RECORDING OF VESTIBULOSPINAL REFLEXES USING CALORIC-INDUCED ELECTROMYOGRAPHIC RESPONSES IN LIMB EXTENSORS

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Title of Thesis/Project/Extended Essay

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ABSTRACT

Vestibulospinal reflexes consist of a pair of complicated organs located in the inner ear which act as gravity-oriented accelerometers. Three semicircular canals in each organ are oriented at right angles to each other. Information about the position and movement of the body is constantly analyzed so that equilibrium can be regained or maintained. It was noted over 100 years ago that stimulation of the canals resulted in a reflex compensatory movement of the eyes. In addition to this vestibulo-ocular reflex there is also a neural connection between the vestibular organs and the so-called anti-gravity muscles (extensor muscles) of the extremities. The vestibulospinal reflex has been investigated since the turn of the century. Early investigators substantiated that it, too, was mediated by the vestibular organs. The present study combined irrigation of the external ear canal with warm water at 44 degrees Celsius with measurement of the electrical activity of the extensor muscles of the arms and legs to detect the effect in humans and to attempt to measure and quantify it. Four male and four female subjects were given four caloric irrigations each in a randomized sequence in a supine position and with the body but not the head tilted at a 45 degree angle.

Results indicate differences between responses measured in the two arms. Extensor muscles on the irrigated side were more active than on the non-irrigated side, although all muscles measured increased their activity to some extent over the level of activity recorded at rest. There was a high degree of variation between responses of different subjects. There was also a general decrease in response with repetition. My experimental protocol was designed to demonstrate that a quantified vestibular stimulus would elicit a predictable vestibulospinal response. The results appear to indicate, however that there is no consistent vestibulospinal response to that stimulus. Emotional factors, prior experience, central nervous system (CNS) preprogramming or fatigue or stimulation of sensory nerves may contribute to the observed variability, as each of these factors may have affected each subject to a different degree. There was no observable difference in results between tests performed in the sitting and supine positions. The responses were not statistically significant despite attempts to analyze the data using many different parametric and non-parametric means of analysis. Some of the responses were not very marked. Although no significant response is demonstrated, the tendency noted towards ipsilateral excitation refutes previous evidence that shows a contralateral effect. The only other similar investigation reported in the literature demonstrated ipsilateral facilitation.

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A. Introduction

The major receptor organs of the body's major senses respond, with one exception, to stimuli from the outside world. The exception is the labyrinth of the vestibular system, which responds to angular acceleration of the head. As a result, labyrinthine responses are not under voluntary control. The continuous activity of the vestibular organs is altered by head movement. Rotation of the head, for example causes excitation of the leading balance organ and inhibition of the trailing organ. This imbalance of sensory information reaching the vestibular nuclei creates the sensation of movement. Unwanted visual or auditory stimulation can be supressed by closing one's eyes or ears, but stimulation of the labyrinths cannot be suppressed (Baloh and Honrubia, 1979). The vestibular system is never directed towards a particular environmental object in the way we turn to see, hear, touch, or smell, but vestibular stimulation occurs each time we turn (Guedry, 1974).

Mach in 1875 was the first to appreciate the existence of a separate organ for the perception of motion. He observed that perception of motion could be altered by changing the position of the head in relation to the body and suggested that the sense organs for the perception of acceleration and head position were located in the head (cited in Baloh and Honrubia, 1979).

It can be shown that the sensation of angular motion is a separate sensation. It can be generated by vestibular stimulation alone and need not be a composite of stimulus perception from other sensory systems, although the sensation is often enhanced by visual and tactile cues. As suspected by Mach, patients without vestibular function (whether they are born without it or lose it later in life) do not experience the sensation of turning when rotated in complete darkness if all tactile cues are removed (Guedry, 1974). This perception, however remains intact in a patient with a cervical spinal cord transection. Rotation of a person generates an associated eye movement even in the dark consisting of a compensatory slow deflection in one direction elicited by the vestibulo-ocular reflex (VOR) and a fast corrective repositioning eye movement. Although there is close interaction between vestibular and visual sensation, the sensation of movement is not dependent on the associated eye movement ("nystagmus"), or even the presence of sight, as blind people or people with complete oculomotor paralysis still experience the sensation of vertigo upon vestibular stimulation (Baloh and Honrubia, 1979). Therefore it must be the case that the brain's awareness of vestibular stimulation can generate eye movement without visual input. This interaction between head movement and appropriate compensatory eye movement forms the physiological basis of the VOR.

Vestibulospinal reflexes comprise all those spinal reflexes that cause movements or changes in position, (or both) as a result of vestibular signals (Peitersen, 1967). If a rabbit on a turntable is rotated at constant velocity and then suddenly stopped, the physiological effect on the labyrinth produced by the deceleration persists for a time, causing a post-rotatory nystagmus (Roberts, 1978). A burst of nystagmus is seen with its slow-phase in the original direction of rotation. The rabbit will also tend to fall in the direction of rotation when the table is suddenly stopped. This falling tendency is counteracted by reflex activation of the antigravity muscles on the side towards which it is falling, producing an increased extensor thrust in the limbs on that side. The extensor tone of the contralateral limbs is diminished and the rabbit successfully thwarts his fall (Baloh and Honrubia, 1979). These limb muscle reflexes are mediated by the semicircular canals and are always appropriate to prevent falling regardless of the direction of the acceleration force (Roberts, 1978). This example demonstrates the existence, role and function of the vestibulospinal reflexes. While the effector organs of the VOR are the ocular muscles, those of the vestibulospinal reflexes are the so-called **anti-gravity** muscles of the neck, trunk and extremities. Most muscles in this group are extensors. The push-pull (agonist-antagonist) organization of the VOR effectors closely parallels the organization seen in the vestibulospinal reflex system (Baloh and Honrubia, 1979). Each flexor muscle has an antagonist extensor and excitation of one is accompanied by inhibition of the other. However the complexity of the vestibulospinal response greatly exceeds that of the VOR. Characterizing any vestibulospinal response by describing the action of an extensor muscle and its antagonist (in the way eye muscle pairs govern eye movements) is far too simplistic as any movement about a joint requires a complex interaction of motor unit recruitment in a multitude of muscles. There are three descending pathways by which vestibular stimulation can activate the spinal cord. All three tracts are located in the anterior horn of the spinal cord. The **lateral** and **medial** tracts synapse directly with neurons in the vestibular nuclei, while the **reticulospinal** tract fibres synapse predominantly with second order neurons from the reticular formation (although some primary vestibular fibres end right in the reticular formation). All three tracts have both crossed and uncrossed fibres serving both ipsilateral and contralateral muscle groups (Gernandt, 1974). It is generally agreed that most fibres in the lateral vestibulospinal tract originate from neurons projecting from the lateral vestibular nucleus. In the spinal cord this tract descends to synapse with anterior horn cell dendrites or interneurons, both of which project to anterior horn cells of limb musculature. The initial descent is ipsilateral but there is a certain degree of crossover. (Electrical stimulation of the lateral vestibular nucleus causes bilateral effects). Stimulation of the lateral tract results in activation of the extensors of the extremities. That the lateral nucleus is involved in global excitation is demonstrated by the fact that its ablation will abolish decerebrate rigidity. Although there is a somatotopic organization of the fibres arising from the nucleus, it remains largely unmapped. The lateral tract is prominent in monkey and cat but is poorly developed in man (Gernandt,1974). The medial tract, the smallest of the three, has far fewer fibres than the other two tracts. It descends via the medial longitudinal fasciculus (MLF) to the cervical vertebrae. Its predominant functional role appears to be mediation of the VOR and cervico-ocular reflexes. Stimulation of the MLF activates neck flexors and extensors. Fibres in the reticular tract originate from neurons in the reticular formation. Fibres descending the spinal cord are both crossed and uncrossed. Although somatotopic mapping has demonstrated some excitatory fibres arising from the more lateral regions of the reticular formation, the tract is predominantly inhibitory on both extensors and flexors of extremity muscles. The main vestibular influence on afferent reticulospinal activity is governed by secondary vestibular neurons and interneurons. The complicated, highly interconnected reticular formation governs information sent down the reticulospinal tract. Although not well understood, it seems to work in concert with the lateral tract to modulate its effects. As a result, a midground between spasticity and flaccidity is maintained. The interaction between the two tracts is also not well understood but both the red nucleus and the substantia nigra are suspected of playing a vital role.

Purkinje in 1827 seems to have been the first investigator to document his observations of the vestibulospinal reflex at work in man (Peitersen,1974). He described a bending in a given direction after rotation and a greater weight on one foot than the other. He reasoned that the rotation caused increased pressure on one side of the brain. Fifty years later Ernst Mach expounded on the initial observations by his countryman:

> "There are cases, indeed, in which the sensation of forward movement is undoubtedly present while that of the movements of the legs is equally undoubtedly lacking. This is true, for instance, of a railway journey, or even the thought of a journey.... The only explanation of this can be that the will to move forward or to turn about, which furnishes to the extremities their motor impulses, - impulses which may be further modified by particular innervations - is of a comparatively simple nature. The conditions existing here are probably similar to, although more complicated than, those connected with the movements of the eyes.... We shall scarcely go far wrong if we suppose that the comparatively simple motor sensations stimulated from the labyrinthe of the brain stand in the closest connexion [sic] with the will to move".

(Ernst Mach, 1875) [1]

Barany in 1906 developed Mach's observations into a clinical test. He demonstrated that irrigating the external ear and tympanic membrane with fluids of different temperatures would produce stimulation of various reflexes initiated by the labyrinths (Dolowitz, 1967). This "caloric irrigation" has evolved into the present-day test for detection of vestibular pathology. A carefully-controlled amount of water at a standardized temperature is used and the slow-phase velocity of the elicited nystagmus (i.e. the vestibulo-ocular response) is

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[1] Mach's original work cited here was entitled "Bewegungsempfindungen". Translated from the German in 1897, it was revised and supplemented in 1911 and re-read by Mach himself before being published in its present form.

measured (discussion of caloric irrigation p 13). Barany developed a method of measurement of the elicited **cristospinal** reflexes (so-called because they arose as a result of stimulation of the crista) using the upper limbs. A patient would sit with one arm raised and one finger pointing straight forward. The patient would then allow his hand to sink to his knee. A normal individual would always touch the same spot. However if the right ear was irrigated with cold water, a left-beating nystagmus was elicited and the finger would drift towards the right in its downward journey. Hot water would produce a movement in the opposite direction. Irrigation of the opposite ear would also produce a movement in the direction of the slow component of the nystagmus.

