THE EFFECTS OF VISUAL AND LABYRINTHINE DEPRIVATIONS ON THE POSTURAL STABILITY OF QUIETLY STANDING DOGS

by

Calvin Y. Nakao, B.A.

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APPROVED:

[redacted]

. . . .
(Professor in Charge of Thesis)

[redacted]

. . . .
(Chairman, Graduate Council)

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INTRODUCTION

DYNAMIC ASPECT OF POSTURE

Rigidity is an important factor in determining the stability of supported structures. The supporting structures of vertebrates are obviously not as rigid as the supporting structures of an oaken table, and therefore not as stable. In the design of the skeletal system, with its moveable joints and surrounding musculature, some rigidity has been sacrificed for the mobility necessary in obtaining food, shelter, and protection from other animals. Thus, the contraction of various muscle groups may cause the skeletal framework to be modified to provide mobility or to be made relatively rigid to provide support.

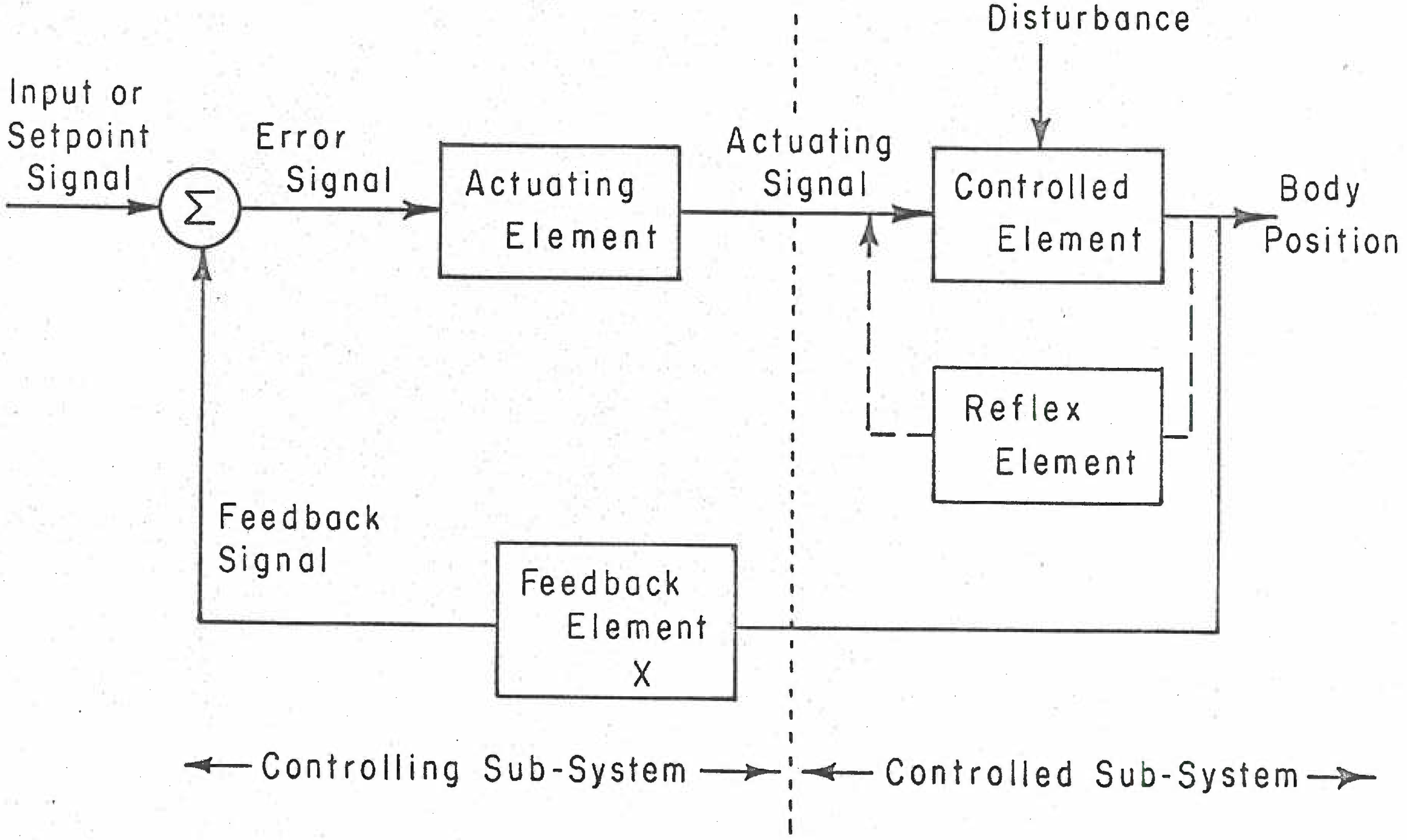
In the normal standing posture the supporting structures are not held as rigid as one might voluntarily hold them. Certainly, if one voluntarily attempts to hold himself at a rigid "attention" position, he will quickly expend a great deal of energy and become fatigued. Perhaps, because of the enormous expenditure of energy involved in maintaining a maximally rigid supporting structure, the standing animal has learned to use postural corrective mechanisms which involve minimum amounts of muscular activity for the maintenance of stability and thus demand less metabolic energy expenditure. The corrective mechanisms permit the postural muscles to remain relatively relaxed until displacement initiates reactions of only those muscles which will tend to correct the displacement. In the quietly standing posture, a series of fine corrective movements are continually occurring in response to displacement by external and internal forces. This dynamic nature of posture is well demonstrated in the patterns traced by body sway in humans (1,2) and dogs (3). These facts imply that standing is accomplished with the aid of a continuously operating control system which detects and corrects deviations from a desired position in space.

THE CONTROL SYSTEM MODEL

Dynamic postural control may be investigated by using the automatic feedback control system as a working model. Yamamoto and Brobeck (4) have explored the relationships between traditional physiology and control systems engineering, and have reviewed recent accumulating evidences compatible with the concept of automatic biological feedback control systems. The model aids in bringing organization and insight into the problems involved in postural control and aids in developing working concepts.

