear to play a major role in modulating vestibulospinal reflexes (Precht, 1979).

Both direct and indirect projections from the cerebellum to the Deiter's nucleus have been identified (Brodal, 1962; Pompeiano, 1974). Direct projections to the Deiter's nucleus originate primarily from the anterior lobe and in less density from the posterior lobe, and were found to monosynaptically inhibit the LVST neurons (Ito et al., 1968; Akaike et al., 1973). Thus, when the cerebellum is intact, it appears to provide constant modulations of ongoing vestibulospinal reflexes in response to positional changes (Orlovsky, 1972; Dutia et al., 1981). Moreover, inhibition of these postural reflexes appear to occur in patterns which coincide with dynamic functional demands (Wylie and Filpel, 1971; Allen et al., 1972; Bruggengate et al., 1975). For example, Purkinje cell firing is apparently harmonized with the phases of step during the gait cycle (Orlovsky, 1972). Furthermore, decerebellation of a decerebrate cat produces strong extensor rigidity which is likely due to disinhibition of tonic vestibular reflexes (Pollack and Davies, 1927).

The dramatic effects of the above lesion experiments serve to illustrate the enormous importance of cerebellar influence upon postural control. More specifically, the extensive convergence of inputs from various sensory modalities (Wilson and Peterson, 1978), including the vestibular nuclei (Wilson and Melville Jones, 1979) at the cerebellum, provide the latter with a means of fine-tuning the muscular activity needed to maintain postural equilibrium under a variety of conditions.

2.3.3 Cortical Inputs

Projection of inputs from the vestibular complex to the cerebral cortex has been confirmed by studies which utilized electrical (Anderson and Gernandt, 1954), caloric (Landgren et al., 1967), and natural (Becker et al., 1979) labyrinthine stimulation. Responses to each of these modes of stimulation were recorded from the region of the anterior suprasylvian sulcus (ASSS) which lies between the auditory and second somatosensory area (Abraham et al., 1977).

Cortical neurons showed clear modulations of activity in all three planes of movement by characteristically signalling the excitatory direction of rotation (Becker et al., 1979). Two major and two minor response patterns, which correlated with the classical patterns of response recorded from the vestibular nerve (Fernandez and Goldberg, 1976a) were identified. The two major patterns were equally represented and consisted of ipsilateral excitation to tilt and contralateral inhibition (Type I), or ipsilateral inhibition to tilt and contralateral excitation (Type II). The two minor patterns responded by either bilateral excitation or bilateral inhibition (Type III and Type IV). In addition, many of these cortical neurons responded to proximal joint displacement of one or several limbs as well as visual input (Becker et al., 1979). These results provide a firm neurophysiological basis for the processing of conscious sensory awareness of postural alterations in space (cf. also section 4.1).

Evidence for interaction between the sensorimotor cortex and vestibular nuclei was provided by Azzena et al. (1983), in a study which utilized electrical stimulation of both the sigmoid gyrus of the cat and the peripheral nerves subserving the fore and hind-limb areas, to determine whether they converged upon the same vestibular nuclear neurons. The majority of the cells recorded within Deiter's nucleus responded to both ipsilateral peripheral nerve stimulation and contralateral cortical stimulation. The latencies of the response recorded from the cortex (4-6 msec) implied that a multisynaptic pathway was involved.

Thus, evidence for cortical influence upon posture and movement regulation as well as conscious sensory integration has begun to accumulate, and the logical progression of these studies will be to include sensory and motor data gathered in the same subject to provide a more holistic understanding of postural control mechanisms in relation to spatial perception. However, before complicating the postural control picture, a closer examination of the role of tonic labyrinthine reflexes in animals and humans will serve to shed more light upon one of the classical reflex mechanisms which underlie equilibrium reactions.

3. Tonic Labyrinthine Reflexes and Postural Control

Tonic labyrinthine reflexes are naturally activated to maintain equilibrium in response to static changes in head displacements relative to space. As mentioned previously, these are probably mediated by utricular and saccular receptors which are sensitive to the angle of tilt (Fernandez *et al.*, 1972). Moreover, spatial distribution of activity in axial and limb musculature differ for each direction of head displacement. This can now be discussed in light of findings from both animal and human experiments.

3.1 Animal Studies

Animal studies which were carefully controlled to elicit tonic labyrinthine reflexes independent of tonic neck reflexes (Roberts, 1967, 1973, 1979), showed that upward tilt of the *head* caused extension of both hindlimbs and flexion of both forelimbs. Downward tilt reversed that response to flexion of both hindlimbs and extension of both forelimbs. On the other hand, lateral tilt evoked ipsilateral extension of both fore- and hind-limbs to restore equilibrium.

It is interesting to note that tonic neck reflexes, evoked by static displacement of the body on the stationary head, were found to have precisely the opposite effect on limb muscle tonus. Thus, downward tilt of the neck resulted in flexion of the upper limbs and extension of the lower limbs, while lateral tilt caused extension of the contralateral limbs and flexion of the ipsilateral limbs (Roberts, 1979). This antagonistic interaction of neck and labyrinthine activities is thought to allow free movement of the head in the intact animal without affecting the stability of the trunk (Roberts, 1973; Pompeiano, 1974; Lindsay et al., 1976; Schor and Miller, 1981).

Interestingly, increases in the extensor tone of muscles of the lower limb may depend upon whether a given stimulus is of a static or dynamic nature (Nashner, 1972). It has been noted that motor patterns recorded from forelimb extensors in response to sinusoidal stimuli below 0.2 Hz (Soechting et al., 1977) were antagonistic to those elicited by static tilt (Lindsay et al., 1976; Anderson et al., 1979). Thus, it has been postulated that EITHER the location of the otolithic receptors with their specific polarization vectors allows them to be excited by differential stimuli, OR that static and dynamic reflexes require different processing at the level of the brainstem and subsequent alteration of response patterns (Chan, 1983).

However, the majority of the above studies were conducted in quadrupeds. Relatively few reports have shed light on the role of vestibulospinal reflexes in man whose bipidal mode of stance may require different equilibrium responses. Now, in light of the findings in animals, studies on motor control of postural reflexes in man will be critically evaluated.

3.2 Human Studies

The control of posture is driven by a multisensory system which includes visual, somatosensory, proprioceptive, neck, and vestibular inputs. Nashner (see review in 1981) reported an increased amplitude of postural sway in normal men during electrical stimulation of the vestibular apparatus in response to inhibition of visual cues and disruption of somatosensory inputs. In addition, Mauritz and Dietz (1980) occluded vision and proprioceptive inputs from the Ia afferents of lower limb muscles and likewise found that postural sway increased significantly. The interaction between neck and vestibular information was investigated by Nashner and Wolfson (1974), who galvanically stimulated the labyrinths while the subjects stood on a sway platform, and found the resultant EMG response to be related to changes in the direction of head on body rotation. Clearly, sensory inputs appear to be coordinated in their efforts to maintain human postural stability.

The relative contribution of vestibular inputs in themselves to postural stability was recently studied by Black and Nashner (1984). They found that patients with reduced or distorted vestibular function were unable to maintain an upright equilibrium when visual and proprioceptive influences were inaccurate. In addition, patients with distorted peripheral vision (paroxysmal positional nystagmus) remained posturally stable solely when their eyes were closed. From these results, therefore, it appears that compensation for vestibular deficiencies can occur provided that visual and proprioceptive inputs are unobstructed, and conversely, compensation for visual and proprioceptive deficiencies can occur provided that vestibular inputs are adequate. Otherwise, it appears that patients have no alternative means of being able to re-weigh orientation references which contribute to postural control.

As mentioned previously (see section 3.1), vestibulospinal reflex activity is an integral part of the motor control system, and in man has been shown to persist in influencing the tone of lower limb extensors which are essential to the maintenance of an upright posture. However, the precise nature of the influence remains unclear in that both non-physiological and natural labyrinthine stimulation were utilized by different authors, and in some experiments, failure to isolate input variables influenced the reported results. For example, Delwaide and Juprelle (1977) employed *caloric* stimulation to excite labyrinthine receptors while examining the excitability of the soleus monosynaptic reflex pathway. Facilitation of the H and Achilles tendon reflexes occurred during the entire period of irrigation for both ipsilateral and contralateral applications. This lack of differential response may be due to caloric stimulation of non-specific cutaneous receptors in addition to semicircular canals. On the other hand, Stejskal (1979) utilized *natural* labyrinthine stimulation by studying the effect of different head positions upon muscular activity, and reported no significant increases or decreases in levels of activity. However, the extent to which the results could be ascribed to normal tonic labyrinthine reflex action is doubtful due to the unrestrained visual inputs introduced during the experiment as well as the fact that this study population consisted of spastic patients with upper motor neuron lesions. Finally, Hayes and Sullivan (1976) studied the effect of tonic *neck* reflexes in man by altering the static positions of the head and arms in accordance with the positions characteristic of tonic neck reflexes (Linday *et al*., 1976), while monitoring the H-reflex and mechanical stretch reflex responses. However, labyrinthine inputs were not isolated, in that rotation of the head upon the body undoubtedly stimulated both the labyrinth and upper three cervical receptors, lending controversy to the authors' interpretation of their results.

Several authors have used modulations of the H-reflex to evaluate the influence of static tilt upon soleus motoneuron excitability in the sagittal plane. Chan and Kearney (1982) found that the H-reflex was minimal in the upright position and maximal at 60° of tilt either forwards or backwards. These findings did not concur with those recorded in decerebrate cats by Lindsay *et al*. (1976) and Roberts (1968, 1979), but were consistent with the findings of Ehrhardt and Wagner (1970) in that the lumbar extensor motoneurons were facilitated regardless of the direction of head tilt. More recently, Aiello *et al*. (1983) utilized a similar experimental method to evaluate static vestibulospinal influences in relation to different body tilts in man. In contrast to the findings of Chan and Kearney (1982), they observed that the excitability of the soleus motoneuron pool was maximal in the upright vertical position (90°) and minimal with the subject lying supine in the horizontal position (0°). These contradictory findings for the same basic experimental procedure have led to further evaluations of methodological details by Chan and Kearney (1984). The latter authors concluded that possible artifacts due to changes in the ankle joint position and progressive rather than random angular displacements of the whole body in the experiment by Aiello *et al*. (1983), may account for the recorded differences. In addition, their results are consistent with the many human studies on dynamic vestibular stimulation which have been reported (Melville Jones and Watt, 1971; Greenwood and Hopkins, 1976; Reschke *et al.*, 1976).

From the foregoing resumé, it has been shown that the central vestibular system consists of information processing in the vestibular nuclei which in turn interacts with the cerebellum, reticular formation, and somatosensory systems to transform the raw signals generated by the labyrinthine receptors to postural control via tonic vestibulospinal reflexes. The motor effector system has been elaborated upon, but the cortical processes which provide "sensory awareness" of postural adjustments in space have not been described. Furthermore, clinical testing for vestibular dysfunctions includes both the evaluation of *motor* equilibrium reactions as well as *sensory* appreciation of movement in terms of accuracy in predicting head and body positions relative to gravity (Gundry, 1979). This project addressed both facets of vestibular function and in this connection, the role of the otolith in the perception of spacial orientation will now be discussed.

4. Role of the Otolith in Perception of Spacial Orientation

4.1 Pathways Mediating Vestibular Sensation

Vestibulo-cortical projects were first recognized to be situated in the region of the suprasylvian gyrus in the cat (Waltz and Montcastle, 1949). In the Rhesus monkey, the localization of sensory vestibular input included the lower end of the intraparietal sulcus (Frederickson _et al_., 1966). In humans, stimulation of both regions evoked subjective sensations of rotation or body displacement (Penfield, 1957).

Moreover, vestibulo-thalamo-cortical projections appear to integrate labyrinthine and somatic proprioceptive inputs to provide information on conscious awareness of body orientation (Abraham _et al_., 1977; Deecke _et al_., 1979; Mergner _et al_., 1979). Upon destruction of the vestibular nuclei, degenerative lesions of the contralateral ventro-posterolateral nuclei (VPL) of the thalamus became evident (Liedgren and Rubin, 1976). In turn, electrical stimulation of the VPL nuclei antidromically activates secondary vestibular neurons.

All subgroups of the vestibular complex project to the thalamus, but the major contribution is made by Deiter's nucleus (Maciewicz _et al_., 1982). The brainstem pathway mediating information to the thalamus appears to run parallel to the auditory pathway, and thus passes through the pontine reticular formation lateral to the medial longitudinal faciculus (Abraham _et al._, 1977). Interestingly, there does _not_ appear to be a relay through the cerebellum, in that ablation of the cerebellum in the rhesus monkey did not alter the responses evoked by vestibular nerve stimulation in the medial geniculate body (Abraham _et al._, 1977).

Likewise, there is anatomical and physiological evidence for cortical integrations of body orienting signals (Liedgren _et al._, 1976; Becker _et al._, 1979), neurons of the VPL nuclei have been found to project to both the precentral and postcentral gyri of the sensorimotor cortex (Liedgren and Rubin, 1976). Furthermore, movements of limbs, trunk, head, and neck all excite both motor and sensory integration centers (Becker _et al._, 1979), providing human subjects with a psychosomatic frame of reference for position and movements (Valentinuzzi, 1980). Thus, the following section will elaborate upon the multiple psychological studies which have been associated with subjective accuracy in estimating body positions in space.

4.2 Psychophysical Studies

Psychophysical studies which correlate the magnitude of displacement with the accuracy of subjective predictions, represent some of the earliest investigations of sensory vestibular functions. Both dynamic studies which investigate the perceptions of linear movement, and static studies which investigate the position-sensing abilities of the otoliths after sustained tilt, have been extensively reviewed (Clark, 1970; Graybiel, 1974; Guedry, 1974; Deeke et al., 1979; Valentinuzzi, 1980; Zacharias and Young, 1981; Bles et al., 1982). Those which relate to the present project include the threshold and accuracy of estimation studies in response to static but not dynamic stimuli. The methodologies comprise postural vertical measurements and visual vertical adjustments, which respectively request that subjects return themselves to the vertical upright position after sustained tilt, or that subjects adjust a luminous line in a dark field to the apparent vertical (Valentinuzzi, 1980). Tilt devices and human centrifuges in rooms with changing intensities of illumination, under partial water immersion, and in simulated no gravity space environments, have most commonly been used to minimize proprioceptive and exteroceptive inputs and to manipulate the force environment in an attempt to isolate otolithic function. The comparative results of normal and labyrinth-deficient (L-D) subjects have been found to be significantly different, thereby establishing these methods as reliable tests for otolithic function. The results of postural vertical and visual vertical experiments will be briefly reviewed below.

4.2.1 The Postural Vertical

On earth, we are constantly experiencing above threshold stimuli to the otolith. Consequently, normal subjects, who were blindfolded and immobilized in the seated position, responded with an accuracy of 2-4° when tilted (whole head-body) up to 40° from the vertical in the sagittal plane (Mann and Dauterive, 1949). Judgements tended to fall in the direction of initial tilt, and greater accuracy of estimation in rotation about the X-axis (coronal plane) has been documented (Passey and Guedry, 1949). Consistent overestimation (E phenomena) and underestimation (A phenomena) as a function of the load of gravity (g) has been systematically recorded over a range of 100° of tilt in the coronal plane. For g values less than 1, the angle of tilt was underestimated, and for g values greater than 1, the angle of tilt was overestimated (Clark and Graybiel, 1964). Thus, angles of tilt ranging from 40°-90°, when 0° is equal to the upright vertical, were associated with greater errors of estimation. Moreover, there was a tendency to perceive the angle of body tilt as being greater than the true angular displacement.