Baldenwick in 1912 (cited in Peitersen, 1974) made further observations about the effects of caloric stimulation. He noted leaning of the body and turning of the head in the direction of the slow phase.

Wodak and Fischer (cited in Dolowitz, 1967) in 1922 also exposed patients to caloric stimulation and described turning, twisting and tilting of the body. They attempted to record these movements by having the patients stand holding pencils in both hands with their arms stretched out in front of them, but found the recordings to be inadequate. In 1924 Fischer and Wodak (cited in Peitersen, 1963) performed more accurate studies by developing stepping tests. They found that persons seemed to rotate on their own axes while "marking time" or walking on the spot while blindfolded with their arms folded across their chests.

In 1938 Unterberger published his results of rotational tests on normal people (done using the same basic protocol as Fischer and Wodak) and found that most people rotated away from their dominant hand (cited in Zilstorff-Pedersen and Peitersen, 1963). Hirsch (1940) described the identical procedure and called it the **waltzing test**. He found that people could mark time without rotating on their axes. Irrigation of one ear with ice water caused rotation of the patient anywhere between 180 and 360 degrees. None of the authors, however detailed results of individual subjects or even reported the number of subjects tested (Dolowitz, 1967).

Fukuda in 1959 developed tests to measure vestibulospinal reflexes in both the arms and the legs. He developed a writing test (Fukuda, 1959a) measuring the arm deviation when a subject wrote vertical columns of letters. He described normal subjects as having little or no spontaneous deviation. It was subsequently shown that the normal deviation was in fact far greater than previously reported and the test had little or no diagnostic value. However Fukuda (1959b) also further refined the waltzing test and tried to correlate carefully-documented results with clinical diagnoses. Using procedures essentially identical to Hirsch's, he had five hundred subjects marking time at the centre of two concentric circles with diameters of one metre and one-half metre. These circles were divided into thirty degree segments. He found that most normal persons remained in the original position after as many as one hundred steps. He also described the limits of variation that he considered normal. However, Jordan (1963) reproduced Fukuda's stepping test and found results for normal subjects that were strongly in conflict with those originally reported.

Henriksson et al.. (1962a,1962b) developed a method of measuring head rotation following caloric irrigation, a reflex that they termed **laterotorsion**. They placed a subject's head between two pneumatic pillows and measured relative changes in air pressure between the pillows. The laterotorsion responses were found to be fairly consistent for a given subject, but some patients with inner ear pathology showed no difference from normals, even though caloric irrigations confirmed the existence of pathology. Peitersen noted (1967) that man's ability to walk in place unaided by vision is one of the human functions that has remained largely unexamined. He assumed that most clinicians had taken this function for granted and that they believed no investigation was necessary. Studies done before that date had been for the most part inconclusive. No accurate methods had evolved for delineating postural pathology because nobody understood how normal posture and gait were maintained.

Zilstorff-Pedersen and Peitersen (1963) had initially drawn attention to the primitive state-of-the-art in the area of vestibulospinal reflex testing. They criticized Fukuda's poor control of experimental parameters and developed a refined stepping test. They excluded all auditory and visual cues that subjects could use for information and even prevented subjects from orienting themselves by feeling the warmth of their own feet on the floor by making all their subjects wear shoes (Peitersen, 1967). The pair also found marked discrepancies between Fukuda's results and their own and in the most intensive and objective study to that time were able to build up a data base of results from normal subjects. They also investigated the effects of rotatory stimulation (Peitersen and Zilstorff-Pedersen,1963) and caloric irrigation (Peitersen, 1963a, 1963b) on stepping test performance and demonstrated alterations in performance in patients with various types of vestibular disease (Peitersen, 1964a) and intracranial disorders (Peitersen, 1964b). Peitersen (1967) concluded that the stepping test was a valuable adjunct to clinical examination, especially in patients with unilateral disease. While advocating the stepping-test as an informative screening technique, he cautioned that the result could not be accepted at face value to represent a single organ function, due to the complex physiology of the upright ambulatory position and the multitude of functions contributing to this act. Generally he advocated the stepping test as a "spontaneous routine method", but admitted that its great sensitivity may be one of its major drawbacks, as any patient more than slightly dizzy could not perform the test at all.

The stepping-test was the first stage towards the development of the present study as it had now been shown that the results of vestibular function tests measuring the VOR (i.e. caloric irrigation) could be more or less correlated with the results of vestibular function tests using the vestibulospinal reflex. Although Peitersen himself (1967) stressed that the stepping test should not be used alone in diagnosis, he had made the first attempt to quantify the vestibulospinal reflex in order to detect pathology. Peitersen himself admitted that his extensive investigations into the stepping-test were less than satisfactory and the end result was a conundrum: the scores of patients with only mild vestibular pathology were hard to distinguish from those of his normal population (because of the extreme variability he found in his normals). Patients with severe pathology on the other hand were too dizzy to even attempt the stepping test. Since Peitersen's work (1963-1967) with the modified stepping-test, little progress has been made in developing a clinical regimen for testing vestibulospinal reflexes. Nashner has been investigating human postural control from a neuromuscular standpoint. His early studies (Nashner and Wolfson, 1974) used electrical current applied bilaterally across the mastoid bones in order to induce sway. This was his method of vestibular stimulation. The existence of a pathway for the stimulation of antigravity muscles was demonstrated. They showed that although the body's total effort in compensating for this sway was a collective effort involving both vestibulospinal activity and cues from the feet and lower leg, the initial postural response to this (or any) disturbance of equilibrium was supplied exclusively by the vestibulospinal system. Nashner admitted that his galvanic stimulation procedure had no future as a clinical tool:

> "The properties of responses evoked by galvanic stimulation have been uncertain, limiting its usefulness as a clinical tool or as a technique for the study of vestibular or motor system physiology."

In order to measure postural reflexes, Nashner had developed a standing platform mounted on strain gauges. It could either be moved actively, or used passively. This platform linked with a computer could either execute a preprogrammed series of movements, or analyze a subject's response to an external stimulus that required a reactive movement to regain postural stability. Nashner et al. (1982) delineated the role played by the vestibular organs in posture maintenance. This was hard to measure clinically because of the threefold nature of postural control:

1. **proprioceptive and cutaneous inputs** from the lower legs and feet,
2. **visual inputs** derived from analyzing angular motions of the visual field, and
3. **vestibular inputs** derived from angular accelerations of the head.

The study delineated the prime function of the vestibular system not as a direct supplier of information, but as a **reference system** against which conflicting or erroneous proprioceptive and visual cues are quickly suppressed. In other words, its job is to find out when sensory information is wrong so it can be ignored. The investigators postulated that this system was on a hierarchically high level and was possibly more important than the hierarchically low-level system which directly mediates postural muscle action. A second study (Forssberg and Nashner, 1982) showed that children under the age of seven and a half years old were actually unable to use their vestibular system to suppress erroneous information although they demonstrated abilities similar to those of adults during experiments designed to test rapid postural adjustments. This proved that the hierarchically lower process matures earlier in life than the higher level adaptive process, indicating the complexity of the latter. In short, Nashner and his colleagues enhanced understanding of the neural control of posture maintenance, but have contributed little to clinical testing of the vestibulospinal system. (Note that Nashner's work could delineate pathology somewhere in the vestibular-vestibulospinal complex, but could not differentiate between vestibular and vestibulospinal pathology.) Clinical vestibular testing today is performed by caloric irrigation. This method stimulates the vestibular labyrinths. It is quantitative, more or less reproducible and fairly well standardized. Response is gauged by measuring nystagmus (i.e. vestibulo-ocular response(VOR)) elicited by controlled thermal stimulation of the semicircular canals via the temporal bone. The external ear canal is irrigated with water above body temperature. A temperature gradient is set up causing a change in the specific gravity of the endolymphatic fluid. The fluid is displaced and the cupula is deflected. During clinical testing in this manner, the patient is in a supine position with the head ventroflexed 30 degrees. This brings the lateral semicircular canal into a vertical plane, thereby maximizing the effect of the specific gravity change. Although differing caloric irrigation techniques exist, the one employed in this experiment, the Fitzgerald-Hallpike technique modified by Barber is one which is widely accepted as clinically accurate. Further details of the technique and its interpretation are given by Barber and Stockwell (1980). Responses are quantified by measuring the maximum velocity of the slow-phase of the caloric-induced nystagmus. During this phase the eye movement is interpreted as movement of the body. which visual input takes place). Irrigations using water above body temperature (i.e. warming of the endolymphatic fluid) cause an increase in the level of afferent information from the irrigated ear, while irrigations below body temperature inhibit the response from that side. Although it is recommended that both warm and cold irrigations be performed, Longridge and Leatherdale(1980) have shown that if the results of the warm irrigations of the left and right ears fall within a certain range of symmetry, cold irrigations are unnecessary.