Figure 1 illustrates in block diagram a typical control system comprised of a controller and a controlled sub-system. Basically, the detection of the difference between the setpoint and the feedback signals results in an error signal which initiates the adjustments necessary to reduce the error signal to zero. In tetrapod vertebrates the controlled elements are known to be the body musculature by which position may be altered through the generation of integrated patterns of nerve impulses from the actuator elements. The feedback channels are assumed to originate in the receptors which are capable of generating signals indicating various parameters of body position relative to itself and to the environment. Some of these receptor signals have direct effect upon the controlled elements primarily via the reflex arcs. The location and the connections of the error detection and

Figure 1. A conceptual presentation of the postural mechanisms based upon the hypothesis that it operates as a feedback regulated control system. The block diagram identifies several specific terms which are explained more fully in the text.



BLOCK DIAGRAM OF A REGULATORY SYSTEM

actuating elements in the central nervous system have not been identified. The setpoint is defined to be external and independent of the control system; we can assume that it comes into being as a result of learning. One learns early in life to align himself with the direction of gravitational force in order to maintain a standing posture. This setpoint is assumed to remain fixed so long as this environmental cue is present.

FEEDBACK CHANNELS OF THE CONTROL SYSTEM

Certain sensory receptors are known to be capable of influencing body orientation and postural control. About the turn of the century Hinsdale (5) first observed and attempted to quantitate the increase in body sway of blindfolded deaf-mutes who were thought to lack labyrinthine function. Sherrington (6) later recognized the importance of proprioceptive muscle afferents and cutaneous sensory nerves in the maintenance of postural tonus in the decerebrate animals. Clinicians have long been aware that patients with posterior column disease are unable to maintain a stable standing posture upon visual deprivation. The classical studies by Magnus (7) have contributed much to the recognition of the importance of the visual, labyrinthine and somesthetic inputs on the righting reflexes.

Magnus also recognized the important fact that animals are able to carry out some aspects of postural regulation even after the loss of one or two of these feedback channels. He found that all three channels were individually capable of activating the reflex righting reactions which bring the head to its normal position. Thus the head righting reflex activated by any one channel could only be studied in the absence of the other channels. Observations on standing humans and animals also demonstrate this compensatory phenomenon from another aspect. It has often been pointed out, on qualitative grounds only, that the deprivation of any one channel does not affect the maintenance of adequate postural control in the human being. However, the deprivation of any two channels does result in minor perceptible difficulties. Ford (8) has observed patients with previous bilateral eighth nerve sections to become unsteady upon visual deprivation. One may speculate that in the intact condition the feedback channels possess reserves which may be utilized to compensate completely for the deprivation of any one channel. Deprivations of any two channels cause the reserve of the remaining channel to be taxed beyond its capacity, and result in overt manifestations of difficulties in maintaining postural control. Deprivations of all feedback channels result in total postural disorientation and incapacitation.

RELATIVE IMPORTANCE OF EACH FEEDBACK CHANNEL

There is much speculation, but no real understanding, concerning the relative importance of each feedback channel in maintaining the upright posture. It is well known that rodents do not demonstrate the visual righting reflexes, whereas these reflexes are very active in higher mammals such as the dogs, cats, monkeys and humans. Magnus and de Kleijn (9) have observed dogs to be totally incapacitated for approximately one week following labyrinthectomy. They interpreted this result to mean that the labyrinth normally plays the dominant role in maintaining the upright posture, and that approximately one week was necessary for the visual and somesthetic channels to compensate for the labyrinthine deprivation. The relationship of this interpretation to the studies in orientation of airplane pilots is not clear. In spite of the sudden lack or distortion of the labyrinthine and somesthetic stimuli, well-trained airplane pilots are able to visually orient themselves to the vertical without experiencing a period of total incapacitation. It is obvious that more information is needed to adequately assess this problem.

CENTRAL CONNECTIONS OF THE FEEDBACK CHANNELS

The optic tract sends the major portion of its fibers to the lateral geniculate and a smaller portion to the superior colliculus and the pretectal nucleus. The anatomical connections between the visual cortex, lateral geniculate, and the tectum of the midbrain remain unclear. Deprivation studies have shown the cortex to be essential in producing the visual righting reflexes (10) but the exact center and the pathways are not known. The tectospinal and the tectotegmentospinal tracts provide for motor responses to impulses correlated at the superior colliculus (11).

The central connections of the somesthetic feedback channel are less clear. Somesthetic impulses reach the brain via the anterior, lateral and posterior columns and are delivered to the thalamus and cerebellum. The effects of cerebellar lesions upon posture and gait are well known but the relationship of the cerebellum with the somesthetic and the labyrinthine control of posture is unclear. Ataxia caused by lesions of the spinocerebellar division of the somesthetic feedback channel is not corrected by visual and labyrinthine compensating mechanisms (12). The lack of cerebellum does not abolish the righting reflexes but certainly impairs the precision and the grace with which the reflex reactions are manifested. The outgoing somesthetic impulses from the thalamus discharge particularly to the primary and secondary somesthetic areas of the cerebral cortex with additional influences on the basal ganglia. Outflow pathways from the cortex reach the brain stem and the spinal cord through the pyramidal and extrapyramidal pathways (11).

The central connections of the vestibular feedback channel have been more extensively studied than other feedback channels. The majority of the vestibular nerve fibers terminate at the four major vestibular nuclei with a few fibers passing directly to the cerebellum. Secondary fibers give rise to the vestibulospinal, vestibulomesencephalic, vestibulocerebellar and the vestibuloreticular pathways. There is physiological evidence of vestibular projections to the thalamus and to the cerebral cortex (11). Some of the fibers from the cerebellum return to the vestibular nuclei while others pass to the red nucleus and relay with the neurons of the rubrospinal system. The main outflow pathways of the vestibular fibers are via the vestibulospinal, rubrospinal and the reticulospinal tracts. Physiological studies have shown the vestibulospinal, vestibulocerebellar and the vestibuloreticular fibers to have profound tonic effects on body posture, but have not yielded more specific information on how these fibers function to enable the postural control system to reduce the error signal. Recent electrophysiological studies by Precht and Shimazu (13) have begun to yield information about the synaptic organization of the vestibular nuclei.