Variables which influence judgement accuracy include the speed of rotation away from the upright, the magnitude of the tilt, and the duration of delay in a given position (Clark and Graybiel, 1964). In addition, increased variability occurs with alteration of somatosensory cues via padding of the tilt device or water immersion (Graybiel *et al.*, 1968), and is apparently dependent upon the position in which the body is immobilized. Clark and Graybiel (1968) tested normal and labyrinth-deficient patients in a standing posture and found no differences between these two subject populations. However, testing in a seated position resulted in pronounced differences which were consistent with the findings of other authors.

In general, L-D subjects showed significantly increased variability and delays in estimating positions. The A and E phenomena occurred at smaller angles of tilt, with more variance, and were more pronounced even though ocular counter-rolling[1] was minimal in L-D subjects (Clark and Graybiel, 1964). Moreover, in water, the L-D subjects had greatly diminished somatosensory cues and had difficulty restoring the tilt chair to vertical because of their greater reliance upon these inputs (Graybiel et al., 1968). Under dry land conditions, both somatosensory and visual cues compensated for their loss of gravito-inertial input (Guedry, 1974).

4.2.2 The Visual Vertical

Most studies once again focused upon the accuracy of judgement. However, the ability to set a luminous line to the vertical without altering the body position is dependent upon labyrinth and somatosensory signals as well as the ability to place a line in a particular orientation relative to the body. Surprisingly, this additional task demanded of

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[1] The involuntary conjugate rolling movements of the eyes in the direction opposite to movement.

the subject does not decrease the accuracy of prediction, but rather increases it (Clark and Graybiel, 1967). Errors of estimation in the range of 2.9° from the true vertical accounted for 75% of the judgements for tilts up to 20° from the vertical (Mann et al., 1949).

Between 20°-60° of tilt in the coronal plane, when 0° is equal to the vertical, there was a tendency to perceive a truly vertical line as being tilted in the direction of body tilt, i.e. the angular displacement was under-estimated. However, with larger tilts, vertical lines were perceived as being tilted to a greater degree than their actual position (over-estimation) (Bauermeister, 1964). Variability appeared to be influenced by alteration in somatosensory cues as well as the position of the head during the procedure (Graybiel and Clark, 1962). In the erect position, with the head upright, thresholds were 1.5°; whereas in the side-down position, with the head laterally flexed in the direction of movement, thresholds were 8.9°. In relation to these findings, it has been reported that under conditions of water submersion, when subjects were held in a particular position before being asked to swim to the surface, dependent upon the position of the head, subjects were able to perform the task with ease or difficulty (Graybiel, 1974). Furthermore, they functioned better under dynamic conditions than after a static delay was incorporated into the experiment, similar to the astronauts who must rely on continuous movement to maintain a sense of equilibrium in space (Baloh and Honrubia, 1979).

When visual cues were uninhibited, they tended to dominate the perception of orientation, but as they were reduced, graviceptors dominated (Gibson and Mowrer, 1938). As visual cues diminished, a subject being tilted experienced the deceptive perception of room tilt to coincide with their body position. This is an example of the "oculogravic illusion", which has been validated as a specific indicator of otolith function by Graybiel and Clark (1965). Under reduced visual conditions, normal subjects increasingly overestimated the angle of displacement with increasing levels of resultant force, whereas L-D subjects showed greater variance at all angular displacements, including some who were unable to make relevant settings. L-D subjects who were given normal visual cues responded with the same accuracy of prediction seen in normal subjects, thus underlining the importance of visual compensation for labyrinthine defects. Moreover, all L-D subjects improved with practice and could learn to respond with the same accuracy seen in normal subjects even when blindfolded, by becoming more attentive to somatosensory cues (Howard and Templeton, 1966; Roberts, 1967).

In summary, psychophysical studies have mapped out the perceptual sensitivity of humans to body <u>movement</u> and different body positions in relation to the vertical line of gravito-inertial forces. Errors in estimating deviations from the vertical are minimal within the range of 0-40° and progressively increase when the g values are greater than 1 (Mann and Dauterive, 1949; Passey and Guedry, 1949; Clark and Graybiel, 1964). Judgements are facilitated by dynamic movements and are increasingly variable after prolonged delay in a given position (Clark and Graybiel, 1964). Variability is likewise increased when the somatosensory cues are diminished or when the head is not immobilized in a neutral position, thus altering the input to neck and labyrinthine receptors (Graybiel *et al*., 1968; Graybiel, 1974). Labyrinth-defective patients consistently make larger errors in estimating their position in space and, after prolonged maintenance in a given position, have difficulty orienting themselves (Graybiel and Clark, 1965). Visual cues can compensate for all potential judgement errors in normal and L-D subjects (Roberts, 1967), and over a period of training, somatosensory cues can likewise compensate for reduced labyrinthine input.

5. Problem Formulation

The preceding literature review served to describe the otolithic mechanisms involved in both sensory awareness and motor control of posture. Perceptual sensitivity to whole body movements in space appears to be highly accurate and dependent upon interaction between somatosensory, visual, and vestibular cues (Graybiel et al., 1968; Graybiel, 1974). Similarly, tonic vestibulospinal reflex activity which contributes to the maintenance of body equilibrium can be modified by inputs from joint, cutaenous, and muscle receptors of both the trunk and the extremities (Wilson et al., 1966). Postural compensations for distortions or deficiencies occur rapidly, provided that these integral peripheral inputs as well as those from the cortex (Becker et al., 1979) and the cerebellum (Wylie and Filpel, 1971; Allen et al., 1972; Bruggengate et al., 1975) are adequate. However, despite observations which shed light upon the time course of recovery and the inputs necessary to drive the compensation following disease or injury to the labyrinth (Black and Nashner, 1984; Bles et al., 1984), very few studies in man focus upon the role of tonic labyrinthine reflexes in the control of upright posture, or the relative contribution of labyrinthine afferents to sensory awareness of whole body positions in space. As mentioned previously, current understanding of postural control mechanisms remains predominantly based upon findings in quadrupeds as opposed to bipeds, and further research is necessary to correlate and compare animal with human studies.

Thus, the primary rationale for the present study was to study one of the basic reflexive components of postural control, i.e. the tonic labyrinthine reflex, and to determine the extent of its influence on the excitability of the lower limb extensor (soleus) motoneuron pool in man. In addition, sensory awareness of static postural alterations in space during whole head-body rotations was investigated in the hope that the results might shed light upon the relative contributions of the tonic labyrinthine inputs to both sensory awareness and motor control of posture.

CHAPTER THREE

METHODOLOGY

1. Introduction

Review of the pertinent literature provided a foundation for development of the experimental protocol utilized. As mentioned previously, animal studies concerning the effect of static otolithic stimulation on motor control of the lower limb extensors emphasized the importance of rigidly fixating the head in relation to the body, to ensure relatively selective stimulation of the labyrinth during static changes in the whole head-body positions relative to space. In addition, visual and somatosensory inputs have been shown to interact intimately with vestibular inputs in response to postural functional demands, and thus must be controlled within reasonable limits to avoid confounding the data gathered. Furthermore, when the experimental objective is focused upon human postural adjustments to alterations of whole head-body rotations in space, the utilization of natural physiological stimulation avoids the recording of artifactual response patterns created by either the mode or non-specificity of stimulation (e.g. caloric or electrical stimulation).

In light of these findings, it was necessary to devise a means of providing precisely controlled step inputs to the otolith in selected planes of movement while the head and body were rigidly fixated in the standing posture. A modified circoelectric bed capable of having its support surface rotated to different positions in relation to space was utilized. It was customized with adjustable partial sansplint casts for fixating the cervical and lower limb articulations to minimize proprioceptive input from the neck and ankles (Fig. 3.1). With visual input likewise limited by either a blindfold or a light-proof crowning, two series of experiments were carried out: (1) Subjects were maintained in randomly allocated positions during whole head-body rotation in the coronal plane, while changes in the excitability of the extensor (soleus) motoneuron pool were monitored via the H-reflex testing technique. (2) Sensory estimation of the visual vertical in relation to whole head-body position during rotation in the coronal plane was recorded. Motor and sensory data were analyzed separately to illustrate the characteristics of the normal response to static tilt in the coronal plane. In addition, a comparison of motor and sensory data, which human subjects can uniquely provide, was attempted in order to delineate any potential functional correlations between perception of spatial orientation and autonomic motor responses in relation to the need for postural adjustments.

The present chapter will describe in greater detail the experimental population, instrumentation, test procedures, data collection, and methods of data analysis.

2. Subjects

Fourteen normal healthy female adolescents ranging from 12 to 16 years of age constituted the experimental population. Excluded from testing were any subjects with a history of neurological or muscular disease. Furthermore, precautions were taken to screen out children with a familial tendency towards development of either idiopathic scoliosis or kyphosis based upon the recent implication of neurogenic postural disturbances in the etiology of these conditions (Sahlstrand and Petrusen, 1979). Utilization of a selective female adolescent population who are at greater risk for development of spinal curvatures (Ponsetti and Friedman, 1950), permits the data to be used in the future as a baseline for comparison with age-matched adolescents with idiopathic scoliosis.

3. Apparatus

As mentioned previously, the fact that experiments investigating the influence of static tilt in the sagittal plane upon the excitability of the soleus motoneuron pool have been documented by Chan and Kearney (1982), the coronal test plane was selected for this study. Thus, a customly constructed hardwood platform was fixated to the tubular steel frame of a circoelectric bed in a position that allowed whole platform rotations in both clockwise and anticlockwise directions. A goniometer, which was aligned to the axis of rotation of the bed, was affixed to the subject support platform and used to continuously monitor the angle of tilt. The bed or support platform could rotate a full 270°, i.e. 135° on either side of the upright vertical position.

Several methods of immobilizing the subject to the platform were utilized, to ensure that artifacts due to body movement or persistent alterations in pressure over the stimulating and recording electrodes would be eliminated. In addition, consistent proprioceptive input from the trunk and the extremities was maintained by these patient-platform interfaces which included: (1) pre-molded sansplint casts affixed to the platform to prevent head, neck, and lower limb movements; (2) canvas corsets for the torso which rigidly prevented it from sliding downwards or laterally during platform rotation; and (3) velcro straps for fastening the upper extremities (Fig. 3.1). The location of these fixation devices was adjustable and modifiable for each subject to ensure comfort and to maintain constant head, neck, knee, and ankle joint angles in relation to the support platform. In addition, the combination of a sling and saddle system and the canvas corset mentioned previously provided a more even weight distribution, and aided in the control of exteroceptive and proprioceptive inputs which strongly influence postural reflexes (see Chapter 1). In fact, the major limitation of this experimental set-up was

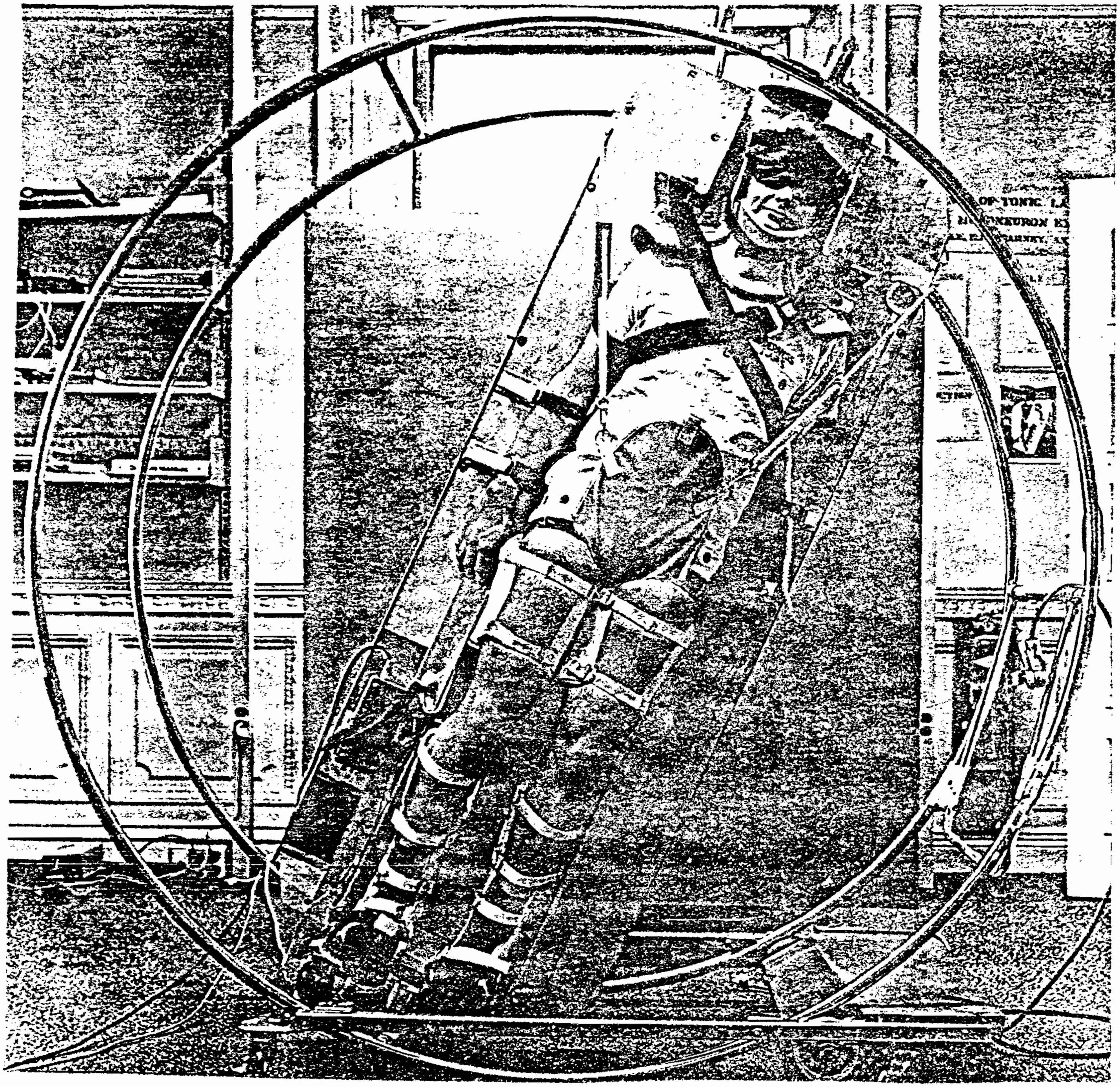

Figure 3.1: Photograph of subject fixated upon the experimental apparatus. Partial sansplint casts for the neck, thighs and lower legs were mounted onto the bed in an adjustable manner. A canvas sheet was secured around the torso, and a sling and saddle system firmly held the trunk in place, while velcro straps restrained the arms at elbows and wrists. The blindfold occluded visual input.

an inability to abolish the cutaneous input from both restraining and supporting devices. With the exception of total body immersion in water, however, this source of potential contamination cannot be practically eliminated. Alternatively, the experimental protocol was designed to ensure adaptation of both phasic cutaneous and phasic labyrinthine receptors. Before recording, subjects were maintained in each test position for one minute. Moreover, full confidence that cutaneous input from the soles due to inadequate support of body weight was being controlled, was reinforced by the following finding: (1) Releasing the foot plate, upon which the partial sansplint casts for the ankle rested, after a subject had been tilted to the control position (30° ipsilateral rotation from the vertical), (2) recording the peak-to-peak H-reflex amplitude (mean of 20 responses) one minute after the position was reached, and (3) replacing the foot plate and after one minute recording the peak-to-peak H-reflex amplitude once again. No significant changes in the excitability of the soleus motoneuron pool were recorded under these conditions, which provided the assurance that cutaneous inputs were not significantly affecting the experimental results.