There has been some criticism about utilizing caloric stimulation of the lateral semi-circular canal as a valid parameter of vestibular function. The caloric stimulus acts only on the lateral canal and the response gives no indication of the function of the other two canals or of the otoliths. The classical theories stated that the semi-circular canals were only sensitive to angular acceleration and their main role was to maintain fixation of the eye during head movement, resulting in corrective saccades, generating nystagmus (Kornhuber, 1974). However it has been shown that there is an intimate interrelation between all parts of the vestibular system. The perception of tilt, for instance (a function classically assigned to the otoliths) can be modified by semi-circular canal stimulation. Perception of angular velocity can be either enhanced or suppressed by otolith stimulation (Guedry, 1974). Because of this association, a technique regarded as measuring angular acceleration might allow quantification of the vestibulospinal response classically recognized as being mediated solely by the otolith organs. A caloric irrigation resulting in a slow nystagmus response causes a subjective sensation of slight movement (usually rotational) or a feeling of unsteadiness. A fast response ususally includes extreme sensations of rotatory motion, falling off the examining bed and general instability. During a response of this nature many patients describe attempts to counteract this motion by "digging in with my heels" or "pressing down with my palms". This is not only a subtle response that is casually mentioned by patients as an afterthought, but is an easily observable phenomenon that I see repeatedly in the laboratory. Patients often report marked insecurity during testing, even though they are supine, and will grasp the bedrails, the mattress or the examiner's arm for reassurance. These actions take place despite repeated assurances that their perceived motion is just that. In other words, the vestibulospinal reflexes are invoked in response to an **apparent** rather than an actual motion. In the same way that antigravity muscles would be recruited to avert a fall off the bed, an isometric contraction takes place to "avert" the perceived fall.

Isotonic contractions result from motor units being continually recruited until the tension in the muscle just balances the weight of the load (force, etc.). As the muscle is allowed to shorten, less force is available and less tension can be built up. Far greater tension is developed in a sustained isometric contraction in which the muscle is prevented from shortening (Roberts, 1978). The vertiginous patient on the examining bed would therefore be making a maximum-strength isometric contraction of his leg muscles to make sure he doesn't roll off.

The experiments to follow test the proposition that, based on this supposition and the repeated observations of patient reactions to caloric-induced vertigo, the anti-gravity muscles will respond to counter this perceived motion. The specific strategy undertaken to counteract the sensation of rotatory vertigo while in a supine position would consist of some combination of two different isometric contractions: firstly an extension of the hip, (coupled with flexion of the knee), and secondly extension of the elbow (if the hand is pronated). By examining the subject in a supine position, the whole-body response to vertigo is channeled into specific groups of muscles in the arms and legs. In the lower extremity the bi-articulate muscle group responsible for hip extension and knee flexion is the "hamstrings" group of muscles. The elbow extensor is the triceps brachii. EMG recordings of these two muscle groups using surface electrodes and analysis of the rectified-averaged signal should provide a direct measure of the vestibulospinal response to standard caloric irrigation.

B. Experimental Procedures

Four males and four females from 20 to 32 years of age acted as subjects for the experiment. All subjects were right-handed. All subjects were medically screened and

1. had never been diagnosed with a neurological problem or affliction,
2. had never had exposure to aminoglycoside antibiotic therapy (a family of drugs which can have toxic side effects on the vestibular system),
3. had no history of vertigo or complaints of hearing loss,
4. had no history of back surgery.

Informed consent was then obtained from all subjects (see Appendix "A").

Electrodes for measurement of electronystagmographic (ENG) signal (for recording induced nystagmus) were placed on the lateral canthi. This electrode position is the standardized position for bitemporal recording of nystagmus. Electrodes for electromyographic (EMG) recording were placed on the triceps brachii and hamstrings group of muscles. The muscle was flexed isometrically and the muscle body located by palpation. The centre point of the muscle body was determined and electrodes were placed 2.5 cm. equidistant from this point on the longitudinal axis of the muscle. This protocol is suggested by Davis(1959).

Electrode sites were cleansed with 70% isopropanol and abraded with pumice cream. Gold cup electrodes were then filled with electrode cream and applied with hypoallergenic surgical tape. A reference electrode was applied to the dorsal aspect of the left hand. All electrode impedances were reduced to a maximum of 3000 ohms. Electrodes were allowed to stabilize for at least 10 minutes to minimize slow potential drift.

The experiment was carried out in a laboratory. The subject and examiner were not distracted by conversation between other subjects. Illumination was kept at a comfortable level. The computer system was situated in a separate room, as were the amplifiers and signal monitor. An assistant timing the experiment sat quietly beside the subject. The left and right ears of each subject were irrigated for 30 seconds with 250 millilitres (ml.) of water at 44.0 ± 0.1 degrees Celsius with the body supine or reclining at 45 degrees. The head was kept at 30 degrees above the horizontal in all cases. A minimum of 5 minutes was allowed from the beginning of one procedure to the beginning of the next one. This is adequate time to ensure that there is no effect on a given test because of the previous one not having worn off (Barber and Stockwell,1980).

The water was held at a stable temperature and the temperature at the irrigating tip was monitored degrees Celsius throughout. All ears were examined for tympanic membrane perforations and also the presence of earwax before irrigation. During the test subjects were instructed to lie in a relaxed manner. The hands were pronated and the arms were kept flush to the body with the fingers together and flat. The legs were together with the knees straight and toes pointing straight ahead. The head was maintained in the caloric test position (i.e. ventroflexed 30 degrees in the horizontal test and dorsiflexed 15 degrees in the 45 degree test position). The subject maintained this position with eyes closed for a thirty second period prior to the start of each irrigation. At this time, EMG's were recorded. Approximately 250 ml. of water was instilled over an irrigation time of 30 seconds using a gravity-feed pump. Subjects were instructed to keep eyes closed during the irrigation and for one minute after the irrigation ended. During this time vigorous alerting tactics were used such as matching Christian names, place names or animals to sequential letters of the alphabet or to recite serial sevens backwards from ninety. Ninety seconds after the irrigation began, the subject was instructed to open his eyes and fixate on a target for a five second period. After the irrigation, the subject recorded his description of the sensation on audio tape.

Each of the five signals (the ENG channel, the two arm EMG and the two leg EMG channels) was routed through a phazo amplifier built especially for data amplification in the Psychophysiology laboratory at Simon Fraser University. A sixth channel was used to store coded digital information about experimental procedure. All data were then digitized at a sampling rate of 500/sec. and collected on magnetic tape on a

Nova 3D computer using a Data General Real Time Disk Operating (RDOS) system. Information on the digital channel was used to locate "epochs" of data which were subsequently stored separately. Frequencies up to 250 Hertz (the Nyquist frequency) could be recorded without distortion at this sampling rate. Appendix "F" illustrates the analyzed epochs of data. The one minute of data immediately following cessation of caloric stimulation represents the response. This is the period of time during which caloric-induced nystagmus is analyzed in the clinical setting. All ENG recordings were scrutinized to make sure that the eyes were not opened prior to the end of data collection. In one case it was found that this took place and the EMG recordings in that instance were analyzed only for the period of time that the eyes remained closed. In one instance no EMG response was recorded for a period of seconds, presumably due to a computer error.

The resting EMG signals were obtained for 20 seconds immediately before each irrigation. In three instances the eyes were opened prior to obtaining the full twenty-second epoch. In three instances it was noted that the subject shifted his position voluntarily. Upon examination of the EMG responses in these instances, peaks of contraction occuring simultaneously on all channels were observed. Peaks such as these were not observed at any other time during examination of the resting data. These three separate episodes lasting under two seconds each were excluded from the calculations. Both the epochs of response and the 20 second resting signals were treated in the following manner:

1. EMG responses were smoothed by averaging successive twenty millisecond (msec.) windows of data so that each 20 msec. was represented by one point.
2. The smoothed EMG data were rectified.
3. The smoothed-rectified EMG data were reduced to a single value by calculating the average amplitude across the whole epoch.

Results were tested both parametrically and non-parametrically. Noise from the Grass electrode panel, which is rated to be 5 microvolts (uV) or less, was ignored during calculations.

Statistical treatment of the responses obtained did not show any significant difference between ipsilateral and contralateral responses. The following statistical analyses of the data were carried out:

1. a paired t-test was used to compare each response with that of the contralateral limb;
2. the average of the arm and the leg response on each trial was compared in the same fashion with the average of the contralateral limbs;
3. the total ipsilateral response of each subject was compared with the total contralateral response in the same fashion;
4. the above three procedures performed on the net responses (i.e. absolute increase in response) were also performed on

the ratio of response increase;

5. steps 1,2 and 3 were also performed on the calculated base 10 logs of the responses (a maneuvre often utilized in EMG analysis to accommodate large variations);

6. the Phillipszoon and Jongkees method of analysis of caloric assymetry (see Barber and Stockwell, 1980) was utilized in each subject to determine if there was a significant directional tendency of response.

The Wilcoxon test for paired comparisons, or Wilcoxon-Mann-Whitney test as it is sometimes called (Noether, 1971) was used in non-parametric analyses.

C. Results

1. All irrigations elicited nystagmus on the ENG channel.

2. All subjects reported subjective sensations ranging from slight sensation of perturbation of position to definite reports of axial rotation. No subject complained of nausea during the course of the testing.