FUNCTIONS OF THE CONTROL SYSTEM

In order to understand the primary functions of the postural control system, it may be helpful to introduce some clear definitions of terms. The center of gravity of a standing animal is elevated some distance above the supporting surface. In any given stance, the animal's weight will be distributed about a point on the supporting surface which may be regarded as a single representation of all downwardly directed forces operating on the points of support. This may be referred to as the center of weight distribution (14). For each animal, there should be one ideal position of the center of weight distribution which can be maintained with the minimum expenditure of muscular forces and metabolic energy. It would be in the best interest of the animal if his posture were regulated in such a fashion that the line between the center of gravity and the ideal center of weight distribution were kept parallel to the lines of gravitational force. The maintenance of this parallelism may be regarded as the primary function of the postural control system in quiet standing animals. Any force which brings about a departure from parallelism may be regarded as a disturbance requiring corrective reactions on the part of the control system.

The feedback channels are equipped with specialized receptors to enable the control system to utilize several different environmental cues in the detection of errors in alignment. The labyrinthine channel primarily acquires information of acceleration and gravity; the somesthetic channel, of touch, pressure, and proprioception; and the visual channel, of the surrounding objects in the visual field.

The setpoint may be defined and learned in terms of environmental cues utilized by the feedback channels. For example, the setpoint may be learned and expressed in terms of a number of cues which reflect, directly or indirectly, the orientation of the body in the field of gravity. It may relate to those visual objects which are recognized to be oriented in a reliable way with direction of gravitational force, or may be that characteristic pressure distribution on the supporting columns when the center of gravity is perpendicularly above the ideal mean center of weight distribution. Changes in the error signal associated with changes in the somesthetic channel reflect the true error in alignment and may initiate appropriate corrective movements independently of the remaining two channels. However, changes in the error signal associated with changes in the visual and the labyrinthine channels do not always reflect the true error in alignment and probably cannot initiate appropriate corrective movements independently of the somesthetic channel. Visual and labyrinthine receptors are incapable of differentiating tilting of the head from tilting of the body and false correction may result unless the differentiating information is provided by the somesthetic channel. Therefore, adequate postural stability probably does not occur in the complete absence of the somesthetic channel. The integration of information is assumed to occur in the actuating elements.

THE PROBLEM

The characteristics and functions of any control system may be examined from several points of view and under a variety of operating conditions. One way in which to study the postural control system is to look at the stability of the output during quiet standing. Since the primary function of the control system is to maintain the center of gravity perpendicularly above the ideal mean center of weight distribution, one measure of the effectiveness of the system would be to examine the deviations between the ideal and the instantaneous center of weight distribution. Because the ideal center of weight distribution reflects the most stable postural attitude, any deviation of the instantaneous from the ideal value would be indicative of instability. Thus we can evaluate instability as an index of the functional characteristics of the system.

Quietly standing posture is the simplest task for the control system to perform and affords an operating condition under which observations and measurements may easily be made. The stability of quietly standing dogs has been previously observed and measured (3). Aside from variations due to displacement forces acting on the body, the normal variations observed in the instantaneous center of weight distribution were suggested to be comprised of a variety of noises which have their sources in the control system. Noises which have their sources in the feedback channels were thought to be generated by variations in the feedback receptor sensitivity over time. Noises in the controlled elements were suggested to be due to variations in muscle tension as a result of random asynchrony in the discharge patterns of motor units during tonic contraction. Discomfort from standing over a long period of time may initiate occasional slight volitional alterations in stance for the purpose of relieving this discomfort.

The problem in this investigation is to study the effects of the labyrinthine and visual deprivations on the normal variations in the instantaneous center of weight distribution. From these observations we may begin to identify some characteristics of the postural control system and its mode of operation.

METHODS

GENERAL

In an earlier study (3), the stability of quietly standing dogs was evaluated using a system of force plates and signal processing units to generate an X-Y plot of the movements of the center of weight distribution. Experience with this method has led to the conclusion that problems of data reduction could be simplified without loss of critical information by registering only the longitudinal and lateral components of these movements on two separate records. Thus, the observational scheme adopted involved the use of animals trained to stand quietly on force plates while records of longitudinal and lateral movements of the center of weight distribution were recorded on two channels of an ink-writing oscillograph.

TRAINING OF ANIMALS

Eight animals of approximately equal build and weight (20-30 kgs.) were trained by gentle tactile and verbal reprimands followed by reward to assume a command posture, a relaxed stance without sudden observable movements, with the head straight ahead and with the snout above the scapulohumeral joint. Visual, verbal and tactile commands were established and used simultaneously during the training period so that the commands could be used interchangeably later in the deprivation conditions. Four of the animals were trained to assume a command posture in previous experiments (3) and required little additional training. All the animals were required to maintain this command posture for six to seven minutes duration in successive trials without being reprimanded. Two of the newer animals were unable to meet these requirements and were eliminated from the experiment.

PRELOADING AND STARTING POINTS

Previous studies indicate each animal has a characteristic and individual stance (3). Practice trials were established to determine the characteristic stance of each experimental animal and to eliminate remnants of changes in position due to training. The establishment of a characteristic stance allowed the investigator to estimate the characteristic preload, the amount of lead weight required on each force plate to simulate the weight and individual pattern of weight distribution. This preload was used to simulate the animal during the calibration procedures.

During the practice trials each animal was observed to adopt an initial stance which varied from trial to trial, gradually drifted into a more stable stance over a period of two to three minutes, and retained this plateau position which was relatively constant from trial to trial. The initial variability in stance was reduced to a minimum by using the plateaus reached during the practice trials to guide the placement and adjustment of the animal before the recording was started. The plateau was characteristic for each animal and was used as the common starting point in all experimental trials for that animal.

INSTRUMENTATION

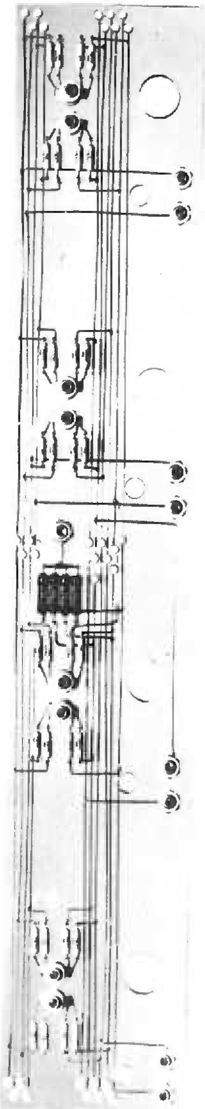
A small room sufficiently isolated from outside noises was selected in which to conduct the experiment in order to minimize auditory distractions.