Visual influence was eliminated by means which differed for the two experimental series. A simple blindfold was utilized in the H-reflex study to exclude visual influence on lower motoneuron excitability. On the other hand, visual input mediating conscious awareness of the head and body in space during the psychophysical (sensory) experimental series was eliminated by encompassing the entire support platform in a light-proof crowning. For the latter experiments, a luminescent dial was aligned with the axis of rotation of the circoelectric bed. It was utilized by subjects to indicate their estimations of the postural vertical after rotation to each new test position. In addition, random distribution of test positions precluded the possible use of auditory feedback as a guideline for sensory estimations, as well as eliminated any systematic errors associated with progressively increasing (or decreasing) amounts of lateral tilt.

4. Labyrinthine Stimulation

The above experimental set-up allowed examination of the effects of changes in the static orientation of the subjects' head and body relative to gravity. Responses to 30° step displacements over a total range of 180° in the coronal plane were studied. Displacements from the upright vertical of 30°, 60°, and 90° in either the clockwise or anticlockwise direction were randomly assigned in order to avoid the effects of systematically graded test positions.

Following the recording of the H-reflex made 60 sec. after each statically maintained test position, subjects were returned to a pre-selected control position (30° anticlockwise rotation from the vertical) in order to ensure that pre- and post-test control values did not differ greatly. On the other hand, repeated return to a control position during the sensory awareness experiments was thought to provide the subjects with learning cues, which might decrease their reliance upon vestibular input for judging spatial orientation. Therefore, a preselected series of randomly distributed test positions was repeated three consecutive times, without return to the vertical. This procedure allowed the variability of the subject's sensory estimation at each of the repeated test positions to serve as its own means of control.

5. Recording

5.1 H-reflex Methodology

As mentioned previously, excitability changes in the soleus motoneuron pool were measured by means of variations in the amplitude of the H reflex. This response is considered analogous to the monosynaptic stretch reflex and has been used to study mechanisms of altered motor functions, including spasticity, rigidity, and peripheral neuropathies (Mayer and Mawdsley, 1965).

More specifically, the technique consists of percutaneous electrical stimulation of group Ia fibers in the popliteal nerve and of recording the monosynaptic electromyographic response from the soleus muscle (Hoffman, 1918; Magladery and MacDougal, 1950). However, the normal H reflex appears to be subject to great variability and has led to the standardizations of the methods used to elicit this electrical potential, to ensure that a stable control reflex capable of reflecting both excitatory and inhibitory influences upon it can be consistently generated (Hugon, 1974; Meinck, 1980). For example, care must be taken to monitor muscle activity, including stretch or contraction to the agonists and antagonists, all of which differentially affect the amplitude of the H reflex.

In our experiment, the leg to be stimulated was strapped in a restraining device with the lower limb articulations at fixed angles. A Grass S88 Square Pulse Stimulator connected to a Grass SIU 5 Stimulus Isolation Unit delivered rectangular pulses of 1 msec duration at 5 second intervals, through a cathode precisely positioned under constant pressure in the popliteal fossa, at a location in which the relative threshold for eliciting the reflex was minimal. A metallic braid strapped around the lower quarter of the thigh served as the anode.

Stimulus intensities capable of recruiting approximately 35% of the motoneuron pool were utilized (Chan and Kearney, 1982), despite the greater stability of the control reflexes equal to 50% of the maximal M response. This decision was based upon the findings that although reflex inhibition is marked over a large range of stimulus intensities, the greatest facilitation is observed when the H-reflex amplitude is below 50° of the maximal M response (Meinck, 1980). This finding, which appears to be unique in man, may be due to the relatively small and narrow subliminal fringe of the human soleus motoneuron pool.

With gradually increasing intensities of electrical stimulation, the responses observed are characterized by the following sequence: (1) The largest Ia afferent fibers, which monosynaptically excite the soleus motoneurons are the first to respond. (2) Submaximal stimulation produces a minimal H response at a latency of approximately 29 msec. (3) The maximal H coincides with the appearance of a just detectable M response, due to the recruitment of alpha motoneurons with increased intensities of stimulation. (4) Increasing antidromic volleys in the motor axons progressively occlude the H-reflex generated by the orthodromic volleys of large Ia afferent nerve fibres. (5) Finally, the maximal M response, which is thought to recruit 100% of the motoneuron pool, completely occludes the H response. Consequently, calculation of the control stimulus intensity needed to activate 35% of the soleus motoneuron pool, was based upon measurement of the peak-to-peak amplitude of the H response divided by the peak-to-peak amplitude of the maximal H response and multiplied by 100 (Taborikova and Sax, 1968; Chan and Kearney, 1982).

Raw EMG activity was recorded from bipolar skin electrodes placed about 3 cm. apart over the soleus. These signals were amplified (gain = 1,000), as well as band-pass filtered with a preamplifier manufactured by the Biomedical Engineering Unit of McGill University. Frequencies below 1 Hz and above 1 KHz were cut off. The signals were displayed and monitored on a Tektronix 5111 storage oscilloscope, with the sweep of the trace externally triggered by a pulse from the stimulator unit (Fig. 3.2).

First, a maximal M-response was recorded in order to standardize the H-reflex stimulus intensity at a mean value of 36.7% of the motoneuron pool. Then 20 responses of the H-reflex were recorded in the following sequence for averaging purposes: (1) at the control position of 30° ipsilateral tilt, (2) one minute after being placed in the test position, and (3) once again at the control position. Any M-response accompanying the H-reflex was monitored and kept constant throughout the experiment to ensure that there were no alterations in the stimulus conditions. Test results were rejected if there were significant differences between pre- and post-test control H-reflex amplitudes, or between the control and test M responses.

5.2 Sensory Awareness

The technique of estimating the visual vertical was used to evaluate sensory awareness of head and body position in space (Clark and Graybiel, 1964; Miller *et al.*, 1968). Subjects were asked to adjust a luminous line in a dark

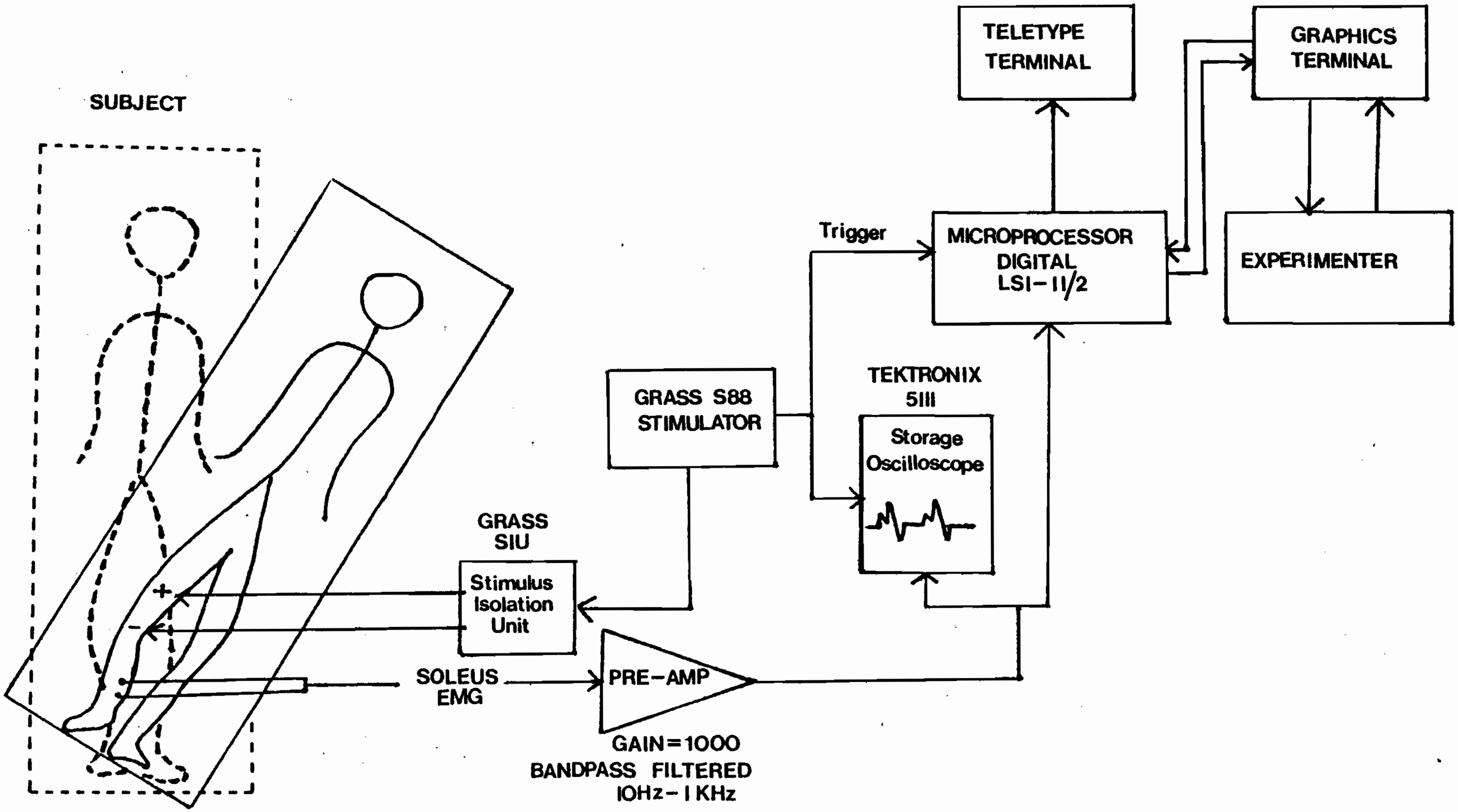

Fig. 3.2 Experimental set-up for the stimulation and recording of the H-reflex as a function of tilt in the coronal plane.

field to the apparent vertical while errors in estimation were recorded for each test position.

The same experimental apparatus was used to apply whole head-body rotations in the coronal plane. Fixation of the head, neck, torso, and limbs was maintained with the exception of one arm which was left free to enable the subject to manually adjust the luminous dial to the subjective sensation of the upright vertical. As mentioned previously, visual input was excluded by means of a light proof crowning which was fixated to the support platform and covered the entire body.

The same sequence of randomly allocated test positions was repeated three times in each experiment. Subjects were maintained in the test position for 60 seconds to allow adaptation of phasic vestibular and cutaneous receptors, and then asked to make their estimation of the visual vertical. However, contrary to the protocols of the other investigators (Graybiel and Clark, 1962; Bauermeister, 1964; Miller et al., 1968), they were never returned to the true vertical until the entire experiment had been completed. This alteration in the standardized protocol was adapted to avoid providing subjects with a consistent reference point from which to make their judgements.

The errors in estimation were recorded manually. A goniometer with a plumb-line suspended from its center was affixed to the midpoint of the axis of rotation of the circoelectric bed. The plumb-line consistently indicated the location of the true vertical in relation to the angle of tilt (Fig. 3.3). With each subjective estimation of the upright vertical, the difference between the two was recorded. Overestimations were given a positive sign (+) and underestimations a negative sign (-), to allow for the evaluation of any consistent patterns of error in judgement. To ensure that the data gathered were reproducible, each subject was tested on three separate occasions over a period of three months. In addition, four subjects were re-tested with their eyes opened and the light proof crowning removed, to objectively measure the contribution of visual input to sensory postural awareness.

6. Data Analysis

6.1 H-Reflex Data

The raw EMG was sampled at 2000 Hz by a digital LSl-11/2 microprocessor, to record the repeated H-reflex responses to each test position and to monitor the repeated M-responses to ensure consistency in stimulus conditions. The on-line program further computed the means of both the H-reflex and M-response data for each test ensemble of 20 responses and their standard deviations. These data were stored on the printout of the teletype terminal for future analysis.

The averaged data for each test position were normalized with respect to that of the mean of pre- and post-test

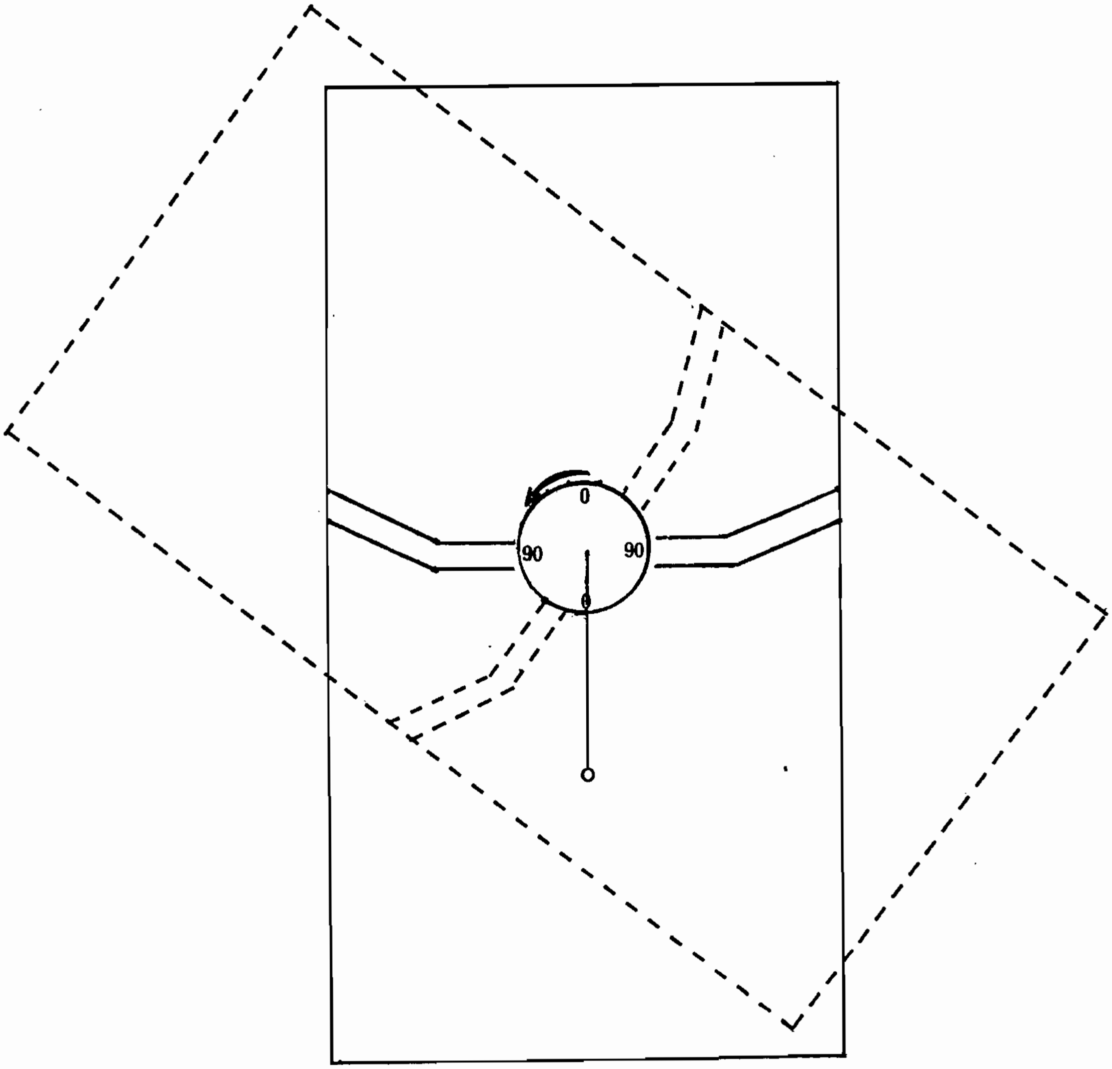

Fig. 3.3: Measurement of errors in estimating the location of the true vertical. The plumb line consistently indicated the location of the true vertical in relation to the angle of tilt.

control values. This ratio was expressed as a percent and graphically plotted against the angle of tilt in order to determine the response patterns of normal subjects.