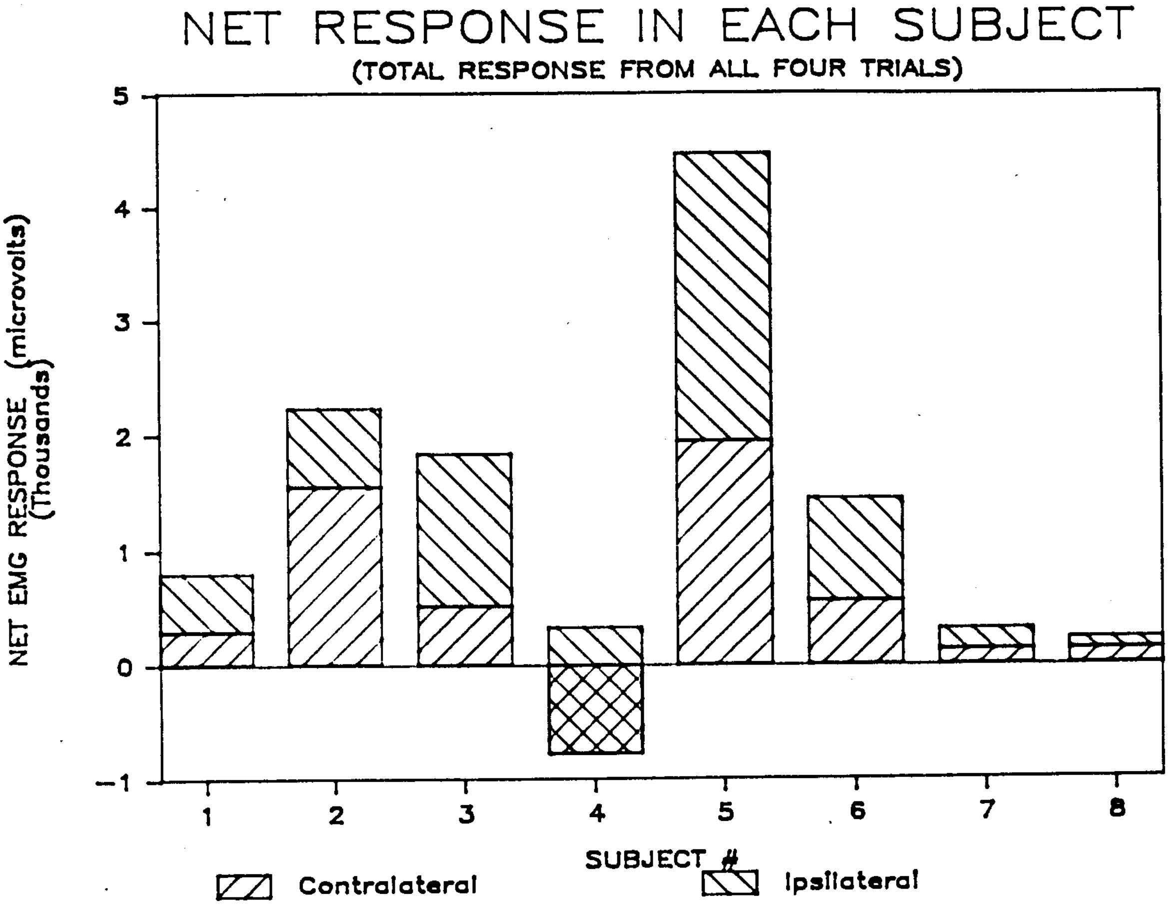
3. There was a wide range of EMG responses, both in the resting data and during the caloric-induced response. Many of the responses reflected extremely low muscle tensions. More vigorous contractions were seldom seen.

3a. The value of resting responses varied from 3 uV to 376 uV, with one extreme value of 1.09 millivolts (mv). Most of the responses remained consistent in individual subjects.

3b. The EMG responses elicited as a result of the irrigations were also varied, both in amplitude (see Appendices) and form. Two subjects who exhibited constant muscle activity on EMG recordings throughout the 60 second recording period did so on all four tests. EMG's in a series of rapid repetitive bursts, on the other hand were seen in 3 subjects during all four trials and in 2 other subjects on 2 of 4 occasions. One subject showed a gradual increase in tension with time in all muscles in 3 of 4 trials (see examples of different kinds of responses in Appendix "G"). Analysis using the Wilcoxson test of all the data together, and also from each experimental condition separately showed that under no circumstances was the d-value small enough to show a significant trend at a confidence level of alpha = 0.1.

The following comparisons were carried out on the data:

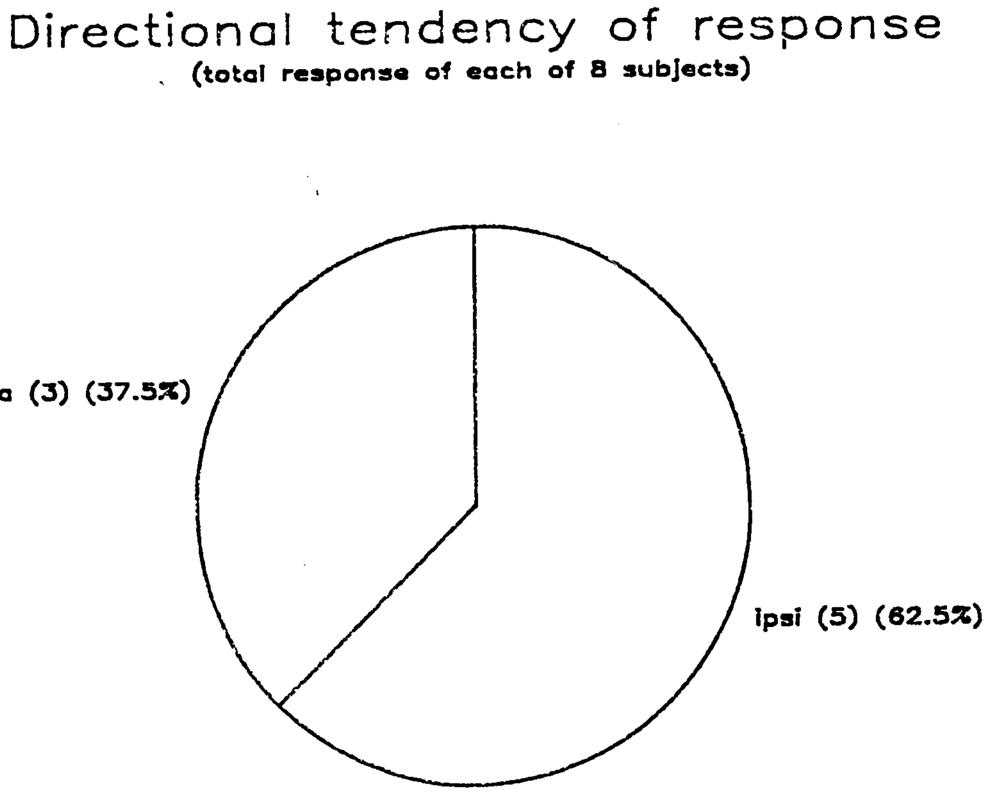
A) All responses in each subject were appropriately added or subtracted to calculate a directional tendency for each subject. This was done by taking the total of all ipsilateral responses and comparing it to the total of all contralateral responses in each subject. The subject was then categorized as either an "ipsilateral" (I) or a "contralateral" (C) roller.



The graph shows the total of ipsilateral responses and contralateral responses in each subject while the pie-chart illustrates the trend across all eight subjects.

Subject No. (Age and sex in brackets)

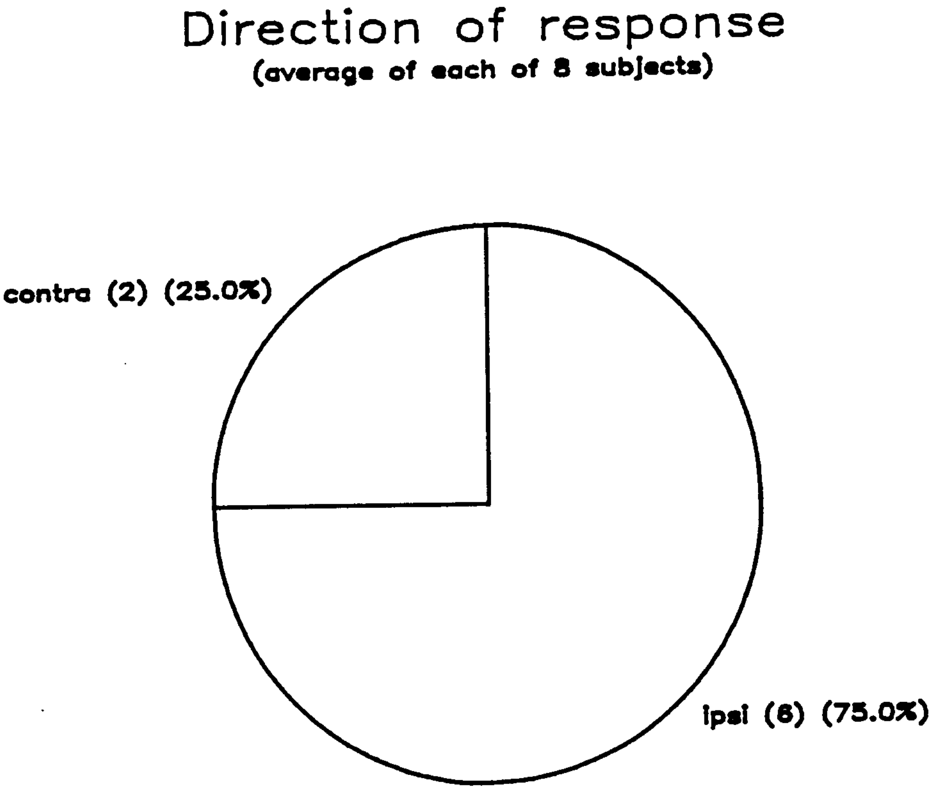
1	2	3	4	5	6	7	8
(25M)	(25F)	(21F)	(29M)	(27M)	(32M)	(31F)	(32F)
I	I	C	C	C	I	I	I



B) The average of all 8 ipsilateral responses in each subject was compared to the average of all 8 contralateral responses. In other words this pie-chart lumps all four trials into a hypothetical "single response".