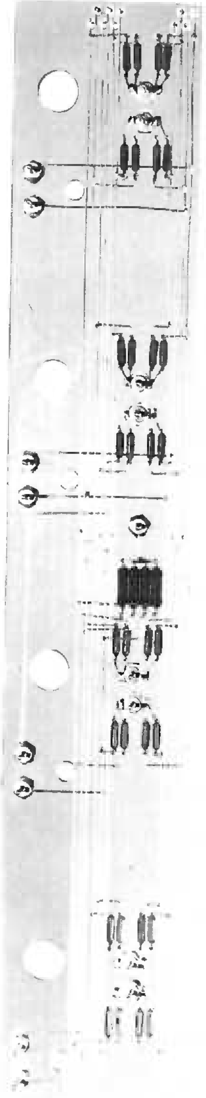
The force plates were constructed in accordance with the modifications recommended by Petersen, Brookhart and Stone (15), increasing the beam thickness from 0.125 to 0.156 inch and substituting stainless steel for beryllium-copper flexures. These modifications permitted increase in the maximum capacity up to 30 kgs. per plate with less than 1% deviation from linearity when the load is placed at one point on the plate. There is a maximum deviation of approximately 5% in the response of the plates to loading on the different corners.

The plates were placed in a rectangular configuration 50 x 15 cm., which permitted all the animals to assume a natural and comfortable stance. A rubber matting was glued to each plate surface to afford better footing, and a 2¼ inch concentric square was marked on this matting to aid in centering the animal's feet upon the plates. Each plate was assigned initials with respect to the animal's feet: right anterior (RA), right posterior (RP), left anterior (LA) and left posterior (LP); and numbered from 1 to 4, respectively. The numbers correspond to the channels of the polygraph from top to bottom.

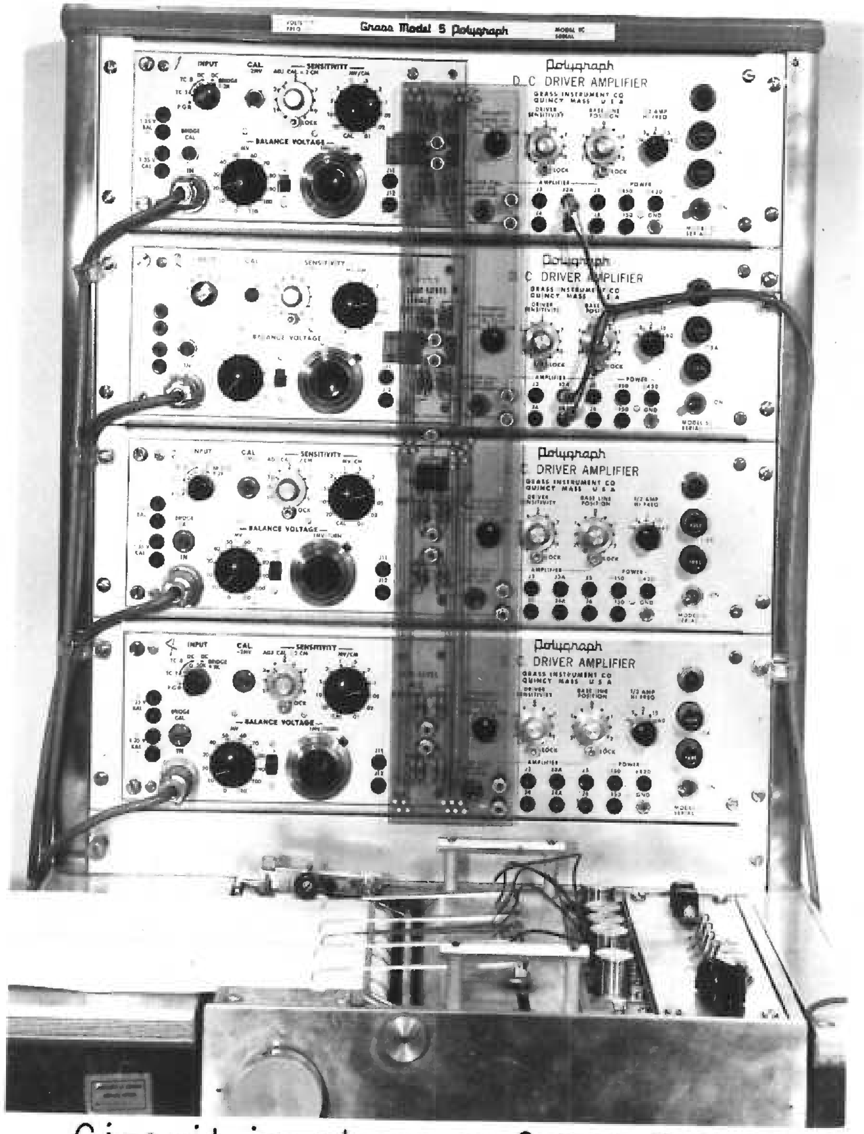
The force plates were connected by four-conductor shielded cables to the 5-P1 Low Level Preamplifiers of a 4 channel Grass Model 5 Polygraph. The preamplifiers were slightly modified by mounting insulated tip jacks on the face plates to exteriorize the output terminals 4 and 8. The calibration switches of the driver amplifiers were placed in the "CAL" position to interrupt the normal circuits between the preamplifiers and the driver amplifiers. A voltage summation circuit was then connected in series between the exteriorized preamplifier output pins and the driver input pins J_1 and J_2. Figure 2 illustrates the voltage summation unit installed on the polygraph for operation.

Figure 2. Voltage summation unit in detailed view and installed on the oscillograph for operation. Front view: the resistors and the bases of the pin plugs are the only components exposed to the front side. The lead wires of the resistors are connected to the circuit through small holes drilled out of the chassis. The larger of the visible holes were drilled out to accommodate the driver calibration switch, and the smaller holes were drilled out opposite the driver calibration signal buttons. Back view: the entire circuit was secured to Teflon stand-offs and pin plugs. The schematic diagram showing the circuit in detail is illustrated in Figure 3. Installed view: the summation unit is plugged into the appropriate jacks of the preamplifier and driver. The output cable to the monitoring oscilloscope appears on the right side, and the shielded cables from the force plates appear on the left side of the illustration.