6.2 Sensory Awareness Data

The mean "error" of estimation was computed for each test position by subtracting the mean subjective estimation of the visual vertical ($n = 3$) from the true vertical. The response accuracy was then computed for each test position and the grouped data of all the subjects were graphically plotted to illustrate the typical response patterns of normal subjects.

The following chapter presents the results obtained from the two series of experiments described above.

CHAPTER FOUR

RESULTS

1. Introduction

The H-reflex and sensory awareness experiments were conducted with all 14 adolescent female subjects. The test positions to which the support platform was rotated for the H-reflex testing included 0° or the upright vertical, 30°, 60°, 90° of ipsilateral and contralateral rotation in relation to the side of recording. Additional data points within the 180° arc of movement in the coronal plane were not investigated in the interest of limiting the period of immobilization necessary for each experiment. Subjects either became restless or drowsy after being immobilized more than 60 minutes, despite greater efforts to ensure their comfort and state of mental alertness. However, the limited time spent in each test position (approximately 70 seconds) for the experiments on sensory awareness allowed us to also document responses at 5°, 10°, 15°, 30°, 50°, 70°, and 90° of ipsilateral and contralateral rotation.

The data will now be considered in light of the one major and two minor response patterns which emerged in the H-reflex study.

2. Presentation of the Data

2.1 H-Reflex Study

The raw data used to calculate the normalized H-reflex amplitude (in % of the control value) as a function of the angle of tilt were condensed in Tables 4.1, 4.2, and 4.3.

These data have been grouped on these three tables according to the one major and two minor response patterns, which became apparent after the ensemble responses had been graphically plotted. The control position of 30° ipsilateral tilt is equal to 100%. For each test position, the first column of the tables provides the mean control H-reflex amplitudes which showed minor degrees of fluctuation over the course of the experiment for each subject. As mentioned in Chapter 3, section 5.1, these pre- and post-test control reflex amplitude values were carefully monitored throughout each experiment, in conjunction with the value of the M-response to ensure that the stimulus conditions remained stable. If significant variations in the pre- and post-test control H-reflex amplitudes were recorded, or alternatively, if the M-response amplitude increased by more than 20%, the data were rejected. Furthermore, if the control response variability increased significantly, the data were rejected.

The second column of each table indicates the amplitude of the mean test H (mV) for 20 responses at each angle of tilt, and the third column the normalized H-reflex amplitudes in % of the mean control value which were plotted as a function of the angle of tilt. Figures 4.1, 4.2, and 4.3 graphically depict the one major and two minor response patterns which became visible, and the following subsections (2.1.2, 2.1.3) will elaborate upon each of the tables with their corresponding graphs in greater detail.

Angle of Tilt (°)	90°I			60°I			30°I			0°			30°C			60°C			90°C		
Subject Code	Mean Control H (mV)	Mean Test H (mV)	% Control	Mean Control H (mV)	Mean Test H (mV)	% Control	Mean Control H (mV)	Mean Test H (mV)	% Control	Mean Control H (mV)	Mean Test H (mV)	% Control	Mean Control H (mV)	Mean Test H (mV)	% Control	Mean Control H (mV)	Mean Test H (mV)	% Control	Mean Control H (mV)	Mean Test H (mV)	% Control
KM +	2.22	6.54	294.5	2.15	4.25	197.6	/	/	100	2.05	2.20	107.3	2.27	4.16	183.2	1.98	4.58	231.3	-	-	-
CS △	3.72	6.76	181.7	3.82	4.89	128.0	/	/	100	3.47	3.74	107.7	3.43	3.84	111.9	3.59	4.19	116.7	-	-	-
AM ◇	2.42	4.50	185.9	2.76	3.76	136.2	/	/	100	2.59	2.73	105.4	3.11	3.45	110.7	2.78	3.69	132.7	-	-	-
CAD ◆	1.71	2.48	145.0	2.03	1.76	86.6	/	/	100	1.89	1.98	104.7	2.23	3.50	156.9	2.17	3.69	170.0	2.33	4.79	205.5
CK ▣	1.32	2.67	202.2	1.58	.81	139.6	/	/	100	1.12	1.46	130.3	1.61	1.31	214.7	1.09	3.71	340.3	.99	3.37	340.4
DD ◉	1.34	5.02	374.6	1.28	1.95	152.3	/	/	100	1.33	1.21	90.9	1.60	3.64	227.5	2.15	4.55	211.6	1.60	5.78	361.2
KS ▼	1.86	3.82	204.3	2.06	2.62	127.1	/	/	100	2.07	2.30	111.1	1.82	1.50	82.4	2.01	3.19	158.7	2.01	2.14	106.4
CO ▲	3.40	6.33	186.1	3.67	4.21	114.7	/	/	100	3.31	3.23	97.5	3.63	3.64	100.2	3.51	4.35	123.9	3.50	5.78	165.1

TABLE 4.1 NORMALIZED H-REFLEX AMPLITUDES (%) AS A FUNCTION OF THE ANGLE OF TILT (°) FOR 8 SUBJECTS WHO RESPONDED TO STATIC LABYRIATHINE STIMULATION IN THE CORONAL PLANE WITH A PATTERN OF BILATERAL FACILITATION. I = IPSILATERAL TILT; C = CONTRALATERAL TILT. THE DIFFERENT SYMBOLS CORRESPONDING TO THE DIFFERENT SUBJECT CODES WERE USED TO PLOT FIG. 4.1.

Angle of Tilt (°)	90°I			60°I			30°I			0°			30°C			60°C			90°C		
Subject Code	Mean Control H (mV)	Mean Test H (mV)	% Control	Mean Control H (mV)	Mean Test H (mV)	% Control	Mean Control H (mV)	Mean Test H (mV)	% Control	Mean Control H (mV)	Mean Test H (mV)	% Control	Mean Control H (mV)	Mean Test H (mV)	% Control	Mean Control H (mV)	Mean Test H (mV)	% Control	Mean Control H (mV)	Mean Test H (mV)	% Control
TL ○	2.01	3.75	186.5	1.95	3.08	157.9	/	/	100	2.01	1.85	92.0	2.09	2.09	100.9	2.11	1.50	71.0	2.00	1.12	56.0
CD □	4.62	7.06	152.8	4.40	5.85	132.9	/	/	100	4.64	4.25	91.5	4.50	3.95	87.7	4.18	3.11	74.4	4.47	.58	12.9
SA ▽	3.95	5.58	141.2	3.74	4.10	109.6	/	/	100	4.11	4.03	98.05	3.58	3.81	106.4	3.96	2.21	55.8	3.43	2.21	64.4

TABLE 4.2 NORMALIZED H-REFLEX AMPLITUDES (%) AS A FUNCTION OF THE ANGLE OF TILT (°) FOR 3 SUBJECTS WHO RESPONDED TO STATIC LABYRINTHINE STIMULATION IN THE CORONAL PLANE WITH A PATTERN OF IPSILATERAL FACILITATION AND CONTRALATERAL INHIBITION.

Angle of Tilt (°)	90°I			60°I			30°I			0°			30°C			60°C			90°C		
Subject Code	Mean Control H (mV)	Mean Test H (mV)	% Control	Mean Control H (mV)	Mean Test H (mV)	% Control	Mean Control H (mV)	Mean Test H (mV)	% Control	Mean Control H (mV)	Mean Test H (mV)	% Control	Mean Control H (mV)	Mean Test H (mV)	% Control	Mean Control H (mV)	Mean Test H (mV)	% Control	Mean Control H (mV)	Mean Test H (mV)	% Control
TM *	2.02	.85	42.07	2.36	1.93	81.7	/	/	100	2.47	2.35	95.1	2.14	3.10	144.8	1.96	2.31	117.8	2.39	1.05	43.9
CA ◆	1.53	.50	32.67	1.97	2.45	124.3	/	/	100	1.72	2.35	136.6	2.29	1.93	84.2	1.92	.47	24.47	2.27	.08	3.52
KB ▫	2.17	.18	8.2	2.17	1.99	91.7	/	/	100	2.16	1.32	61.11	1.91	2.70	141.3	2.13	1.40	65.7	2.27	.12	5.2

TABLE 4.3 NORMALIZED H-REFLEX AMPLITUDES (%) AS A FUNCTION OF THE ANGLE OF TILT (°) FOR 3 SUBJECTS WHO RESPONDED TO STATIC LABYRINTHINE STIMULATION IN THE CORONAL PLANE WITH A PATTERN OF BILATERAL INHIBITION.

2.1.1 Major Response Pattern

In 8 of 14 subjects studied, the H-reflex was progressively facilitated bilaterally with increasing angles of ipsilateral and contralateral tilt (Table 4.1, Fig. 4.1). The upright position was associated with minimal alterations in the excitability of the soleus motoneuron pool as seen in column 4 of Table 4.1. With the exception of subject CK, the amplitude of the H-reflex in this test position ranged from 90.9% to 111% of the control reflex values, and therefore did not consistently signify a trend towards either facilitation or inhibition of the excitability of the soleus motoneuron pool. Subject CK who exhibited a tendency towards facilitation (130% of the control value) of the H-reflex in the vertical position, also showed a remarkably increased excitability (202% to 340% of the control value) of the H-reflex at the extremes of lateral tilt. Thus, her results may simply reflect a greater sensitivity of response to natural labyrinthine stimulation.

In fact, all of the subjects in this group showed levels of sensitivity to tilt in the coronal plane which greatly exceeded those reported by Chan and Kearney (1982) in response to tilt in the sagittal plane. The excitability of the soleus motoneuron pool increased by 165-375% for the majority of these subjects at 90° of tilt in either an ipsilateral or contralateral direction (Table 4.1), in contrast to the maximum increase of 240% seen in response to fore-aft

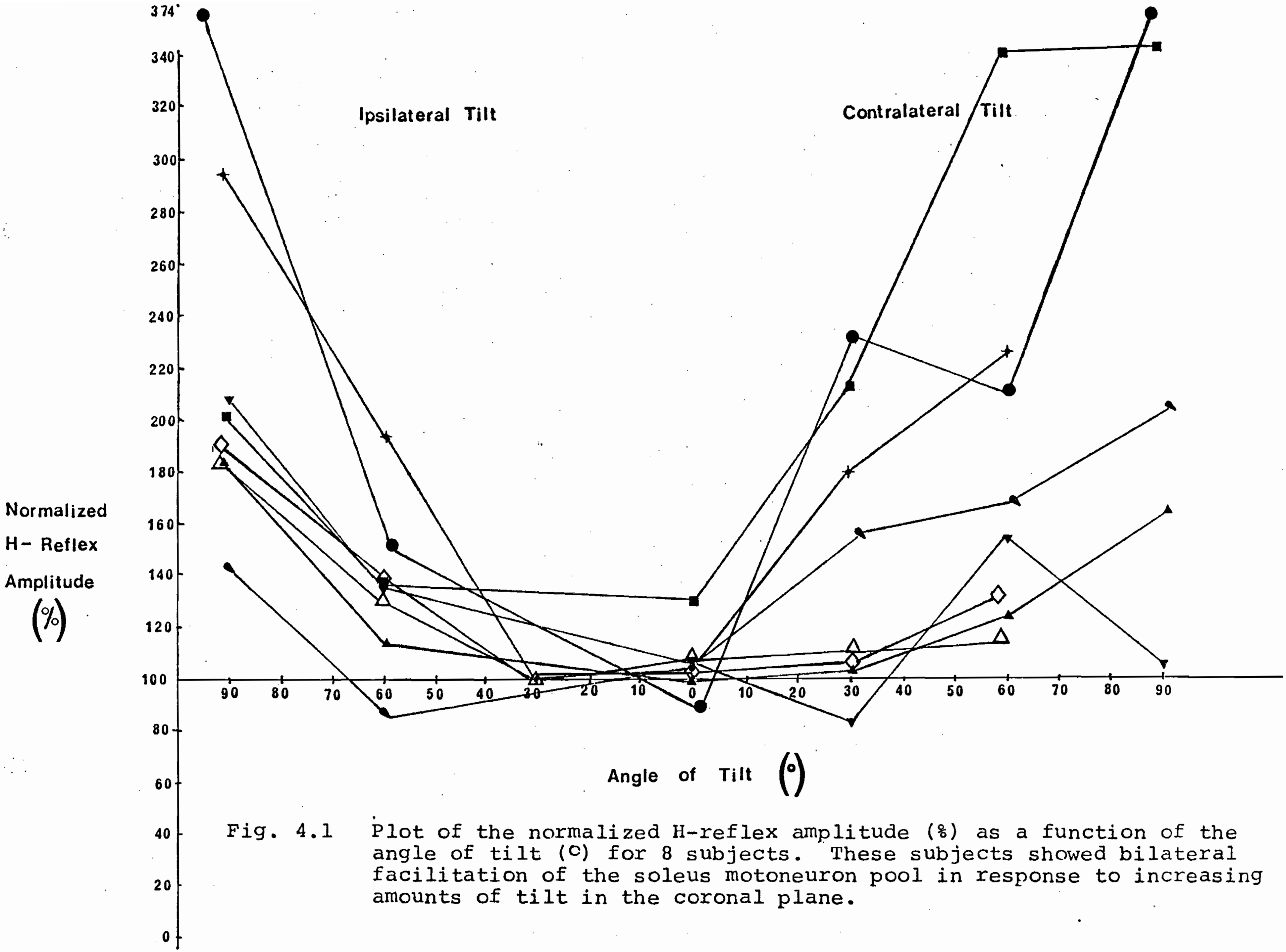

Fig. 4.1 Plot of the normalized H-reflex amplitude (%) as a function of the angle of tilt (°) for 8 subjects. These subjects showed bilateral facilitation of the soleus motoneuron pool in response to increasing amounts of tilt in the coronal plane.

tilts over the range of 30°-150° (Chan and Kearney, 1982). Furthermore, in our study, the variations in the amplitude of the H-reflex (20 responses) recorded at each test position for individual subjects became progressively more stable at the extreme angles of tilt (S.D. = .01).

The results recorded from 3 subjects (KM, CS, AM) when maintained in 90° of rotation in the contralateral direction were discarded (Table 4.1) due to their reported discomfort in this position. The discomfort was related to the close-fitting sansplint neck restraint which in these individuals applied pressure over the mandible when lying directly on the left side. It was noted that the H-reflex response was inhibited by this discomfort.

Finally, it was recognized that a sinusoidal regression analysis of the H-reflex data would have been appropriate, given the pattern of progressive bilateral facilitation illustrated by Fig. 4.1. Nevertheless, the complexity of this analysis placed it beyond the scope of this project.