Subject No. (Age and sex in brackets)

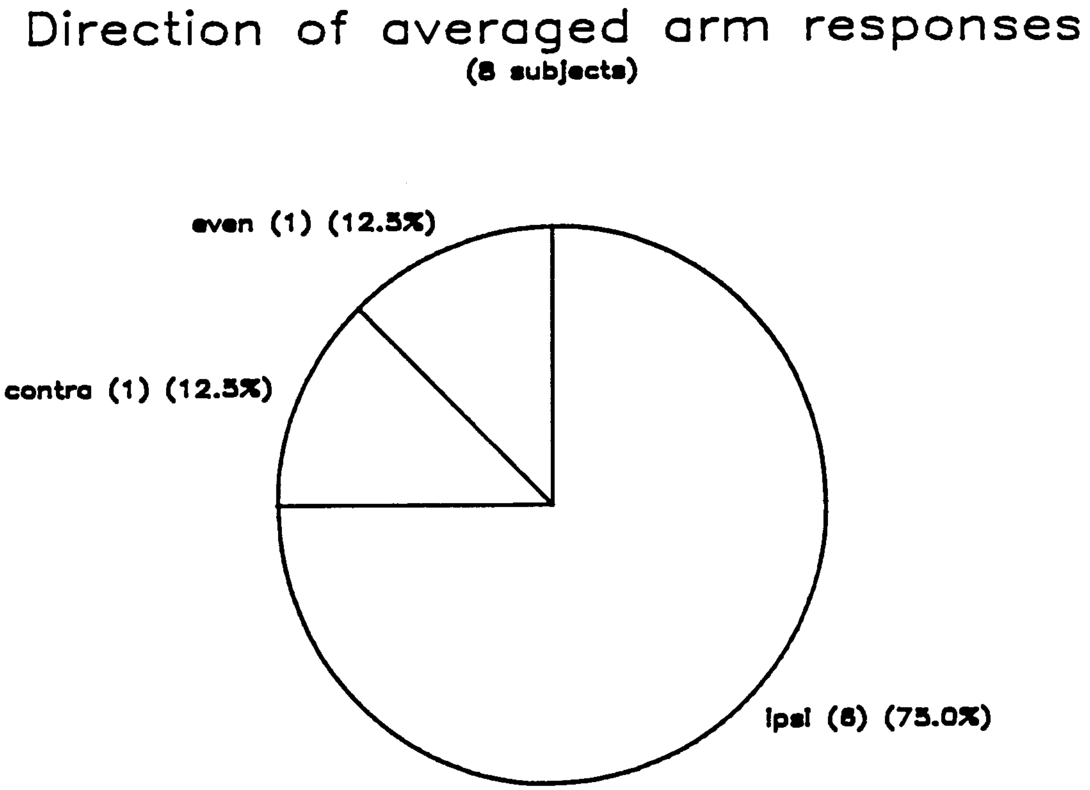
1	2	3	4	5	6	7	8
(25M)	(25F)	(21F)	(29M)	(27M)	(32M)	(31F)	(32F)
I	C	I	I	I	I	I	C



C) The average arm response was also computed in the same manner to determine if arms would show a directional tendency.

Subject No. (Age and sex in brackets)

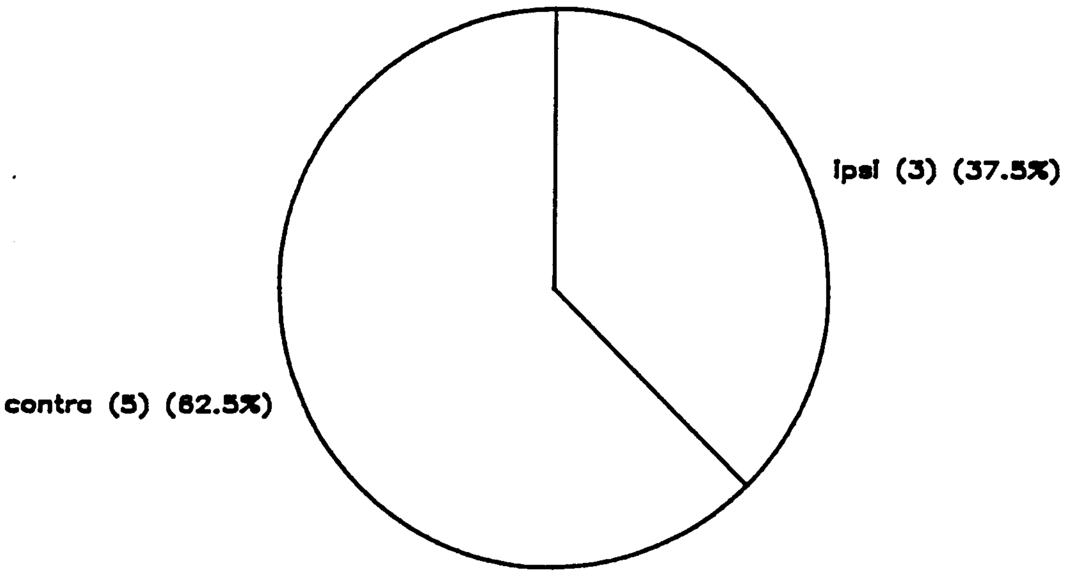
1	2	3	4	5	6	7	8
(25M)	(25F)	(21F)	(29M)	(27M)	(32M)	(31F)	(32F)
I	C	I	I	I	I	I	—


Direction of averaged arm responses
(8 subjects)

D) The average leg response was also computed in the same manner to determine if legs would show a directional tendency.

Subject No. (Age and sex in brackets)

1	2	3	4	5	6	7	8
(25M)	(25F)	(21F)	(29M)	(27M)	(32M)	(31F)	(32F)
I	C	C	I	I	C	C	C



Direction of averaged leg responses

(8 subjects)

E) The following table summarizes the direction of total response of individual trials in each subject.

Right ear irrigation in supine position

1 (25M)	2 (25F)	3 (21F)	4 (29M)	5 (27M)	6 (32M)	7 (31F)	8 (32F)
C	C	C	I	C	I	C	I

Right ear irrigation in inclined position

1 (25M)	2 (25F)	3 (21F)	4 (29M)	5 (27M)	6 (32M)	7 (31F)	8 (32F)
I	I	I	I	C	C	C	C

Left ear irrigation in supine position

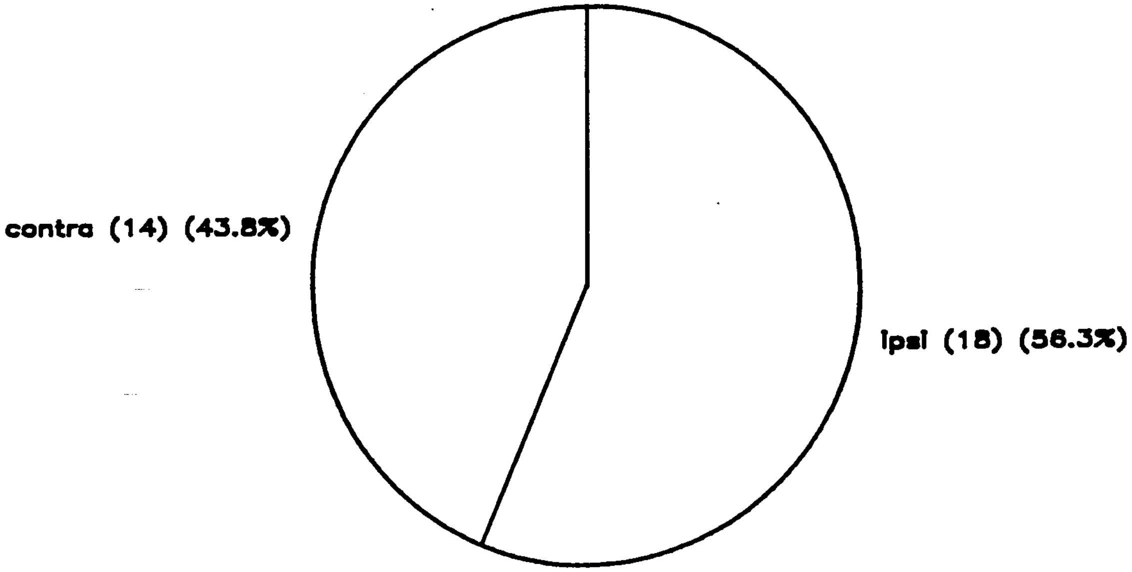
1 (25M)	2 (25F)	3 (21F)	4 (29M)	5 (27M)	6 (32M)	7 (31F)	8 (32F)
C	I	I	I	I	I	I	C

Left ear irrigation in inclined position

1 (25M)	2 (25F)	3 (21F)	4 (29M)	5 (27M)	6 (32M)	7 (31F)	8 (32F)
I	C	I	I	I	C	I	C

Direction of Total Response

(each trial in each subject)



D. Discussion

The results of the total-limb recordings indicate a generalized excitation of limb extensors in response to the supplied vestibular stimulus. A decline in response is also indicated when trials are compared sequentially (Appendix "E") As many of the net responses were extremely low, (see table), one must be cautious in reading trends into the appearance of the data. (For instance a response that averaged only fifteen uV could not be considered to be exemplary of a pattern just because the response doubled in size over a sixty-second period (i.e. from ten to twenty uV)). Again considering the absolute amplitude of the responses, such responses must be considered unremarkable. The conjecture can be made that the limb musculature, after being made aware of the stimulation, tends to activate anti-gravity muscles. (These muscle groups classically play a role in stabilization of the body, opposing any gravitational force which has the potential to perturb or disrupt an assumed bodily position. (Roberts, 1978)) While caloric irrigation is an unnatural stimulus applied to the labyrinth, it closely simulates the subjective sensation of a motion that might have the potential to cause injury (rolling off a bed or a platform) and must be successfully opposed.

Using the gross muscle responses (Appendix "B") the comparison of lower limb response shows no tendency towards lateralization, but the upper limb muscles show a suspicion of lateralization. If we analogize the trunk as a barrel which can roll off the bed (which is essentially the case), the effect of the arms (which are placed laterally to the barrel) is analogous to that of a wedge placed under the barrel to prevent rotation. The role of the legs, on the other hand, (which are not at all lateral) is analogous to a rod driven end-to-end through the barrel, to which torque must be applied to oppose the rotation. While this is an overly simplified analogy, it serves to illustrate how the arms serve the purpose of lateral stabilization in a supine position. Despite the best efforts to reduce this role of the arms in our experiment (by forcing subjects to keep their arms at their sides with fingers together), it is still the strategy of preference to make sure that stability is maintained. The flexion of the arms serves to "wedge" the trunk along its entire length, and the muscular force is applied at the centre of gravity, which is the theoretical point of rotation of the trunk. For this reason the amount of tension in the arms relative to that seen in the legs is irrelevant: a given amount of tension would have far more effect in the arms in "wedging" the body.