Front View


Back View

VOLTAGE SUMMATION CIRCUIT



Circuit in place on Grass Polygraph

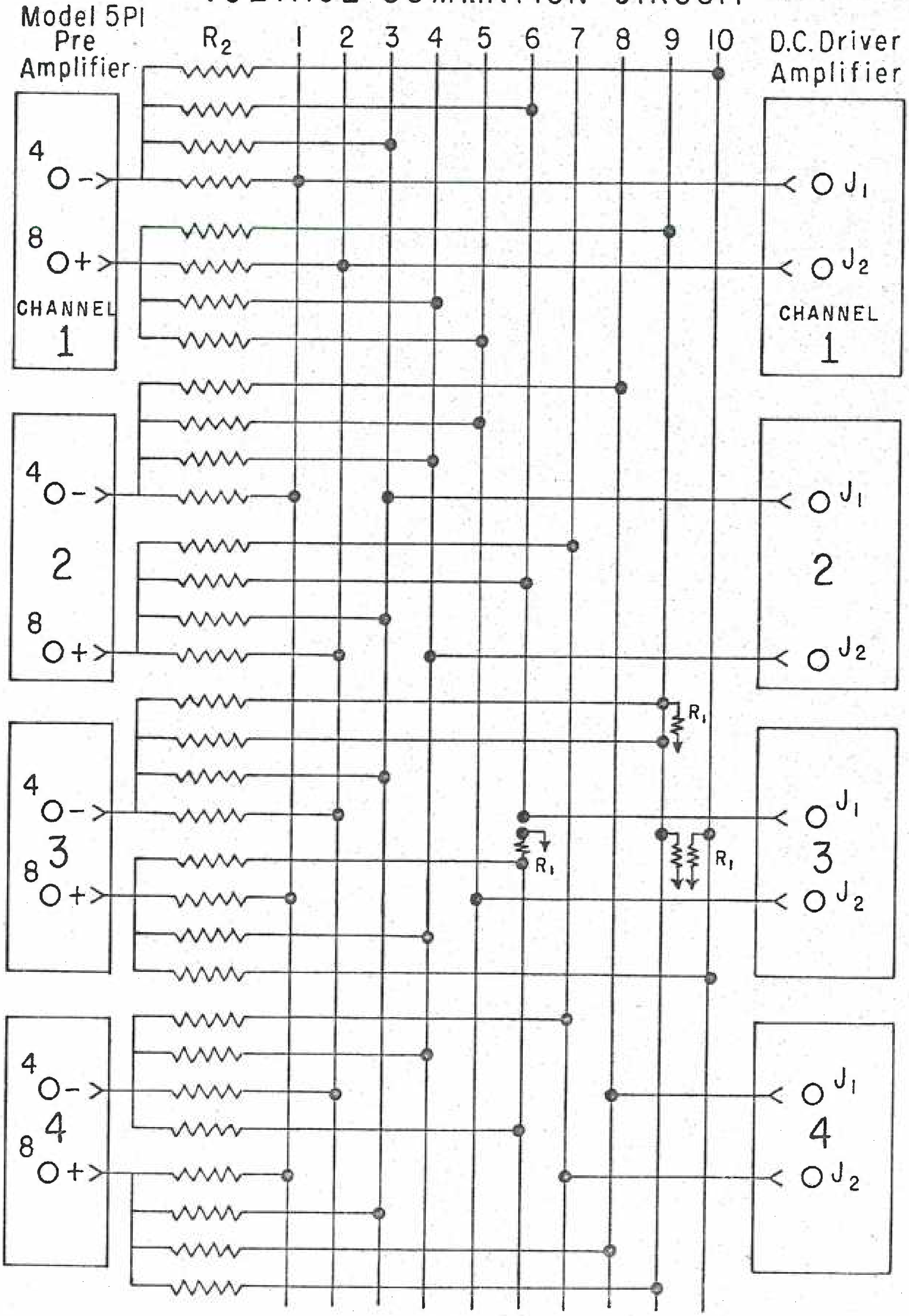
The summation circuit was designed so that the signals presented to the channel #1 driver amplifier caused it to generate an output which represented the longitudinal displacements of the center of weight distribution. Similarly, the signals presented to the channel #2 driver amplifier caused it to generate an output which represented the lateral displacements of the center of weight distribution. The channel #3 driver amplifier output represented the shift of weight between the two anterior plates, and the channel #4 driver amplifier represented the shift in weight between the two left lateral plates. The circuits for the latter two channels were originally designed to obtain ancillary information about diagonal shifts in weight. However, it was later found that the amount of information from these two channels was insufficient, and subsequently no attempt was made to evaluate the diagonal shifts.

Figure 2 illustrates details of the voltage summation unit which was constructed as a "plug-in" unit using a 50 x 9 x 0.5 cm. plastic sheeting for the chassis. Tip plugs mounted through the chassis served as the input and output terminals, and provided adequate anchorage and a clearance of approximately ¾ inch from the face plates when installed. The bases of the tip plugs projecting through the chassis served as check points for the calibration of the preamplifiers. Four ¾ inch holes were drilled in the chassis to accommodate the calibration switches of the driver amplifiers. The entire circuit as illustrated in Figure 3 was secured on the inner aspect of the chassis with Teflon stand-offs.

Since the polygraph tracings could not be seen while aligning the animals with the starting points, a type 512 Tektronix oscilloscope monitored the driver amplifier outputs from channels #1 and #2. A

Figure 3. Schematic diagram of the voltage summation circuit used to compute from the preamplifier outputs the longitudinal and lateral displacements of the center of weight distribution. The preamplifier channel numbers correspond to the numbers assigned in the text to the force plates. The driver channels 1 and 2 represent the longitudinal and lateral displacements of the center of weight distribution, respectively; channel 3 represents the weight difference between the anterior plates; and channel 4 represents the weight difference between the left lateral plates. The numbers 4 and 8 on the preamplifiers represent the output jacks as numbered on the chassis. The numbers J_1 and J_2 represent the input jacks as labeled on the chassis. Numbers were assigned to the vertical bus bars to aid in wiring the circuit. The resistors had the following values: $R_1 = 5M \pm 1\%$, $R_2 = 1M \pm 1\%$.

VOLTAGE SUMMATION CIRCUIT



double pole, double throw toggle switch was used to connect the oscilloscope to either of the two channels at terminals J3A and J4A.