2.1.2 Minor Response Patterns

Two minor patterns of response emerged within our total population of 14 subjects. In 3 subjects, the H-reflex was facilitated by ipsilateral tilt and inhibited by contralateral tilt (Fig. 4.2), and in the 3 remaining subjects, the H-reflex was inhibited by both ipsi- and contra- lateral tilt (Fig. 4.3).

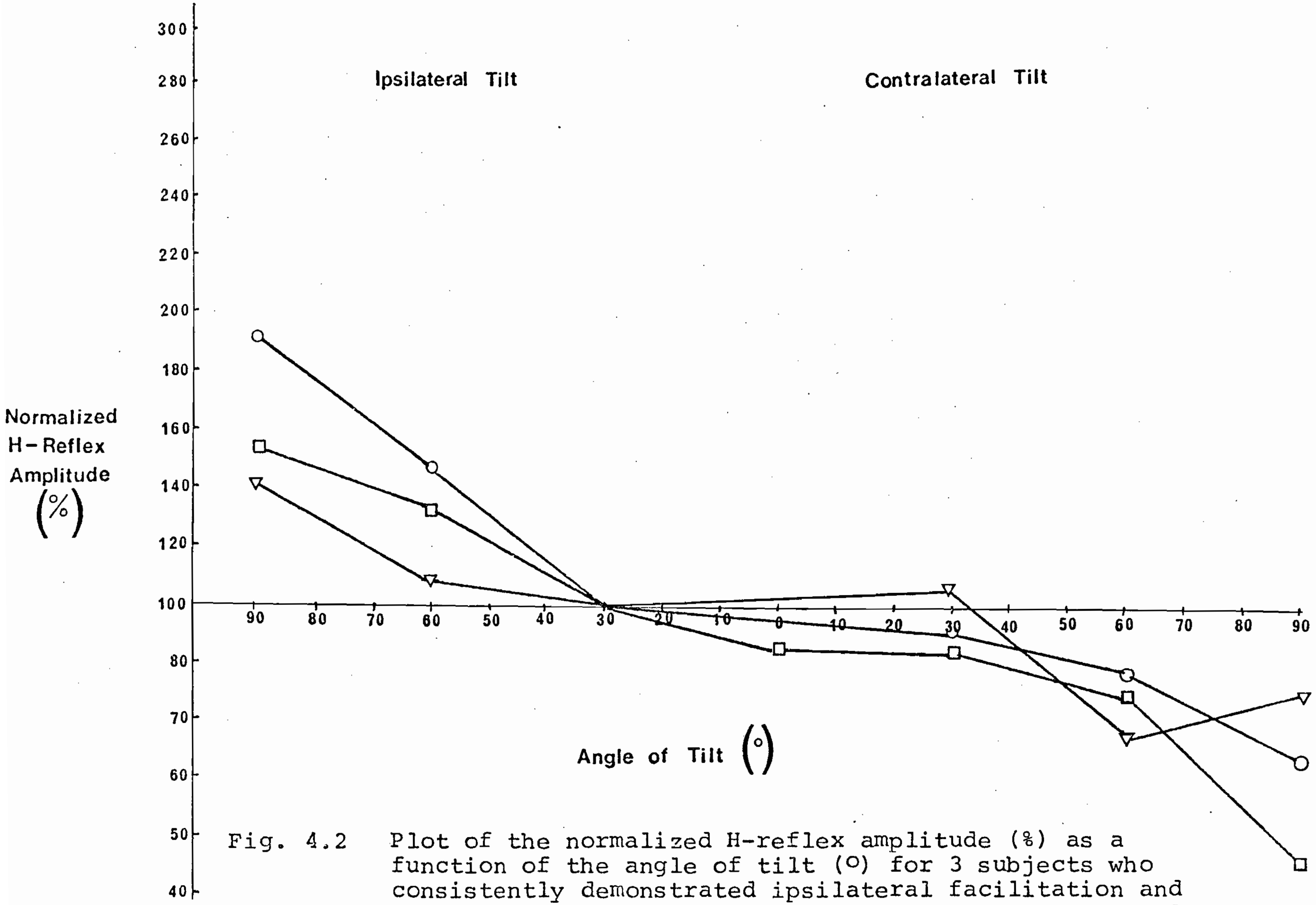

Fig. 4.2 Plot of the normalized H-reflex amplitude (%) as a function of the angle of tilt (°) for 3 subjects who consistently demonstrated ipsilateral facilitation and contralateral inhibition of the soleus motoneuron pool in response to tilt in the coronal plane.

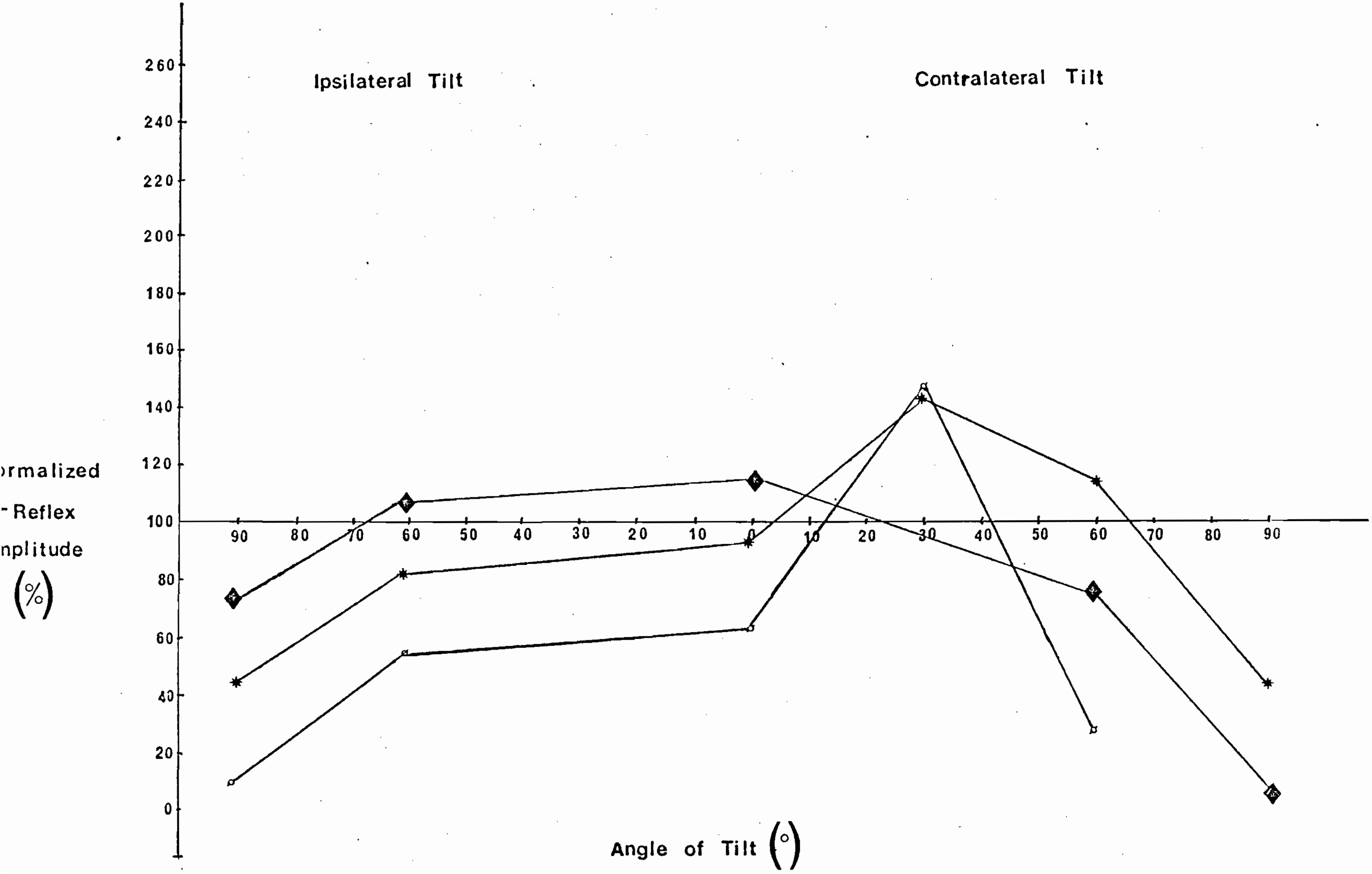

Fig. 4.3 Plot of the normalized H-reflex amplitudes (%) as a function of the angle of tilt (O) for 3 subjects. These subjects showed bilateral inhibition of the soleus motoneuron pool in response to increasing amounts of tilt in the coronal plane.

2 of these 3 subjects (CA, KB) showed a greater variability in their responses at the upright vertical position (Table 4.3, Column 4 for 0°), despite having ensured that they were absolutely comfortable and experiencing no anxiety which might have influenced the results. Furthermore, the progressive patterns of inhibition were relatively symmetrical (Fig. 4.3), and pronounced to the point that at 90° of contralateral tilt for subjects CA and KB as well as at 90° of ipsilateral tilt for subject KB, the H-reflex was so inhibited as to be barely discernable.

2.1.3 Consistency of Response Pattern in the Same Subjects

The 3 patterns of H-reflex modulation by lateral tilt represented real *inter-subject* differences as demonstrated by the fact that upon repetition of the experiment with 2 subjects, with several months interval between tests, the same pattern (Fig. 4.4) of response was reproduced. TL (O) responded with a pattern of ipsilateral facilitation and contralateral inhibition upon related testing whereas CA (◆) responded with a pattern of bilateral inhibition. In addition, some of the same test angles were repeated during each experimental session to ensure *intra-subject* consistency, and invariably the same response was generated. Hence, it appeared that extrinsic variables were being well-controlled, and that confidence in the reliability of the experimental protocol was established.

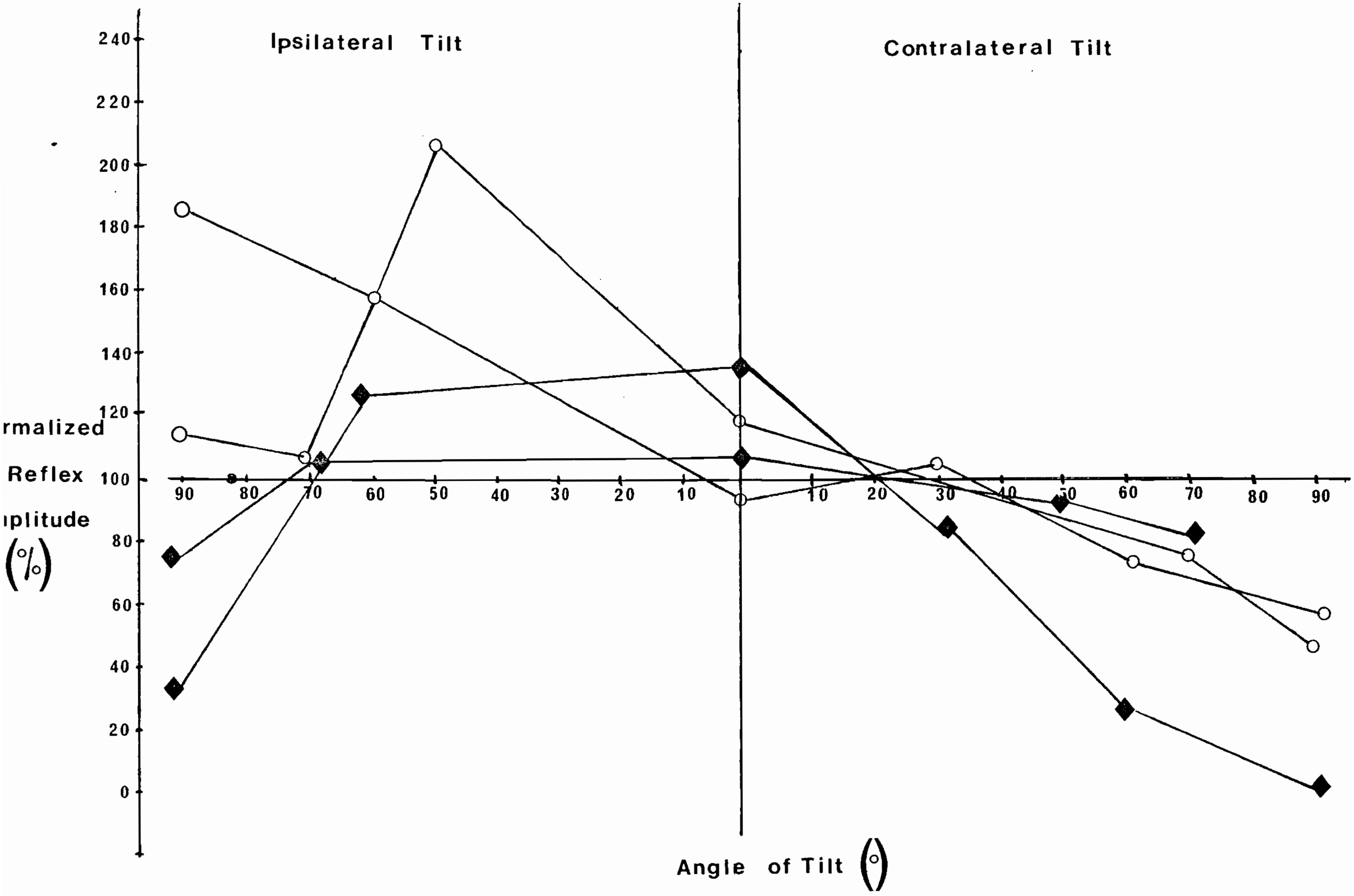

Fig. 4.4 Plot of the normalized H-reflex amplitude (%) as a function of tilt (°) for 2 subjects, in which 2 full experiments were repeated with several months interval between tests. They demonstrated response consistency in the pattern, although not the absolute values, when the same subjects were tested on different occasions.

2.2 Sensory Awareness Study

2.2.1 Major Response Pattern

Within the group of 14 subjects, 2 responded with great variability upon repeated trials and hence these data were rejected. In contrast to these 2 subjects, 8 out of 12 subjects (57.1%) responded to clockwise and anticlockwise tilt in the coronal plane with symmetrical errors in estimating the location of the upright vertical, despite the random allocation of test positions and the absence of return to the vertical between test positions (Fig. 4.5). Fig. 6 plots the mean data (± 1 standard deviation) obtained from the 8 subjects. It could be seen that from 0-30° of tilt from the upright position, the mean error of estimation rarely exceeded 2.5° for these 8 subjects. With tilts of 50°-90° to either side of the vertical, however, the accuracy of estimation progressively deteriorated from a mean error of 5.7° at 50° of ipsi- and contralateral tilt, to a mean error of 17.35° at 90° of contralateral tilt. The standard deviation of the mean error likewise became larger, from 2.58 at 5° of ipsilateral tilt to 18.3 at 90° of ipsilateral tilt.