While flexion of the leg muscles in the supine position is less relevant to opposing specifically a directional force, the standard theories of excitation and inhibition (both of the counterpart on the opposite limb and of the antagonist to the excited muscle group) may play a prominent role in predicting responses of anti-gravity muscles to stimuli. Berthoz(1974) likened all agonist-antagonist interactions in limbs to the simplistic push-pull interactions of the oculomotor muscles in which facilitation is accompanied by reciprocal and contralateral inhibition. This is mediated by the oculomotor nuclei and is the system responsible for the ocular movements in nystagmus (cited in Delwaide, 1977). It is difficult to ascertain the contribution of contralateral inhibition in our findings. While the results show excitation bilaterally (but moreso ipsilaterally), these findings may actually represent "contralateral inhibition" of an underlying excitation as a result of cutaneous stimuli, anxiety or other factors. Delwaide's (1977) study of the changes in the tonic vibration reflex (TVR) and tendon reflexes after caloric irrigation in different muscle groups showed a generalized facilitation of all reflexes, but a greater degree of facilitation ipsilaterally after warm and contralaterally after cold irrigations. (In other words, facilitation predominated on the side of the more active labyrinth). Various extraneous influences are discussed. For instance facilitation is also seen when irrigations at "caloric 0" (37 degrees C.) were performed. It was suggested that this may reflect facilitation due to a cutaneous stimulus. The Jendrassik maneuvre (selective isometric contraction of the forearms) caused facilitation of the TVR in a slightly different fashion, implicating (it seems) two systems exerting a similar effect via different pathways. The effects of the Jendrassik maneuvre on the TVR will vary from subject to subject (Delwaide and Toulouse,1983). The varying influence from subject to subject of many extraneous factors on the vestibulospinal reflex probably plays a large role in the variation seen here between subjects.

In primates some evidence has been provided that a system of co-contraction may be part of a more generalized network for producing postural stabilization throughout a limb (Humphrey and Reed, 1983). It is reasonable to assume then that incorporated into this generalized network is **contralateral** co-contraction during deflection of the body away from its centre of gravity. This system would result in postural stabilization of the whole body rather than one limb. This observation appears to be confirmed by my data which show a definite increase in muscle tone bilaterally. As discussed previously (and according to Delwaide), it is unclear whether or not there is such a phenomenon as contralateral inhibition of a muscle response in a limb. Perhaps it is in fact an asymmetrical facilitation, or the inhibition is masked by the generalized increase in muscle tone. It may be that any perturbation of an anti-gravity muscle will cause an activation of this network in the anticipation that action will be required in order to regain and/or maintain upright posture. The vestibular system has been shown to operate as a reference against which all conflicting information can be compared. It has been proposed that since this capability is absent in children under the age of seven and a half years, perhaps it represents the evolution of a hierarchically higher system because of its late ontogenetic development (Forssberg and Nashner, 1982). Perhaps the evidence of Humphrey and Reed (1983) for the existence of the generalized posture stabilization network reflects the development of a **phylogenetically** higher function for the maintenance of bipedal, as opposed to quadrupedal gait. We may surmise that any vestibulospinal response that can be recorded will be somewhat adulterated by cerebellar input but will also be greatly influenced by higher centres in the motor cortex. In other words, the elicited "reflexes" are in fact under a good deal of cortical control. With the participation of supraspinal structures, muscle response to stretch might be widely adjustable in advance by setting the characteristics of supraspinal processing mechanisms according to expectation and behavioural set. Transcortical involvement would be intrinsically varied by emotional set, prior experience (Chan, 1983) and perhaps even knowledge of conscious techniques of muscle relaxation (eg. yoga, etc.). The effects on vestibulospinal response could be widely varied in an individual who was

-extremely anxious about a laboratory setting,

-anxious about anticipated discomfort,

-adversely upset by the experience of a vertiginous sensation.

On the other hand an individual who was familiar with the experimental procedure and resulting sensation could well respond in a much less definitive fashion and the responses of someone totally nonchalant about the whole experimental procedure could be totally inappropriate. In electrodiagnostic testing it is in fact a difficult task to obtain good test results from a physician. Observations such as these are strongly supportive of a higher, cortical level of influence on the vestibulospinal reflex. Investigations in humans (Marsden et al., 1983) suggest a theory of cortical control of movement (or perceived movement) in which the long-latency stretch reflexes "fine-tune" inaccuracies in the motor program that has been initiated. Gross inaccuracies or continued perturbations require a **conscious** intervention from the individual so that the initial intentions can be fulfilled. In other words, there are a number of intrinsic factors, the interaction of which could cause drastic changes in the response (initiated by this consciously-controlled intervention mechanism). As discussed before, these would include unfamiliarity, anxiety, prior experience, knowledge of relaxation techniques or level of fitness. Note how these various factors could influence both the cerebellar-brainstem co-contracting mechanisms (via efferent information from the motor cortex) as well as the long-loop motor cortex-controlled system.

Nashner (1976) demonstrated an adaptive ability of the so-called functional stretch reflex (FSR). Subjects on a servo-driven platform were swayed forward and exhibited an appropriate compensatory response to prevent falling forward on their face. But a random movement of the platform in an upwards direction, (which would render the response inappropriate), resulted in the response on the succeeding 3 to 5 trials being attenuated. This adaptation could play a role in the decrease of response on serial tests in subjects. Acting synergistically with this "learning effect" is the concept of CNS habituation, which also serves to decrease serial responses. As a result of repetitive muscle contractions (or sustained isometric contraction), muscle fatigue becomes a factor. When fatigue sets in, the same CNS command will result in decreased tension (McCloskey et al., 1983). However the postural muscles (predominantly slow-twitch muscles) show very little decrease in mean force over a period of 60 seconds (Kernell, 1983). Although primary neurons themselves show a slight decrease due to adaptation this fact cannot account for the extent of the adaptation in human subjects and the explanation of the fatigue factor observed here lies elsewhere. It is suspected that such CNS adaptation arises from an interplay between mechanisms in the vestibular end organs, as well as complicated nervous activities such as habituation as described originally by Albert in 1965 (cited in Precht, 1974).

Cutaneous afferents are also known to produce a non-specific excitation of the lower limb extensors that gradually decreases in amplitude (Conrad et al., 1983). Although there was probably reduced effect of this in our experiment (our subjects kept their shoes on), it could conceivably have contributed to the gradual decline in response. These findings may contribute partially to the unspecificity of the lower limb responses with respect to the upper limb responses. In the inclined position the cutaneous effect may have had some bearing as the soles of the feet were in contact with a platform and subjects would have been aware of some pressure sensation even with shoes on. In the supine position there may also have been some effect due to cutaneous input from the legs on the bed (all subjects wore shorts during the experiment). The cutaneous effect could have been eliminated by suspending all subjects in a parachute harness (cf. Aiello et al., 1983).

The vestibulospinal reflexes elicited by caloric irrigation are a phenomenon repeatedly observed in the clinical setting. Turning of the head (cervico-ocular reflex), grabbing the edge of the bed, digging in with the heels and clutching the examiner for reassurance are behavioural responses that I see daily. The degree to which the patient reacts is sometimes in keeping with the amplitude of the elicited nystagmus (an accurate indication of the degree of sensitivity of the balance organs), but not always. Aside from the differing amounts of cortical influence other unexplained phenomena result in differing reactions to vestibular stimulation. Motion sickness, for example, is not a pathological state but an idiopathic hypersensitivity to vestibular stimulation. Such people cannot tolerate any applied vestibular stimulation whatsoever, even though the responses on the ENG recording show levels that are well tolerated by many other people. In other words, a certain amount of stimulation (eg. our caloric stimulus) will elicit identical ENG responses in two normal subjects, but one will report extreme vertigo while the other reports very little subjective sensation. After studying both the values of elicited EMG responses and the subjects' voiced reports about the sensation, one must reach the conclusion that my subjects were at no time concerned about the applied stimulation, with one (subject five) and possibly two (subject three) exceptions. Presumably our subjects had sufficient afferent feedback from cutaneous and proprioceptive receptors to reassure them of a large support surface which was solid enough to provide ample resistance to the vertiginous sensation. No subject was concerned enough about falling on the floor to take any evasive action. This has probably been the major factor in generating the negative results we have obtained. There cannot be documentation of any reflex until it is proven that "Caloric zero" has no effect on EMG activity (i.e. water at body temperature introduced into the ears) and until it is proven that there is some kind of reversal phenomenon of any response that may be observed in the future.

It is possible that the low responses reflect an error in picking appropriate muscle groups from which to record. For instance, if the **antagonist** muscle was mistakenly selected and responses recorded from it, one would see relatively low responses and a reversal of the expected phenomenon, due to reciprocal and contralateral inhibition. The dramatic responses observable in the neck make this a prime candidate as a recording site for recording of the vestibulospinal effect.

E. Conclusion

My objective was to elicit and quantify a vestibulo-ocular response to controlled thermal stimulation of the vestibular labyrinths and investigate the possibility that it could be correlated with a vestibulospinal reflex appropriate to counteract the vertiginous sensation and associated perception of motion that could also be elicited and quantified. The response to caloric stimulation of the vestibular labyrinths shows a wide variation of response between subjects and in successive trials. The hypothesis has been partially supported. An increase in EMG activity in antigravity muscles of the extremities is seen in response to the caloric stimulus. This excitation is greater ipsilaterally in 18 of 32 trials. These findings indicate a possible lateralization of response but it is unclear whether there is an inhibitory element as well that is masked by underlying "global excitation" of muscle tone. The results are similar to the only comparable experiment reported, but results contradict the classically-accepted beliefs about the direction of perceived movement after vestibular stimulation. Many adaptive mechanisms may play a role in modulating, biasing or otherwise masking the vestibulospinal reflex. Cortical control consisting of hundreds of preprogrammed motor responses derived from thousands of past experiences (themselves altered by emotional factors prior to storage) could result in a unique response from each individual. A fatiguing of the response over successive trials was seen. It is uncertain whether this results from a decrease in the "degree of laterality" or a decrease in the absolute amplitude of the elicited response. The major elements of the fatiguing could include

1. CNS habituation
2. habituation of the learning phenomenon, preprogramming and emotional state
3. Habituation of cutaneous stimuli.