INSTRUMENTATION ERROR

The force plate-recording system was tested for probable error of registration under the conditions used for the experiments. Since the placement of the animal's feet within the designated 2¼ inch square area on the surface of the force plates can be accomplished with confidence, the probable error in registration of the force plate-recording system was computed by applying force at different points within this square. A 3 kg. weight having a two inch diameter base was utilized to simulate the supporting area of the animal's foot, and to obtain the differences in registration between the center and each of four points established by the tangents of the base with two sides of the square. These differences represent the maximum error in registration as a result of the inability to place the animal's foot at the exact center of the square. The mean differences were computed from a sample of 20 differences associated with each point. The 16 mean differences obtained from all four force plates were summated appropriately in 256 possible combinations to obtain the average error of .007 ± .016 mm./kg. for the longitudinal displacements of the center of weight distribution. Therefore, it may be assumed that the heaviest animal (30 kgs.) had a maximum error of 1 mm. in the final recording 95% of the time. The probable error for the lateral displacements was assumed to be the same order of magnitude as the error for the longitudinal displacements since the same recording instruments were used for both measures.

Two possible sources of drift arise from the Grass recording instrument itself and from the force plates, possibly due to slippage of the epoxy bonding between the strain gauges and the beams. The average drift at the end of 10 minutes with preloaded plates and with sensitivities as used in the experiment was 0.20 ± 0.20 mm. for a population of 20 trials.

Each calibration deflection was read to the nearest 0.2 mm., which represents an error of 1% on the final data. The recordings were read to the nearest 0.5 mm.

Since all of the data were treated as repeated measures, the errors identified above are not considered significant.

CALIBRATION PROTOCOL

After allowing at least 30 minutes for the Grass Polygraph to achieve thermal stability, the plates were preloaded with lead weights approximating the weight distribution of the animal. Each plate in turn was balanced to zero voltage output with the aid of a voltmeter across the preamplifier output terminals 4 and 8 while the remaining three preamplifier sensitivity dials were in the "CAL" position to open the circuit and prevent interference from the unbalanced plates. The sensitivity of each preamplifier was then adjusted to 0.8 volts/kg. With the entire circuit closed the voltage baseline generated by the driver amplifier was made to coincide (± 0.2 mm.) with the center baseline of the graph paper by using the baseline controls of the driver. The driver sensitivity was adjusted to approximately 1 cm./kg. for channel #1, and 1 cm./2kgs. for channels #2, #3, and #4. The paper speed was set for 1 mm./sec., and 2 kgs. were placed successively on each plate to determine the sensitivity as read on channel #2.? Similarly, 4 kgs. were placed successively on each plate to determine the sensitivity as read on channel #2. The preloads were then removed in preparation for the trials.

CORRECTION FACTOR

Due to the nature of the summing function carried out by the summation network, coupled with the impossibility of attaining precise equality of sensitivities of the preamplifiers, it was impossible to attain an overall recording sensitivity such that one millimeter of pen deflection was precisely equivalent to one millimeter of movement of the center of weight distribution. However, the calibration procedure yielded a measure of sensitivity, which along with the weight of the animal, permitted the establishment of correction factors for each trial. Thus, the recorded movements could be converted to actual movements through the use of these correction factors. Correction factors are tabulated in Appendix A.

SENSORY DEPRIVATION PROCEDURES

The blindfold was constructed of ¼ inch foam rubber sheets formed into cups enclosing the orbits and secured in place by elastic bands around the snout and neck. The cup arrangement permitted the animals to open their eyes with the blindfold in place and was much better tolerated than a simple towel blindfold, which was heavy and seemed to irritate the eyes.

Labyrinthine deprivation was accomplished through partial destruction of the membranous labyrinths. Cawthorne (16) has found that total loss of vestibular and cochlear functions always occurred from tearing the membranous labyrinths or by coagulation with diathermy. Information about the procedure was obtained through personal communications with Dr. W. A. Stotler, who has made similar lesions in cats with a high degree of success.

Under anesthesia with pentobarbital the tympanic bulla was approached ventrally using the hyoid bone as the principal landmark. Care was exercised in avoiding injury to the adjoining carotid artery and the hypoglossal nerve when exposing and entering the bulla. A hooked probe was inserted into the round window and the bone enclosing the base of the cochlea was elevated. As much of the structure of the adjoining labyrinth was destroyed with the probe tip, followed by electrocautery to ensure maximum destruction. After ensuring hemostasis, the wound was closed without inserting a drain.

Two of the experimental animals developed sterile abscesses at the wound site where the skin sutures were too tight to permit adequate drainage. Reopening the wound was sufficient treatment and the animals recovered without further complications.

In the first postoperative day all animals were unable to maintain a standing posture and demonstrated violent lateral movements of the head when attempting to move about. None of the animals demonstrated gross nystagmus or lateralizing signs. During the next four to five days all the animals were able to regain balance and minimize the lateral head movements. Dog C-6 was observed at this time to have a 30 degree tilting of the head to the left with no other lateralizing signs. This tilting of the head remained permanently.

Two weeks following surgery the lateral movements of the neck were no longer present. The animals demonstrated some clumsiness in gait and were unable to prevent themselves from bumping their snouts upon the floor when jumping from a height of four to five inches. They were also unable to stop suddenly and avoid collision upon approaching an obstacle. After three months the animals demonstrated only a minimal amount of clumsiness in gait.

RESULTS

CONDUCT OF EXPERIMENTAL TRIALS

After the calibration procedures were completed, the animals were centered upon the force plates and the stance adjusted to bring the position of the center of weight distribution into alignment within 5 millimeters of the predetermined starting point. Past experience had indicated that tense or apprehensive animals tend to assume a crouching position and resist attempts at slight adjustments in stance. To ensure against tension or apprehension, the animals were handled gently and not reprimanded prior to or during the experimental trials. Each trial was of six minutes duration with the last five minutes being used for sampling. The initial minute gave the animals opportunity to relax and adjust themselves to match the setpoint. After each trial the animals were given generous rewards for their efforts and were permitted ten-minute rest periods between trials to minimize fatigue. No more than four successive trials were run on the same day.

Trials were discarded for any one of the following three reasons: sudden observable movements, a slow drifting of the snout below the level of the scapulohumeral joint or beyond 30 degrees laterally, and deflection of the writing pen beyond the range of the graph paper.