Moreover, 2 of these 8 subjects responded with a truly remarkable ability to estimate the location of the upright vertical throughout the range of test positions. As shown in Fig. 4.5, subjects AM (◇) and CS (△) maintained a 2° error of estimation from 0°-50° of tilt in either an ipsi-

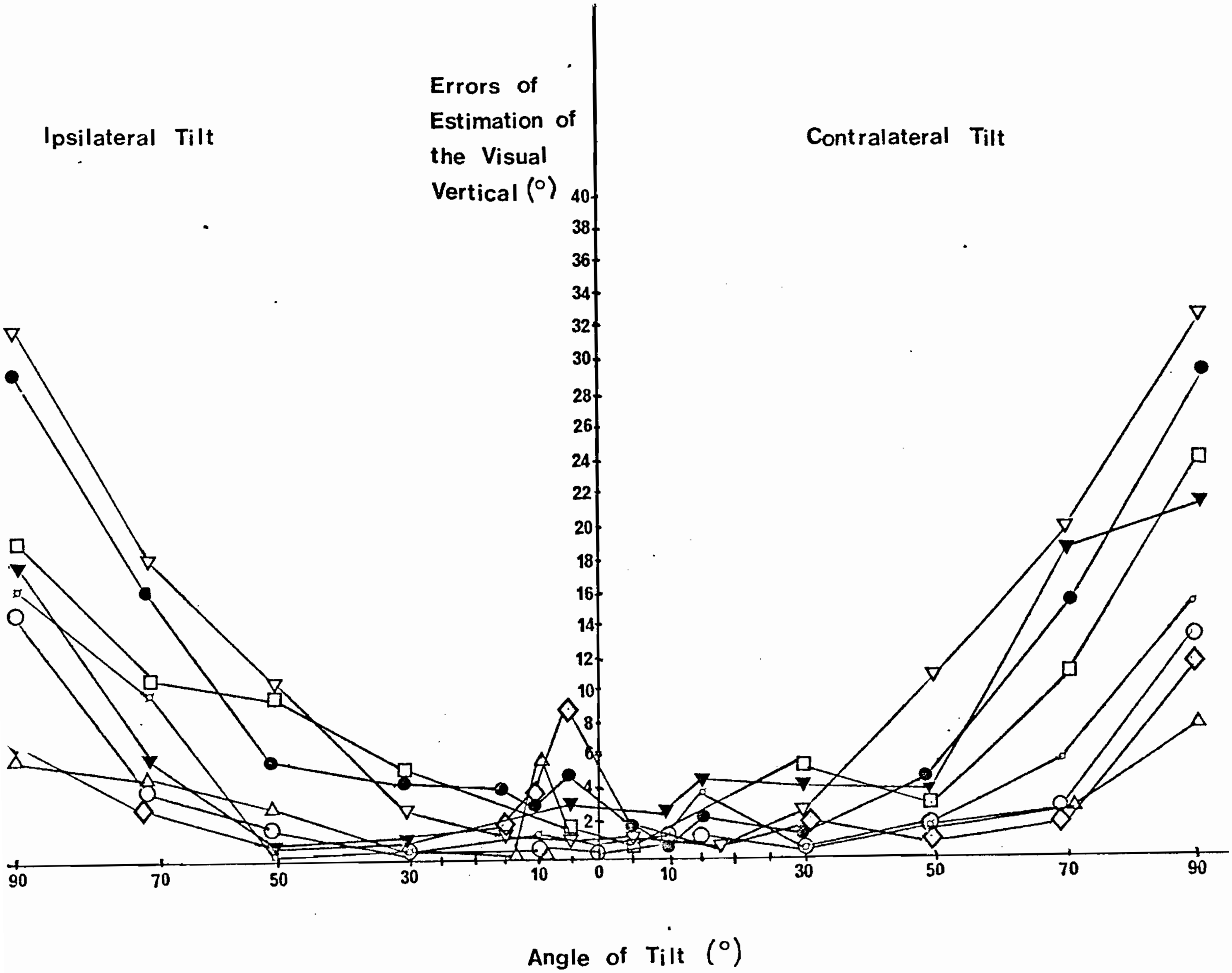

Fig. 4.5 Plot of the error of estimation of the visual vertical in response to increasing degrees of tilt (180 °) in the coronal plane for 8 subjects. Each data point is the mean error for 3 estimates for each subject per test position.

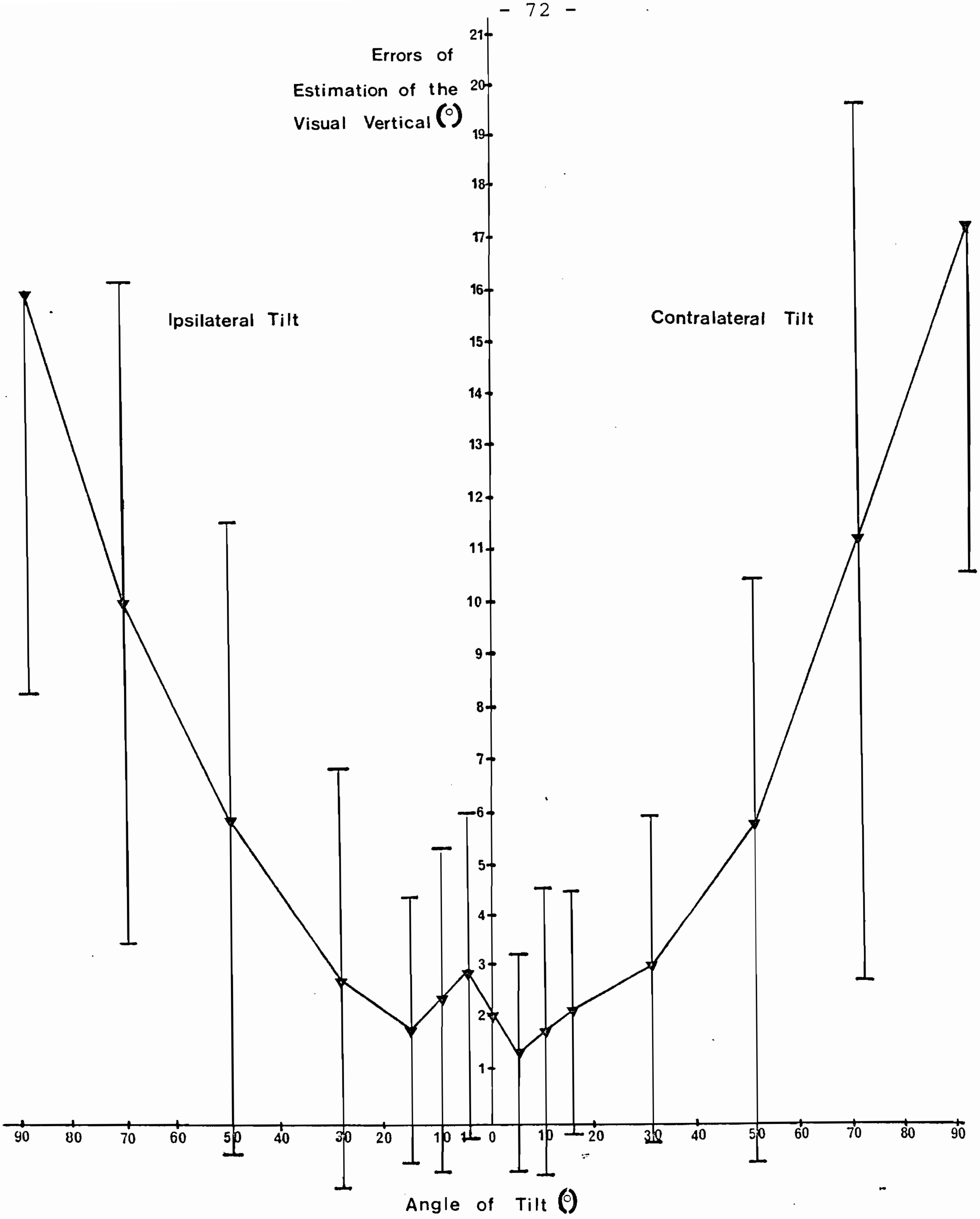

Fig. 4.6 Plot of the mean error of estimation of the visual vertical for 8 subjects and the standard deviations associated with each test position. Note the high standard deviations associated with greater angles of tilt.

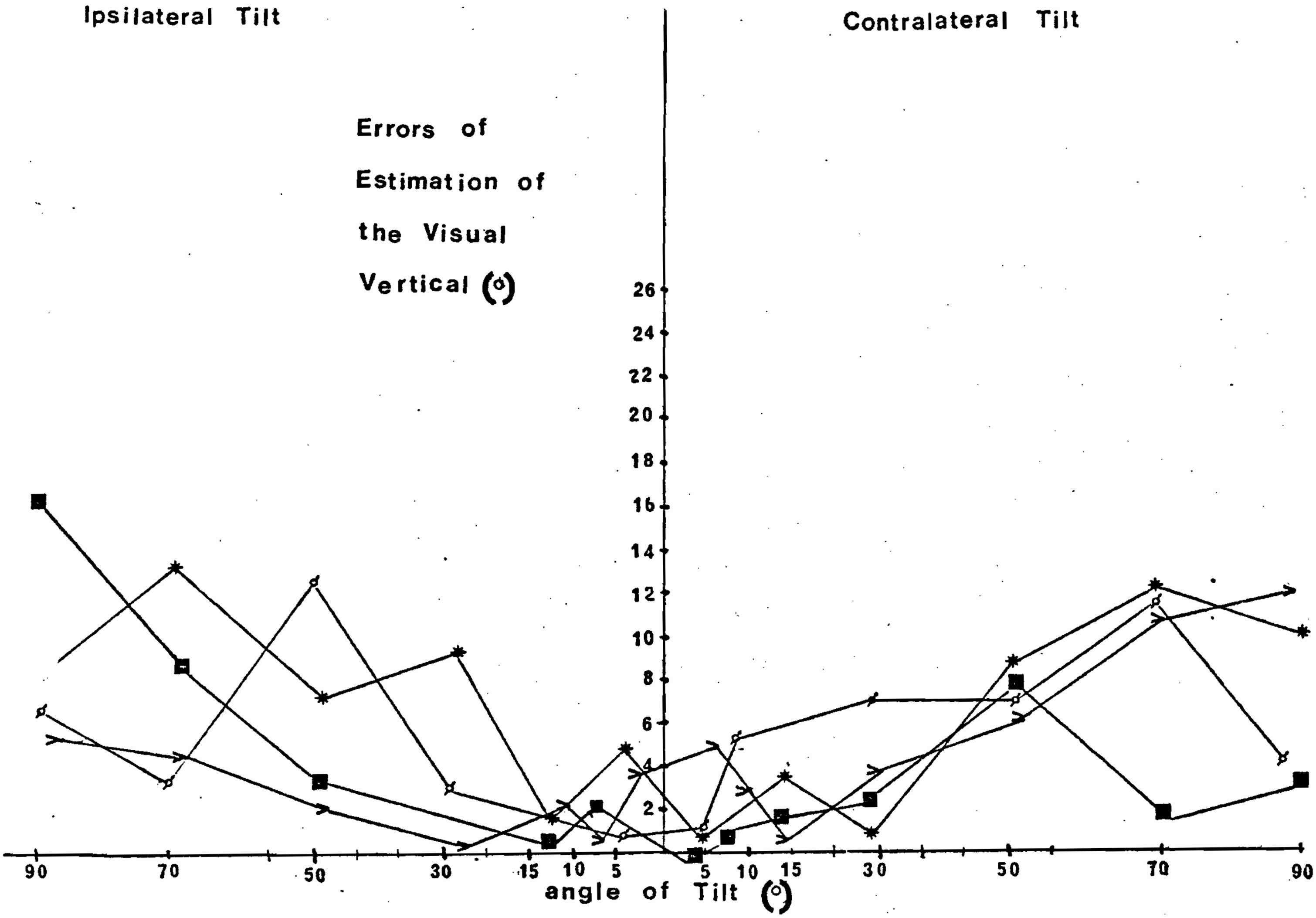

Fig. 4.7 Plot of the errors of estimation of the visual vertical in response to increasing degrees of tilt (0-90°) in an ipsilateral and contralateral direction for 4 subjects. The response patterns did not coincide with that of the majority of subjects, and in particular demonstrated greater variability in the errors of estimation.

lateral or contralateral direction, increased to 4° at 70° of tilt and never exceeded 11° at 90° of tilt in either direction. Upon closer examination of their levels of physical activity, it was found that both of these subjects were highly athletic. One was a competitive gymnast and the other a diver, which might well account for their exceptional ability to estimate their whole head-body positions in space.

Contrary to the findings of other investigators (Graybiel, 1974), no consistent pattern of either overestimation and underestimation at the various test positions could be found. Therefore, the absolute value of each estimated error was utilized for all determinations of the means and standard deviations at each test position.

2.2.2 Minor Response Patterns

The response patterns of the remaining 4 subjects did not coincide with that of the majority. Fig 4.7 shows that subjects TM (*) and SL (ø) responded with less accuracy of estimation at 50°-70° of tilt than at 90° of tilt. In addition, subjects CK (■) and DH (>) responded asymmetrically, with higher errors of estimation of the visual vertical when tilted in one direction and lower errors of estimation when tilted in the opposite direction.

Upon repeated experimental testing, the same patterns of response were found to be consistent in the same subjects, and therefore the anomalous results could not be accounted for by the alterations in the conditions of the experiment.

2.2.3 Visual Contribution to Sensory Awareness of Whole Head-Body Position in Space

Four subjects were tested with their eyes opened and with their eyes blindfolded in random order (Fig. 4.8). With visual input maintained, consistently small errors of estimation were made. The largest mean error of estimation of the vertical was 7° at 90° of ipsilateral tilt. With visual input removed, the accuracy of estimation consistently and symmetrically deteriorated with increasing angles of tilt from the vertical. For example, with the eyes opened, the mean errors of estimation for subjects tilted from 0 to 30° on the contralateral side progressed from 1° to 2° of error. For the same range of test positions with visual input removed, the mean errors of estimation progressed from 3° to 6° of error. Likewise, at 90° of contralateral tilt, the mean error of estimation of the visual vertical when the eyes were opened was equal to 3°, whereas with the eyes closed the mean error of estimation for the same test position increased to 12°. Thus, visual input appears to play a significant role in providing information concerning whole head-body positions in space. However, the residual errors in estimation which persisted despite the contribution of