It appears from the results of the experiment that the legs are employed to stabilize the body in general during an apparent perturbation away from the centre of gravity. The arms may be more stimulus-specific and react more to the particular task of opposing directional forces, participating to a lesser degree in the total-body response. In order to elicit more clearly the vestibulospinal reflex and determine the net effect of caloric stimulation on the anti-gravity muscles of the extremities, attempts must be made to reduce the effect of cortical influence. Other parameters should be introduced to test the validity of our findings. For instance, caloric irrigation using water below body temperature causes inhibition, rather than excitation of the vestibular system. One would expect the stimulus to cause a reversal in the observed response. Further investigations will shed light on why the responses appear to refute classic theory. The Danish investigator Peitersen should be allowed the final thoughts on the subject of vestibulospinal testing since it is he, who after the most extensive studies done to date expressed most accurately the frustrations involved: retrospectively he laments that the state of knowledge is so backwards because man's ability to walk has unfortunately been taken for granted (1967). During his investigations he realized that his stepping test for evaluating vestibulospinal function is only of value "...only if the subjects are not too unsteady and {do not} show a tendency to fall" (1964).

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APPENDIX A

Consent was obtained from all experimental subjects. They were instructed in the following manner:

> "This experiment is designed to test your balance reflexes. These reflexes are generated by the balance organs in your ears. They will be measured while you are reclining. Your balance organs will be stimulated by warming your inner ear with water. This will feel like spinning in an office chair. The response of your balance organs will show up in your eyes and the response will be measured. Although your head thinks you are spinning, the rest of your body feels itself lying down. This confusion is called dizziness and it will last for about two minutes. Sometimes there is also a feeling of mild nausea. A computer will record your eye movements and also the muscle activity in your arms and legs before, during and after the dizziness. You will also be asked to describe the feeling in your own words and your responses will be taped. The warm water test is a standard test used to measure balance organ function. A medical examination of your ears before the test will tell me if there is any reason you should not participate in the experiment. Aside from the dizziness and nausea, there are no side effects from this experiment. If for any reason you feel unwell after the test, you will be looked after until you feel better. All medical information obtained and recordings made are strictly confidential. If you are referred to in a publication the reference will be anonymous. You may end your participation in the experiment at any time and for any reason. This is not a test in which anything else is being observed or recorded aside from what I have explained to you. There are no unexpected surprises in the experiment. Before we begin all of your questions will be answered to your satisfaction."

APPENDIX B

A:Gross Response of Muscles to Vestibular Stimulation
(all values in microvolts)

I=ipsilateral limb
C=contralateral limb

Right ear irrigation in supine position

Subject No. (Age and sex in brackets)

	1 (25M)	2 (25F)	3 (21F)	4 (29M)	5 (27M)	6 (32M)	7 (31F)	8 (32F)
Left arm(C)	6	309	333	155	1313	33	55	79
Right arm(I)	35	228	332	160	158	602	36	126
Left leg(C)	118	44	109	20	413	14	74	18
Right leg(I)	55	162	23	133	356	26	20	17
Right ear irrigation in inclined position								
Left arm(C)	4	182	198	164	243	69	43	43
Right arm(I)	224	861	301	470	60	36	37	54
Left leg(C)	17	343	48	20	26	298	8	56
Right leg(I)	77	38	207	124	17	19	11	25
Left ear irrigation in supine position								
Left arm(I)	8	227	259	382	1883	319	32	66
Right arm(C)	134	156	360	91	56	74	52	164
Left leg(I)	168	49	47	42	523	23	35	57
Right leg(C)	96	51	16	52	482	18	20	19
Left ear irrigation in inclined position								
Left arm(I)	7	195	996	130	317	110	185	72
Right arm(C)	73	1328	334	105	41	52	97	201
Left leg(I)	61	81	78	92	93	14	78	50
Right leg(C)	46	30	130	104	21	208	60	81

APPENDIX C

B:Activity of Muscles at Rest
(all values in microvolts)
I=ipsilateral limb
C=contralateral limb

Right ear irrigation in supine position

Subject No. (Age and sex in brackets)

	1 (25M)	2 (25F)	3 (21F)	4 (29M)	5 (27M)	6 (32M)	7 (31F)	8 (32F)
Left arm(C)	8	94	137	76	278	25	54	158
Right arm(I)	13	113	135	64	58	52	46	0
Left leg(C)	26	61	97	8	28	11	16	52
Right leg(I)	11	305	14	67	47	21	13	16
Right ear irrigation in inclined position								
Left arm(C)	7	115	103	74	157	55	40	43
Right arm(I)	21	461	197	64	47	35	77	63
Left leg(C)	14	24	15	76	38	8	7	15
Right leg(I)	37	39	173	55	28	10	13	24
Left ear irrigation in supine position								
Left arm(I)	4	75	284	71	376	59	33	97
Right arm(C)	15	206	604	1090	46	42	45	105
Left leg(I)	26	24	60	10	18	7	10	20
Right leg(C)	33	71	17	18	45	10	10	25
Left ear irrigation in inclined position								
Left arm(I)	6	118	54	75	294	66	51	54
Right arm(C)	69	305	24	108	39	41	92	76
Left leg(I)	5	25	10	18	7	9	6	93
Right leg(C)	29	15	12	37	20	9	11	51

APPENDIX D

C:Net Response of Muscles to Vestibular Stimulation (all values in microvolts)

I=ipsilateral limb
C=contralateral limb

Right ear irrigation in supine position

Subject No. (Age and sex in brackets)

	1 (25M)	2 (25F)	3 (21F)	4 (29M)	5 (27M)	6 (32M)	7 (31F)	8 (32F)
Left arm(C)	-2	215	196	79	1035	8	1	-79
Right arm(I)	22	115	197	96	100	550	-10	126
Left leg(C)	92	-17	12	12	385	3	58	-34
Right leg(I)	41	-143	9	66	309	5	7	1

Right ear irrigation in inclined position

Left arm(C)	-3	67	95	90	86	14	3	0
Right arm(I)	203	400	104	406	13	1	-40	-9
Left leg(C)	3	319	33	-56	-12	290	1	41
Right leg(I)	40	-1	34	69	-11	9	-2	1

Left ear irrigation in supine position

Left arm(I)	4	152	-25	311	1507	260	-1	-31
Right arm(C)	119	-50	-244	-999	10	32	7	59
Left leg(I)	142	25	-13	32	505	16	25	37
Right leg(C)	63	-20	-1	34	437	8	10	-6

Left ear irrigation in inclined position

Left arm(I)	1	77	942	55	23	42	134	18
Right arm(C)	4	1023	310	-3	2	11	5	125
Left leg(I)	56	56	68	74	86	5	72	-43
Right leg(C)	17	15	118	67	1	199	49	30

APPENDIX E

D: Comparison of Serial Responses
from All Subjects
(all values in microvolts)
(values indicate net EMG response
from all four limbs on trials
in the order in which they
were performed on each subject)

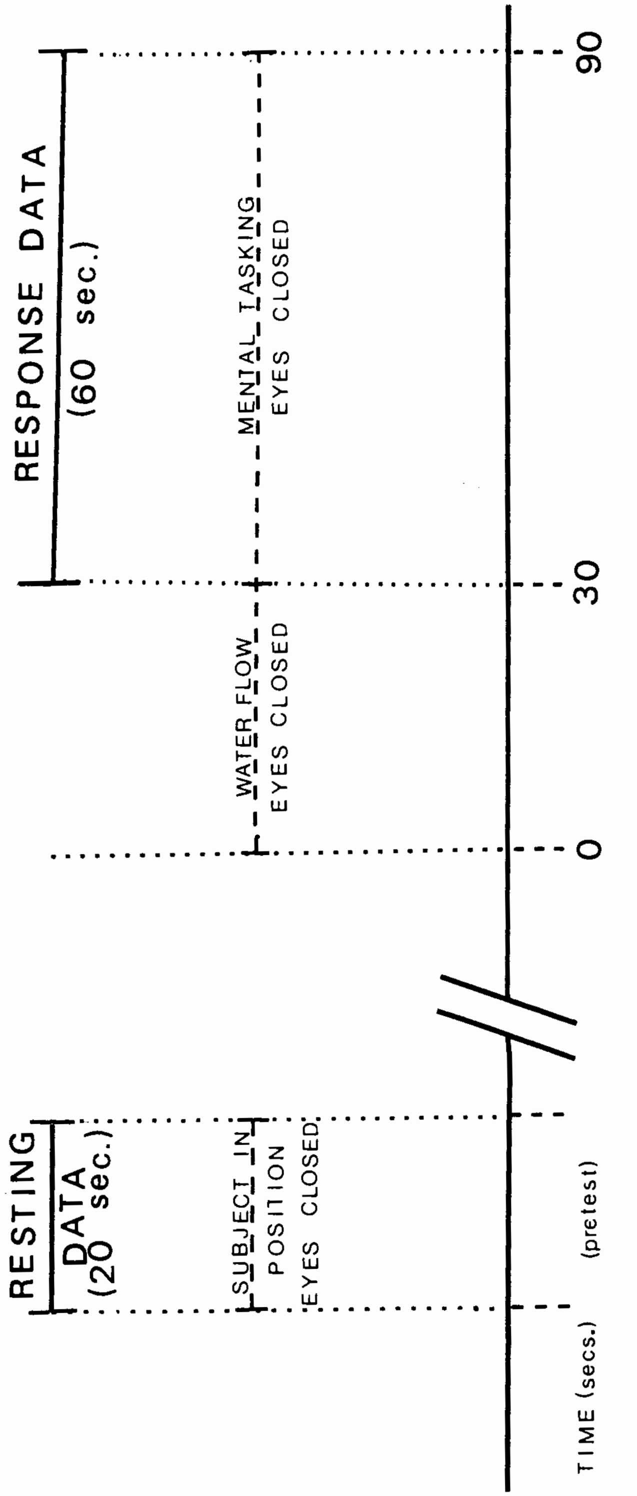
	Subject No.							
	1	2	3	4	5	6	7	8
	(25M)	(25F)	(21F)	(29M)	(27M)	(32M)	(31F)	(32F)
First trial	153	785	1438	-622	1829	316	-38	130
Second trial	328	1131	414	509	2459	314	260	14
Third trial	243	170	-283	193	76	257	56	59
Fourth trial	78	107	266	253	112	566	41	33