CATEGORIES OF EXPERIMENTAL TRIALS AND THEIR SPECIAL ADJUSTMENTS

Ten consecutive trials were observed in each of four conditions consisting of control, acute visual deprivation, chronic labyrinthine deprivation, and combined acute visual and chronic labyrinthine deprivations.

For convenience the conditions will henceforth be designated as "C", "B", "L", and "LB" conditions, respectively.

There was no special problem in the "C" condition other than auditory and visual distractions which caused reflex turning of the head with consequent large variations in the tracings, necessitating abortion of the trial. To minimize the distractions the experiment was conducted within a small room sufficiently removed from outside noises. The investigator was seated directly in front of the animals so that the animals were able to observe all movements made by the investigator without having to turn their heads. Gentle verbal commands were repeated at constant intervals during the trials to reinforce the command posture.

All the experimental animals initially reacted to the blindfolding with apprehension and tension, and failed to maintain their snouts above the scapulohumeral joint throughout the trial. Further training was consequently required to re-establish the command posture. The initial reactions to blindfolding were probably due to the new experience rather than to compromise of the postural control system. Verbal commands were gently repeated during the trial to reinforce the command posture.

The experimental trials in the "L" condition were run approximately three months after the surgical procedure when maximal recovery and compensation were thought to have occurred. No re-training was necessary even though the animals were deprived of their auditory function and were not able to receive verbal commands. Visual commands, which were used with verbal commands previously, appeared to be sufficient to maintain the command posture during the trials.

In the "LB" condition dog C-6, with the tilting head, was unable to maintain the command posture and consistently allowed his head to drift down and to the left during the trials. Intensive training failed to re-establish the command posture and the animal was consequently eliminated from the experiment. The remaining five experimental animals encountered no difficulties in maintaining the command posture and retraining was not necessary prior to the experimental trials. Gentle tactile commands were sparingly used in positioning the animals upon the force plates but were not used during the trials. All animals appeared to maintain the command posture without the use of verbal or visual commands during the trials.

CALORIC TESTING

The experimental animals were tested for labyrinthine function approximately eight months after the surgical procedure. Caloric testing was used in preference to histologic examination of the eighth nerves because the animals were to be used for further postural control experiments and could not be sacrificed. Galvanic and rotatory stimulation were tried but did not produce responses in the control animals which were adequate in either magnitude or reliability.

Three control animals were tested for responses to caloric stimulation under chloralose anesthesia. Chloralose was selected because the reflexes of interest are still observable under the anesthetic dose of 100 mg./kg. body weight. Approximately one hour after the chloralose was given intravenously the control animals were tied down in a supine position with the long axis of the head in a vertical position. All control animals responded to irrigation of the external canal with ice water by rotating the homolateral eye and moving it toward the inferior-medial quadrant. The eye was held in this position for one to two minutes or until irrigated with warm water. Warm water produced an opposite but smaller response in the homolateral eye. Movement of the contralateral eye was not observed during caloric stimulation, nor was nystagmus observed in either eye. The response of the homolateral eye was consistent with successive alternation between warm and cold water.

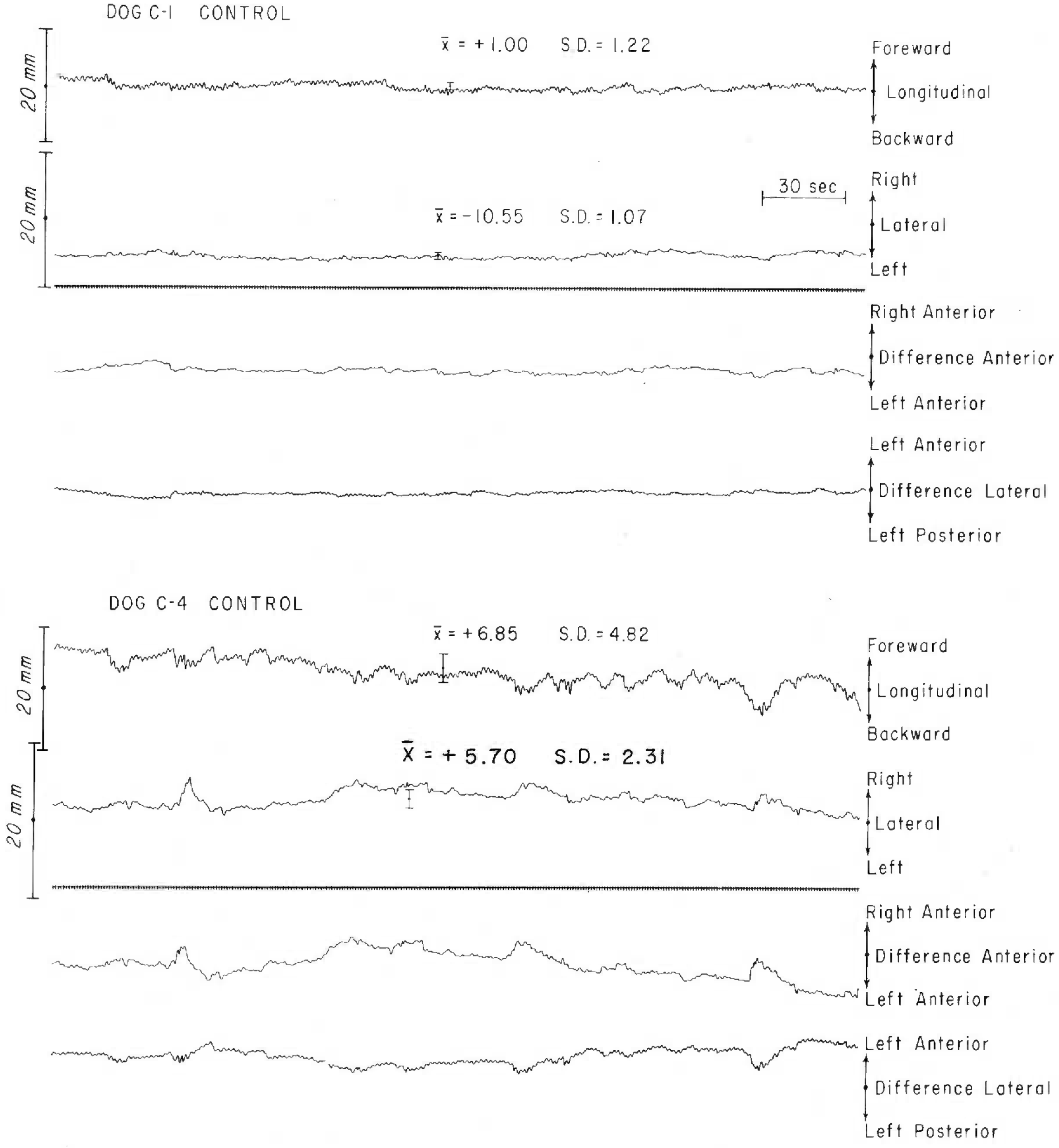
Four of the five experimental animals demonstrated no consistent response to caloric stimulation. Dog C-4 consistently demonstrated a slow and delayed movement inferiorly of the right eye in response to ice water irrigation, but did not demonstrate rotation of the eye. The left eye did not respond to caloric stimulation. The response of the right eye probably represents a partial recovery of labyrinthine function, but strongly suggests that labyrinthine function was severely compromised.