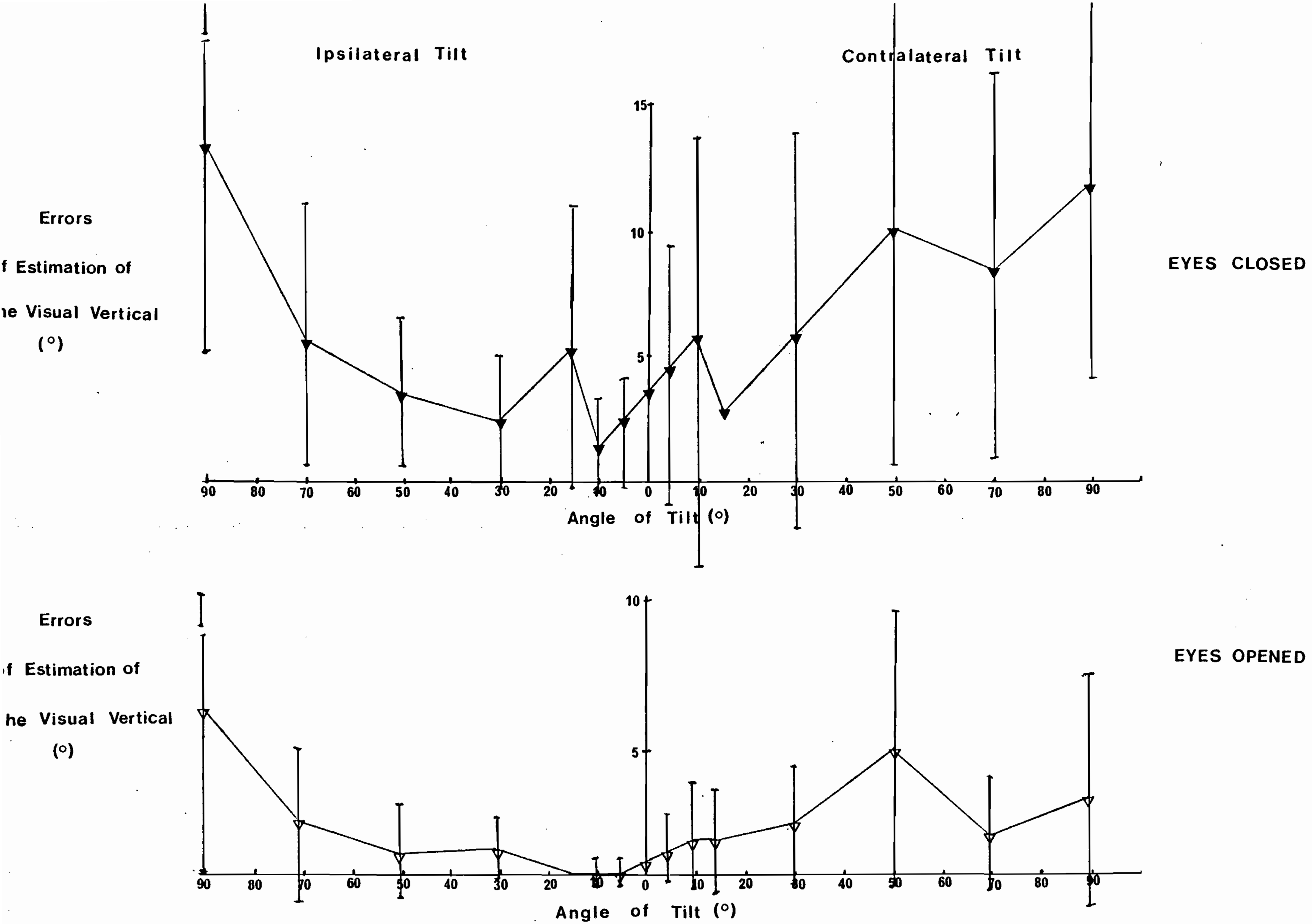

Fig. 4.8 Plot of the mean errors of estimation for the visual vertical in 4 subjects who were alternatively tested with their eyes opened and their eyes closed, to evaluate the contribution of visual input to sensory awareness of head and body displacements in space.

visual receptors and the presence of intact labyrinthine input, are to be noted.

3. Summary of Results

3.1 H-Reflex Study

In summary, 1 major and 2 minor response patterns were recorded in the soleus muscle following natural tonic labyrinthine stimulation provided by static whole head-body tilt in the coronal plane. 8 subjects responded with bilateral facilitation which progressively increased as a function of the angle of tilt (Table 4.1, Fig. 4.1). Conversely, 3 subjects responded with bilateral inhibition (Table 4.3, Fig. 4.3), but showed no significant increases or decreases in the excitability of the soleus motoneuron pool in the upright vertical position. Finally, the remaining 3 subjects responded asymmetrically to tilt in the coronal plane, with facilitation when rotated in an ipsilateral direction, and inhibition when rotated in a contralateral direction (Table 4.2, Fig. 4.2). It should be noted that these patterns of response coincided with those recorded from the otolithic afferents by Fernandez and Goldberg (1976a).

3.2 Sensory Awareness Study

Eight (8) out of twelve (12) subjects responded to randomly chosen angles of clockwise and anticlockwise tilt with symmetrical and consistent errors of subjective estimation of the visual vertical (Fig. 4.5). Increased absolute errors and variability in response accuracy were recorded at greater degrees of tilt (50°-90°) in all of these subjects (Fig. 4.6).

Although sensory awareness of head and body positions in space appeared to be relatively accurate with visual input *removed*, when visual input was *retained*, sensory awareness of head and body positions in space became highly accurate, despite the lack of input from the neck and proprioceptors of the trunk and lower limbs (Fig. 4.8).

CHAPTER FIVE

DISCUSSION

1. Introduction

Despite the differences between animal and human modes of stance, the results of our study on tonic vestibulospinal reflex activity in man during lateral tilt correlated well with responses recorded from limb motoneurons (Erhardt and Wagner, 1970), vestibular nuclei (Peterson, 1970) and peripheral macular neurons (Fernandez *et al.*, 1972) in animals. Three patterns of soleus motoneuron facilitation and inhibition emerged in response to static tilt in the coronal plane (Table 4.1-4.3, Fig. 4.1-4.3), providing concrete evidence for the distinct influences of relatively selective otolithic contribution to the control of upright human posture. In addition, natural tonic vestibular stimulation was shown to provide untrained subjects with significant information on the position of their heads in space in relation to angular displacements of whole head-body positions in space (Fig. 4.6). In the absence of vision, with constant neck and proprioceptive input, as well as minimized exteroceptive influences, subjects maintained the ability to estimate the orientation of the visual vertical in response to movements within the coronal plane (Fig. 4.8).

The following discussion will elaborate upon our *motor* and *sensory* findings in light of previous animal and human studies, as well as develop a conceptual framework for the *functional correlations* between *unconscious* reflex and *conscious* sensory contributions to static postural control.

2. H-Reflex Study

As mentioned in Section 1.1 of Chapter 2, Fernandez and Goldberg (1976a) used static tilt to define the functional polarization vectors of saccular versus utricular components of the otolithic maculae. They found that angular displacements in the coronal plane primarily activated utricular units, 75% of which responded to ipsilateral tilts (Type I) and 25% of contralateral tilts (Type II). In addition, 2 minor response patterns consisting in either bilateral facilitation (Type III) or bilateral inhibition (Type IV) were recorded from the vestibular nerve.

The patterns of response recorded in our study of the H-reflex in adolescent female subjects largely coincided with responses to stimulation of the otolith recorded by Fernandez and Goldberg (1976a), with the exception of the proportion of patterns seen in our population, and our failure to detect a Type II response in the relatively small study population. The predominant pattern of bilateral facilitation (Type III) was found in 8 subjects (Fig. 4.1), in whom the amplitude of the H-reflex recorded from the soleus muscle increased by 145-375% of the control reflex amplitude when the whole body was maintained at 90° of tilt to the side of the recording (Table 4.1). Increasing angles of tilt in either ipsilateral or contralateral directions were associated with progressive increases in the amplitude of the H-reflex. 3 subjects responded with an asymmetrical pattern of ipsilateral facilitation and contralateral inhibition (Type I) (Table 4.2, Fig. 4.2), and the remaining 3 subjects responded with bilateral inhibition (Type IV) to tilt in either direction (Table 4.3, Fig. 4.3), thus providing a striking similarity between the response repertoires recorded from otolithic afferent nerve fibers in animals and human output patterns of response to natural static labyrinthine inputs.

To be noted is also the fact that, despite the small fluctuations in test reflex amplitudes recorded at 50° and 70° of tilt for any given set of 20 responses recorded per subject per position, the test reflex amplitudes recorded at 90° of tilt in either the ipsilateral or contralateral direction were always consistent, non-fluctuating, and clearly reproducible upon re-testing during the same experimental session. This observation served to highlight the remarkably strong influence of the maculae upon the tonus of the lower limb extensors in man, when exteroceptive input was limited and visual input blocked. In fact, the high degree of sensitivity to tilt in the coronal plane, as evidenced by the magnitude of reflex facilitation in this plane of movement (a maximum of 375%, cf. Table 4.1), superseded that reported by Chan and Kearney (1982) in response to tilts in the sagittal plane (a maximum of 240%). These findings corroborated with the greater sensitivities to utricular stimulation shown in animals with rotation in the coronal plane (Fernandez and Goldberg, 1976a).

Electrophysiological studies of neuronal discharges in Deiter's nucleus, which receives 80% of the input from the utricle (Peterson, 1970), have indicated that their responses to tilt are of course closely related to labyrinthine input at this level of the neuraxis. Moreover, descending impulses relayed to the lumbar cord via the lateral vestibulospinal tract (LVST) also correspond closely to the patterns of the static labyrinthine input (Wilson and Yoshida, 1969; Grillner et al., 1970; Pompeiano, 1972). In this connection, Roberts (1967, 1973, 1979) found that lateral tilt evoked ipsilateral extension of both fore- and hind-limbs to restore equilibrium, and our results largely coincided with certain aspects of his findings, given the fact that eleven (11) out of fourteen (14) subjects showed H-reflex facilitation with tilt to the ipsilateral side.

However, despite the apparent response congruities between animals and humans, some investigators have questioned the validity of the experimental method used to gather the reported data. Myklebust et al. (1984) questioned the considerable inter-subject variability and the contradictory findings of two separate groups of investigators (Chan and Kearney, 1982; Aiello et al., 1983) who mapped the H-reflex response to static tilts in the sagittal plane. As already reviewed in Chapter 2, Aiello and his colleagues (1983) reported progressive increases in the amplitude of the H-reflex as the body was tilted from the horizontal to the vertical in progressive step increments, whereas Chan and Kearney (1982) found the H-reflex to be minimal in the upright vertical position and increased as a sinusoidal function of tilt away from the vertical. In an attempt to resolve this controversy which focused upon methodological details (Chan and Kearney, 1984), Myklebust et al. (1984) recently duplicated the reported experimental procedure by testing both the tendon jerk reflexes and H-reflex responses to whole head-body displacements in the sagittal plane. Although 3 out of 5 subjects demonstrated greater reflex excitability in off-vertical positions, they noted significant variations in the threshold for stimulation of the M-wave in 2 subjects, and concluded that although vestibular influences were likely responsible for the recorded findings, these influences were minimal and the results were more likely due to orientation-induced artifacts.

However, in our study, great precautions were taken to minimize movement during tilt - not only at the ankle joint, but also at all the other joints. Partial casts fixated the ankles, knees, neck and shoulders to limit alterations in proprioceptive input from these articulations. The canvas corset for the torso, and the saddle harness used to support the upper body, firmly held the body in place and did not allow downward and/or lateral slip during tilt. Additionally, responses were rejected whenever changes occurred in the

M-responses suggesting an alteration in the conditions of either the stimulating or recording electrodes. It was however noted that over time, accommodation to the stimulus intensity occasionally occurred in some subjects, and in order to maintain the control amplitude of the M-wave, small increments in the stimulating voltage were made without altering the amplitude of the control H-reflex. These increments were never made during maintenance of the subject in the test positions.

Further correlations or corroboration of our results with that of other studies on the contribution of the labyrinth to static postural control are limited by the fact that other investigators focused upon functional interactions between vestibulospinal, somatosensory, and visual inputs in the control of upright stance in man (Mauritz and Dietz, 1980; Lund and Broberg, 1983; Black et al., 1983; Black and Nashner, 1984; Bles et al., 1984), or alternatively used non-physiological forms of labyrinthine stimulation (Delwaide and Juprelle, 1977; Molina-Negro et al., 1980) to study the response patterns of lower limb extensor motoneurons. These authors used methodologies which enabled them to conclude that (1) vestibulospinal reflex activity is relayed to the muscles of the lower limb in man (Molina-Negro et al., 1980; Lund and Broberg, 1983). (2) Abnormal vestibular function disrupts spatial references to the vertical resulting in increased postural instability (Black et al., 1983), and (3) loss of vestibular input results in an inability to re-weigh support surface and visual orientation references when they are inaccurate, leading to increased postural instability (Black and Nashner, 1984). Hence, they resolved interrogations concerning absolute and relative contributions of the labyrinth to postural control, but did not define the precise nature of responses which underlie functional adaptations.

3. Sensory Awareness Study

The sensory facets of macular function in relation to static labyrinthine inputs were investigated two decades ago, via psychophysical studies designed to evaluate the perceptual sensitivity of man to different body positions in relation to the vertical (Bauermeister, 1964; Clark and Graybiel, 1964). These studies were reviewed more recently by Graybiel (1974) and Guedry (1974). At present, the focus of attention is upon the evaluation of motion sickness (Gundry, 1979) and sensory awareness of the dynamic characteristics of movement (Bles et al., 1982). Nevertheless, we were able to generate some unique data on static position-sensing abilities by (1) randomly allocating positions in the test sequence without returning to the vertical during any given trial, (2) repeating the same sequence of positions per trial three times during each experimental session, (3) repeating the experiment three times per subject for the majority of subjects (11) on different occasions, and (4) evaluating the contribution of visual input to estimations of the vertical in space while maintaining exteroceptive and proprioceptive inputs from joint and muscle receptors at a minimum. This mammoth aggregate of data gathered, allowed us to more specifically evaluate static macular sensory accuracy and acuity, by controlling some of the factors which have a direct bearing upon a subject's ability to estimate the visual vertical (Guedry, 1974). In this context of procedural control, we therefore eliminated the upright vertical position as one of the test positions to avoid providing the subjects with a reference position. Moreover, the repetition of the same sequence of positions per trial allowed us to decipher whether the order of testing influenced judgements. Finally, repetitions of the testing procedure in the same subjects on different occasions served to shed light upon the innate sensory awareness of positions in space in individual subjects, versus the acquired ability to improve estimation accuracy through learning, despite the lack of direct feedback on the errors of estimation. To achieve this goal, the accuracy of estimation for the initial experiment was compared to the final level of accuracy recorded during the third experiment.

Comparison of our findings with those of previous authors (Bauermeister, 1964; Clark and Graybiel, 1964) indicates that the additional procedural controls implemented did not dramatically alter the patterns of response. Increased angles of tilt away from the vertical remained associated with greater errors of estimation (Fig. 4.6) (Clark and Graybiel, 1964). However, the phenomena of overestimation (E-phenomena) and underestimation (A-phenomena), respectively for g values greater than 1 and less than 1, were not discernable in our experiment. For any given test position, the absolute errors of estimation remained consistent, but the direction of misjudgement did not have any consistency. This may be the result of reduced reference cues and the random order of presentation of test positions utilized in our study. When the subjects commence their experimental trials in the vertical position and are progressively tilted away from the vertical, an initial judgement error could potentially affect all the following angular estimations. In addition, a systematic presentation of test positions could possibly bias a subject's ability to estimate the visual vertical. However, we can state with confidence that the order of presentation did not bias the accuracy of estimation because progressively greater or smaller step increments were avoided in our experiment.

Interestingly, 2 of our subjects (Fig. 4.5, ◇ , △) appeared to have a remarkable ability to estimate the vertical position from all the test positions during their initial experimental trial and for all subsequent trials. Their average error of estimation for all the positions was 2.5° versus 10° for the remaining subjects. Upon closer examination of their backgrounds in physical activity, it was identified that both of these subjects were gymnasts. Thus, it appears likely that improvement of orientation abilities in space occurs with training. In fact, it has been shown that labyrinth-defective subjects improved their accuracy of estimation and decreased their response variabilities after training (Howard and Templeton, 1966; Roberts, 1967). To further substantiate this hypothesis, our subjects showed a strong tendency towards improvement in judgement accuracy with repeated experiments, despite time intervals of 4 - 5 weeks between experiments. Thus, in the absence of verbal correctional feedback, visual input, or alteration of proprioceptive cues from joint and muscle receptors, perceptual sensitivity to different body positions in relation to the vertical nonetheless improved upon repetition.