Totals:
First trial - 3991
Second trial - 5469
Third trial - 771
Fourth trial - 1456

APPENDIX F

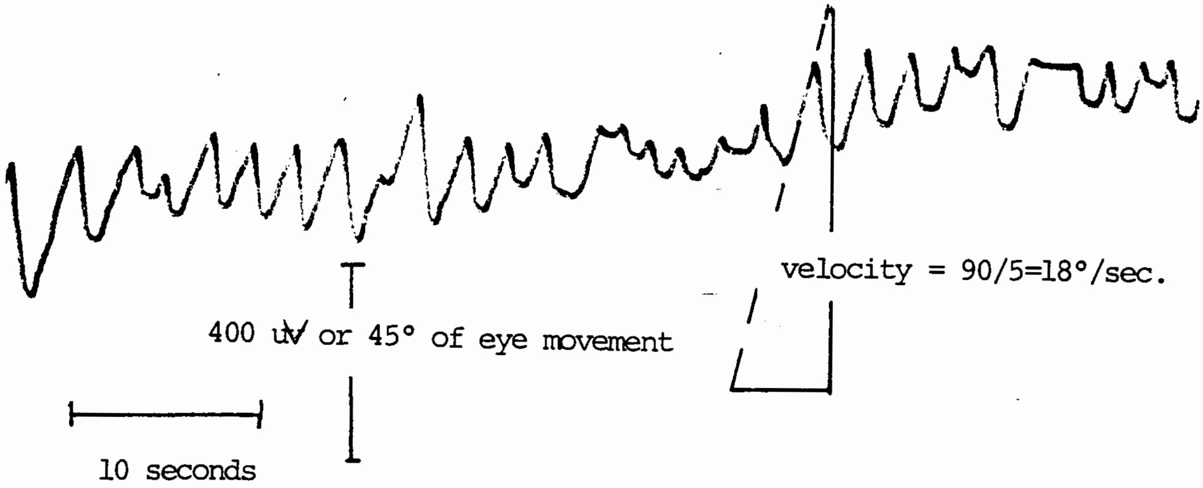
The Data Collection protocol is diagrammed below.

DATA COLLECTION PROTOCOL



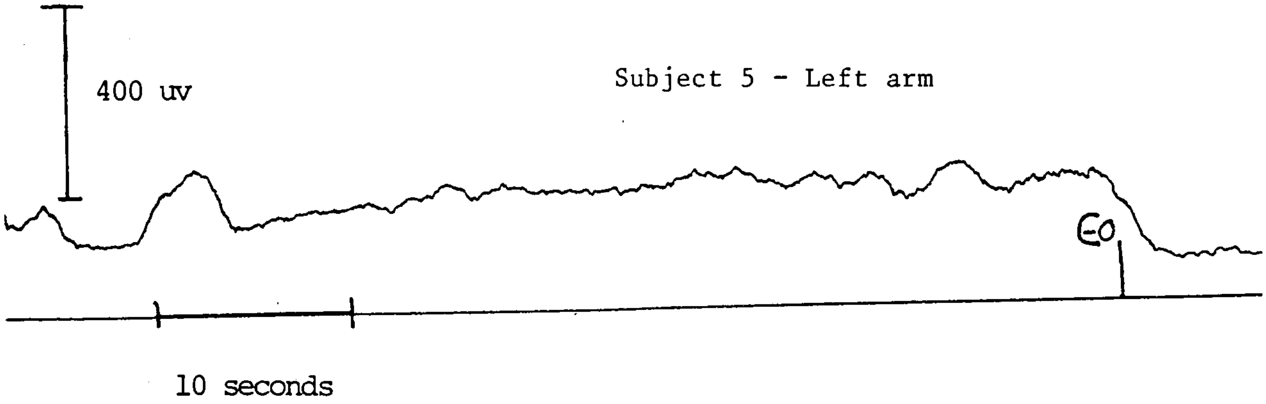
APPENDIX G

These traces are exemplary of some of the different kinds of responses in different subjects. All responses were recorded during the period of time that data were being collected (i.e. during the response data period outlined in Appendix "F".)



scale - one inch=10 seconds (horizontal)
one inch=400 uV(vertical)

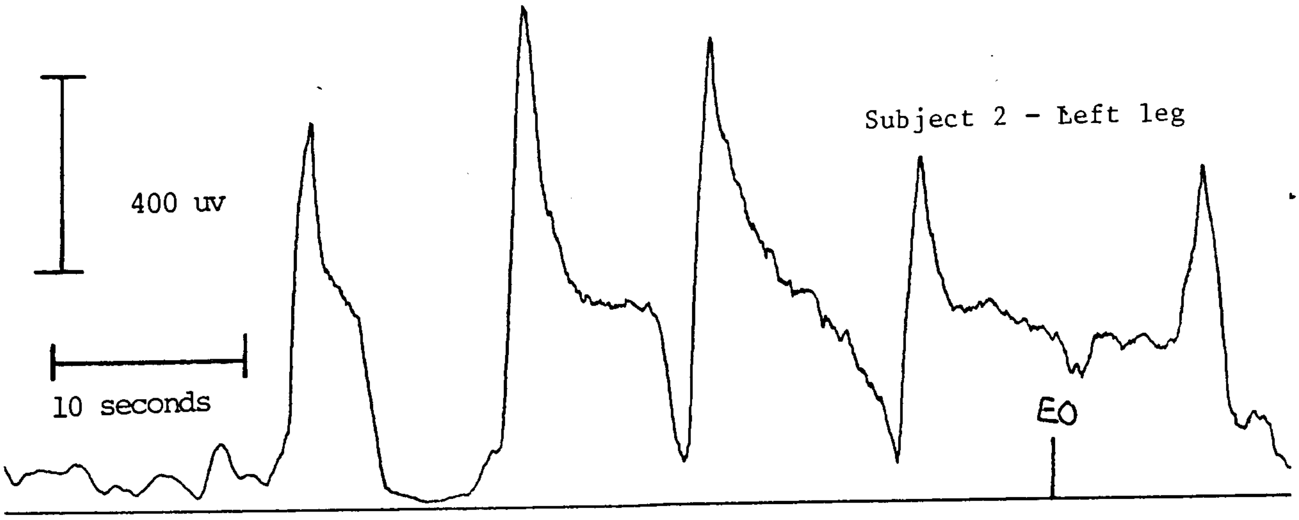
1. Recording of nystagmus with eyes closed plotted against a baseline demonstrates vestibular response to caloric stimulus.



scale - one inch=10 seconds (horizontal)

one inch=400 uV(vertical)

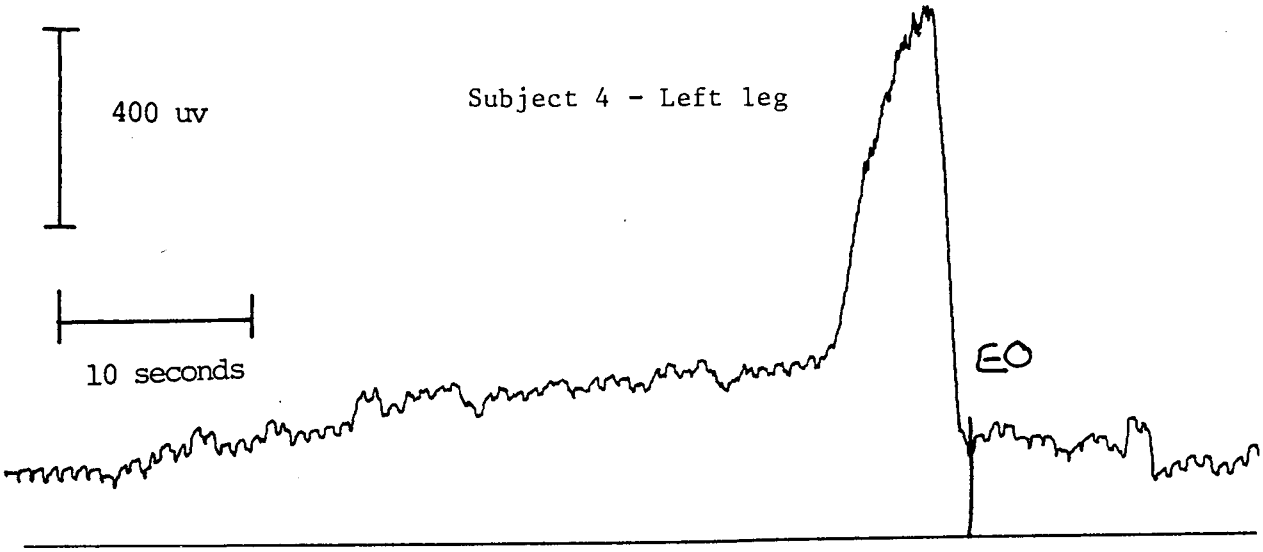
2. Rectified-averaged recording of EMG showing maintenance of constant tension for duration of response period.



scale - one inch=10 seconds (horizontal)

one inch=400 uV(vertical)

3. Rectified-averaged recording of EMG showing rapid, repetitive bursts of tension for duration of response period.



scale - one inch=10 seconds (horizontal)

one inch=400 uV(vertical)

4. Rectified-averaged recording of EMG showing gradual increase in tension for duration of response period.