Integration of visual cues to the task of vertical orientation with limited proprioceptive inputs from joint and muscle receptors, facilitated the estimation ability of 4 subjects who were alternatively tested with their eyes closed and their eyes opened (Fig. 4.8). Similarly, other investigators have found that labyrinth-deficient subjects could react normally when given adequate visual cues (Howard and Templeton, 1966; Roberts, 1967) and studies on dynamic sensory perceptions have stressed the importance of visual-vestibular interactions (Deecke _et al._, 1979; Bles _et al._, 1982). However, in _our_ study, despite the addition of visual inputs, errors of 3-7° persisted in the extremes of range and inter-subject variability persisted (Fig. 4.8). In addition to the absence of proprioceptive input from joint and possibly muscle receptors, this phenomenon could be partly attributable to the absence of neck inputs imposed by the _neck restraints_. Neck proprioceptive inputs have been shown to interact with labyrinthine inputs in detecting displacement of the trunk in space or in recognizing the finally achieved head position (Deecke _et al._, 1979). Furthermore, inputs from the neck and labyrinth converge in the anterior suprasylvian gyrus (Becker _et al._, 1979) which has been found to be the locus of sensory postural orientation (Penfield, 1957).

Thus, a convergence of inputs from the labyrinth, eyes, neck proprioceptors, limb proprioceptors, and cutaneous receptors appears to be essential to spatial perception and orientation. Anatomically, these modalities have been found to converge upon the thalamus (Abraham _et al._, 1977) as well as the cortical vestibular field (Mergner, 1979). Together, they were thought to provide the human organism with a conscious awareness of positions in space. Moreover, it appears that all the sensors must be coordinated for a correct perception of the vertical (Valentinuzzi, 1980). Our last study was devised to evaluate the relative contribution of static labyrinthine, visual, and proprioceptive inputs from joint and muscle receptors to the perception of the vertical. From our results, we could conclude that (1) labyrinthine contribution to the awareness of the vertical during whole head-body rotations in the coronal plane provides highly accurate sensory feedback to the organism over the range of 0-30°, resulting in a persistent, non-decaying awareness of small deviations from the upright (Fig. 4.6). (2) Further head-body rotations of 30°-90° in either a clockwise or counter-clockwise direction are associated with increases in the errors of estimation, and are likely the result of a greater need for coordinated input from visual and proprioceptive of labyrinthine sensory input (Fig. 4.6). (3) Response accuracy increased and variability decreased significantly when visual input was restored (Fig. 4.8). The residual errors in estimation despite visual input suggested that the contribution of unrestrained exteroceptive as well as proprioceptive inputs from joint and possibly muscle receptors, might be essential for full response accuracy at the extremes of tilt.

4. Correlation between Motor Response and Sensory Awareness to Static Labyrinthine Influences

As mentioned previously in Chapter 2 (section 2.3.3), electrophysiological evidence for the interaction between the sensorimotor cortex and vestibular nuclei has been provided by several authors (Becker et al., 1979; Deecke et al., 1979; Azzena et al., 1983). The majority of the cells recorded within Deiter's nucleus responded to both ipsilateral peripheral nerve stimulation and contralateral cortical stimulation. Furthermore, cortical neurons have been found to be modulated by movements of the head and neck relative to space in all the three planes, and characteristically signal the direction of rotation as well as the patterns of facilitation and inhibition seen in both upper and lower limbs in response to alterations of orientation in space. Thus, the logical progression of these studies is to determine the degree of mutual interaction between conscious sensory awareness of positions in space and the unconscious reflex control which govern the maintenance of postural equilibrium.

To date, human psychophysical data has been compared to neuronal responses recorded from the sensory cortex of the cat, as well as those recorded from the first order vestibular neurons in animals (Mergner et al., 1981). In addition, psychophysical data have been compared to the theoretical deflection of the cupula together with nystagmus in man (Guedry, 1974). However, no correlations between motor and sensory interactions to natural labyrinthine inputs have been evaluated either theoretically or experimentally. Our study provided us with the unique opportunity to study the influence of static labyrinthine inputs to both sensory awareness and motor control of postural equilibrium in the same subjects with use of the same experimental procedure.

Interestingly, it appears that there is evidence for functional interactions between conscious and unconscious control mechanisms. Sensory awareness of static whole-body rotations in the coronal plane is highly accurate in positions proximate to the vertical (Fig. 4.6). The vertical position, being one of equilibrium, is also associated with minimum alteration in soleus motoneuron pool excitability, as reflected by negligible changes in the H-reflex in 11 of 14 subjects (Table 4.1-4.3). However, increased tilt in either an anticlockwise or clockwise direction leads to increasing errors of estimation of the visual vertical in normal subjects (Fig. 4.6), to the extent that it would appear necessary for some reflexive control mechanism to compensate for the unreliable conscious feedback. In keeping with this need, when visual and proprioceptive inputs are absent, our results demonstrated that static vestibulospinal reflexes can unconsciously influence the tone of lower limb extensors in such a way as to maintain upright equilibrium. Indeed, the majority of our subjects responded to <u>ipsilateral tilt</u> with a functionally appropriate response, in that the ipsilateral soleus motoneuron pool excitability increased as a function of tilt (Fig. 4.1, 4.2). Conversely, all the subjects within our study population demonstrated an increased difficulty in estimating their positions in space with ipsilateral tilts greater than 50°.

Consequently, we can conclude from the data gathered in our study, that tonic labyrinthine input maintains a significant postural influence in man. It contributes to both a highly accurate awareness of small head displacements away from the vertical, and provides facilitatory reflex motor support on the ipsilateral side to maintain postural equilibrium, especially in response to large off-vertical displacements in the coronal plane.

CHAPTER SIX

SUMMARY AND CONCLUSIONS

1. Summary of Project

The global objective of this project was to determine the contribution of the otolith to the motor control of posture and sensory awareness in response to static natural labyrinthine stimulation. Thus, two series of experiments were devised to separately evaluate the sensory and motor components of this objective, as well as to allow comparison of these data in the same subjects. More specifically, while neck and visual inputs were eliminated, and exteroceptive stimulation minimized, (1) changes in the excitability of the ankle extensor (soleus) motoneuronal pool were monitored via the H-reflex testing technique, and (2) errors in subjective estimation of the visual vertical, in relation to randomly allocated whole head-body displacements in the coronal plane were recorded over a range of 0-180°.

The importance of these studies is highlighted by the fact that current understanding of postural control mechanisms remains predominantly based upon findings in quadrupeds as opposed to bipeds. Accordingly, this project was designed to allow direct comparison of previous findings in animals (Ehrhardt and Wagner, 1970; Lindsay et al., 1976; Roberts, 1979) with the human data generated here. In addition, the utilization of static natural labyrinthine stimulation minimized the possibility of recording artifactual response patterns created by either the mode or nonspecifity of stimulation used by some of the previous researchers (e.g. caloric or electrical stimulation). Moreover, other investigators have focussed upon the analysis of deficient or distorted vestibular function in humans (Lund and Broberg, 1983; Black and Nashner, 1984; Bles et al., 1984) which permits solely indirect conjecture upon basic motor and sensory mechanisms underlying the control of normal upright human posture. Hence, this research had the potential of partially bridging a significant gap of knowledge in the realm of human vestibular function.

The clinical importance of our findings relates to the evaluation of vestibular dysfunction, and hence treatment to promote improved function. So far, tests have been designed to rely largely on qualitative (Guedry, 1974) rather than quantitative methodologies, and there has been a preponderance of tools intended to detect dynamic rather than the less complex static postural dysfunctions (Baloh and Honrubia, 1979). Therefore, the apparatus utilized in our series of experiments, which provided precise and controlled step inputs to the otolith while both reflex motor and conscious sensory data were gathered, could feasibly be developed as a prototype for a more holistic clinical evaluation. The two series of experiments will now be briefly summarized before further elaboration upon the clinical implications of their methodology and results.

1.1 H-Reflex Study

The circoelectric bed which was customized to allow clockwise and anticlockwise rotation of the subject support platform in the coronal plane, could be maintained in positions ranging from 0-270° (i.e. 135° on either side of the upright vertical position). Subjects were blindfolded to eliminate visual input, and fixated to the support platform via partial sandsplint casts for the neck and lower limbs to minimize afferent input from these sources. In addition, a canvas corset for the trunk and body straps prevented the torso and upper limbs from sliding downwards or laterally. These extensive immobilization devices were needed to control all the factors which might influence tonic vestibular input, as well as to ensure the safety and comfort of the adolescent subjects.

The testing procedure for the H-reflex study comprised of rotating the bed to a randomly ordered test position, maintaining it for one minute, then recording the peak-to-peak H-reflex amplitude (mean of 20 responses). This was followed by a return to the control position and further recording of 20 H-reflex responses after a time lapse of one minute. The procedure was repeated for each test position applied randomly in 30° steps over a range of 0-180° while the M response was continuously monitored to ensure that the stimulus conditions had not altered. Test results were rejected if there were significant differences between preand post-test control H-reflex amplitudes, or between the control and test M responses.

Fourteen adolescent female subjects participated in the study, and after normalizing their H-reflex data for each test position with respect to the control reflex amplitude, the results were analyzed by examining the patterns of response which emerged as a function of the angle of tilt. After the ensemble responses had been graphically plotted, one major and two minor response patterns became apparent. 8 subjects responded with bilateral facilitation which progressively increased as a function of the angle of tilt (Table 4.1, Fig. 4.1). They showed minimal extensor (soleus) motoneuron excitability in the upright vertical position and maximal facilitation in either 90° of ipsilateral or contralateral tilt. Conversely, 3 subjects responded with bilateral inhibition (Table 4.3, Fig. 4.3), and the remaining 3 subjects responded asymmetrically to tilt in the coronal plane — with facilitation when rotated in an ipsilateral direction and inhibition when rotated in a contralateral direction (Table 4.2, Fig. 4.2). The patterns of response largely coincided with those recorded from the vestibular nerve by Fernandez and Goldberg (1976a). In addition, a high degree of sensitivity to tilt in this plane was recorded, as evidenced by the magnitude of H-reflex facilitation in this plane of movement (up of a maximum of 375° of the control reflex value). These findings corroborated with the greater sensitivities to utricular stimulation shown in animals with displacements in the coronal plane (Fernandez and Goldberg, 1976a). Furthermore, Roberts (1967, 1973, 1979) found that lateral tilt evoked ipsilateral extension of both fore- and hind-limbs to restore equilibrium, and our results largely coincided with certain aspects of his findings, given the fact that 11 out of 14 subjects showed H-reflex facilitation with tilt to the ipsilateral side.

1.2 Sensory Awareness Study

The technique of estimating the visual vertical was used to evaluate sensory awareness of head and body positions in space (Clark and Graybiel, 1964; Miller *et al.*, 1968). Subjects were asked to adjust a luminous line in a dark field to the apparent vertical while *errors* in estimation were recorded for each test position. The same experimental apparatus was used to apply whole head-body rotations in the coronal plane, and the same method of fixating the head, neck, torso, and limbs was maintained with the exception of one arm which was left free to allow for adjustment of the luminous dial according to the subjective sensation of the upright vertical. Moreover, visual input was excluded by a light proof crowning as opposed to the blindfold utilized in the H-reflex study.

We were able to generate some unique data on static position-sensing abilities by (1) randomly allocating positions in the test sequence without returning to the vertical during any given trial, (2) studying the effect of training via frequent repetition (3X) of the same experiment in the same subject over a period of time, and (3) evaluating the contribution of visual input to estimation of the vertical. We found, however, that in accordance with the findings of other investigation (Clark and Graybiel, 1964), greater errors of estimation were associated with greater angles of tilt for the majority (8) of our subjects. In other words, random allocation of test positions did not appear to reduce estimation abilities. Nonetheless, it became clearly evident that our subjects showed strong tendencies towards improvement in judgement accuracy with repeated experiments - despite time intervals of 4-5 weeks between experiments. Finally, the integration of visual cues to the task of vertical orientation greatly facilitated the estimation ability of 4 subjects, who were alternatively tested with their eyes closed and their eyes opened (Fig. 4.8). However, minor errors in estimation (3-7°) persisted despite the inclusion of visual inputs. This finding was thought to be partly attributable to the absence of neck and proprioceptive inputs. Thus, a convergence of inputs from the labyrinth, eyes, neck and limb proprioceptors, as well as cutaneous receptors, appears to be essential to spatial perception and orientation.

As mentioned previously, our study provided us withe the opportunity to study the influence of static labyrinthine inputs upon both sensory awareness and motor control of postural equilibrium in the same subjects, with use of basically the same experimental procedure. Interestingly, there appears to be evidence for functional interactions between conscious and unconscious control mechanisms, in that sensory awareness of small head displacements (0-30°) away from the vertical is highly accurate (Fig. 4.6) while reflex facilitatory influences upon extensor (soleus) motoneurons are minimal (Fig. 4.1-4.3). Conversely, sensory awareness of large displacements (50°-90°) away from the vertical are less accurate (Fig. 4.6) when reflex facilitatory influences upon the extensor (soleus) motoneurons are maximal at 90° of ipsilateral tilt in a large majority of subjects (11 out of 14) (Fig. 4.1-4.2). Consequently, we can conclude from the data gathered in our study, that with visual and proprioceptive inputs from the neck and limbs eliminated, tonic labyrinthine input maintains a significant postural influence in man.

2. Implications for Clinical Evaluation of Labyrinthine Function

Physiotherapists are commonly consulted to treat patients with balance and equilibrium difficulties, which stem from either primary vestibular disease and dysfunction, or arise as a problem secondary to diverse neurological conditions or the process of aging. Presently, the tools for evaluation consist predominantly of subjective tests which are capable of characterizing the gross functional disability, but incapable of determining the relative contributions of labyrinthine, visual, neck, and limb afferent inputs to the problem. As a result, the treatment tools are largely non-specific and do not take into consideration the tremendous potential for compensation and adaptation to postural equilibrium difficulties driven by the above-mentioned inputs. Thus, the adaptive potential of this interactive system is not being utilized to its full advantage.

Our apparatus and methodology selectively controlled the variables which influence balance and orientation abilities in space, so that evaluation of both motor and sensory outputs in response to natural labyrinthine (in particular otolithic) inputs could be ascertained. The results shed light upon tonic vestibulospinal reflex responses in man which have been assumed to mirror those of other quadrupedal mammals, and added the dimension of evaluating the influence of the otolith upon conscious sensory awareness of orientations in space. This combination of tests provided a more holistic determination of the human responses to static natural labyrinthine stimulation, and could feasibly be utilized clinically to provide information concerning the relative deficiencies and contributions of the various sensory afferent inputs to a given equilibrium dysfunctional problem.

In addition, we utilized a selective adolescent female study population in light of recent findings implicating abnormal labyrinthine control mechanisms in patients with scoliosis of idiopathic origin. Briefly, Sahlstrand *et al.* (1978) recorded increased sway amplitudes in scoliotics, particularly when their visual input was removed. Moreover, in a later study, Sahlstrand and Petruson (1979) reported a significant occurrence of spontaneous and positional nystagmus in scoliotics compared to controls ($p = .001$), with sensitivity dominance on the convex side of the curve. These findings may reflect peripheral biomechanical imbalances, central deviations of postural reflexes, or an interaction of BOTH these factors. Thus, our study methodology and the data gathered in these preliminary experiments could be used as a baseline for comparison with a population of subjects with adolescent idiopathic scoliosis, in an effort to more specifically determine whether tonic vestibulospinal reflex activity is altered.

In conclusion, there is no doubt that the findings of our study can be utilized to improve evaluation and ultimately treatment skills. Further research has the potential of shedding light upon other basic postural control reflexes in man and will provide a solid foundation for the process of rehabilitation.

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