GENERAL CHARACTERISTICS OF THE RECORDINGS

Figure 4 illustrates representative trial runs of two animals in the control condition. The small variations of uniform amplitude and frequency which are less than two seconds in duration from peak to peak and seen best in the longitudinal displacements of the center of weight distribution in dog C-4 were associated with respiratory movements. They were greatly attenuated by filtering in the driver amplifiers. Filtering also eliminated tail wagging as an identifiable cause of variations in the recordings. Observable head and body movements which caused variations in the recordings were unacceptable under the criteria established for aborting trials and thus were not a cause of variations. However, occasional large rapid variations such as the one observed in Figure 4, lateral displacements, were due to unobservable shifts in body

Figure 4. Representative examples of records of trial runs of two animals in the control condition. The pair of tracings above the time line (seconds) represent movements of the center of weight distribution. The two tracings below the time line represent changes in the differences between the weights borne on selected pairs of feet. The directional significance of the movements of the recording pens is indicated by the labels to the right of each tracing. The scale factors are indicated to the left of the tracings. The records were measured in terms of the magnitude of deviation from the baseline position indicated by the dot on the scaling bar. The trial means and standard deviations are given for the records concerned with the center of weight distribution. The sign of the value is given relative to the baseline position. The records of the differences between pairs were not measured, nor were these data utilized. Note the small rhythmic variations in the longitudinal direction related to respiratory movements.

TRIAL RUNS


DOG C-1 CONTROL
x̄ = +1.00 S.D. = 1.22
20 mm
Foreward
Longitudinal
Backward
30 sec
x̄ = -10.55 S.D. = 1.07
20 mm
Right
Lateral
Left
Right Anterior
Difference Anterior
Left Anterior
Left Anterior
Difference Lateral
Left Posterior
DOG C-4 CONTROL
x̄ = +6.85 S.D. = 4.82
20 mm
Foreward
Longitudinal
Backward
X̄ = +5.70 S.D. = 2.31
20 mm
Right
Lateral
Left
Right Anterior
Difference Anterior
Left Anterior
Left Anterior
Difference Lateral
Left Posterior

position. Variations of this type were generally less than 30 seconds in duration, few in number, and may have been associated with minor weight redistribution in the interest of comfort. Since they were not expected to contribute significantly to the final data, these variations were accepted and treated as the results of reactions of the control system to external disturbances.

The variations in the recording, with the exception of those identified to be due to respiratory movements, were assumed to be evidence of instability in the postural control system. The variations may arbitrarily be classified into short term variations with a peak to peak duration range from one second to two minutes and long term variations with peak to peak duration greater than two minutes. The long term variations, over which were superimposed the short term variations, were sometimes longer than five minutes in duration and appeared as slow drifts in the tracings.

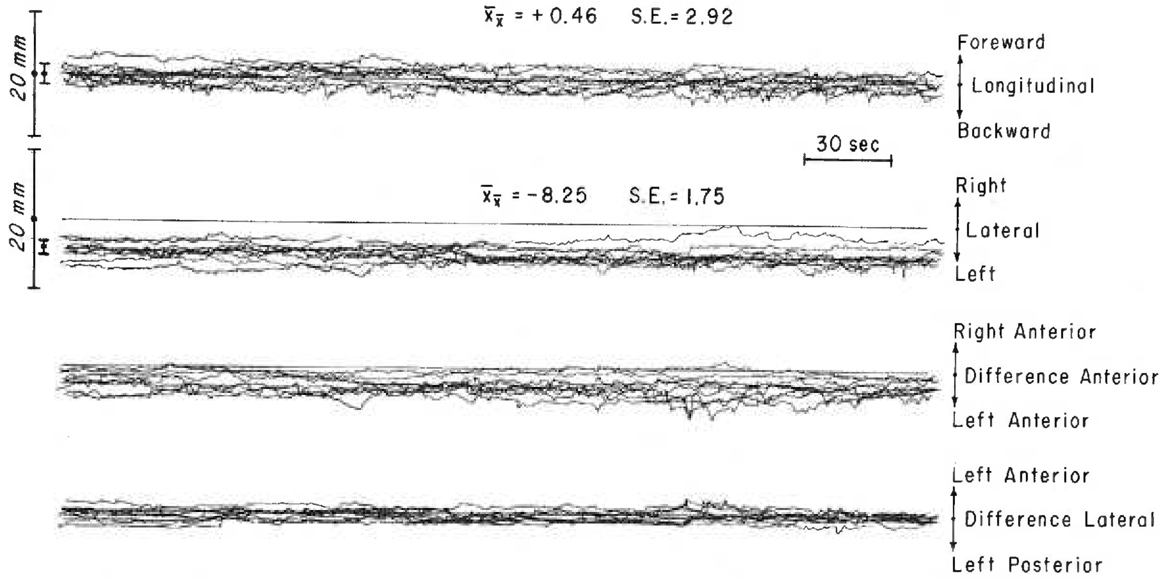
Figure 5 illustrates representative examples of composites of the ten trials within a condition. The randomness of the variations in the control condition reinforces inference that the variations constitute signs of instability in the control system. The uniform drift of the tracings posteriorly in the "LB" condition, longitudinal displacements, of dog C-1 may have been due either to errors in establishing the proper starting point or may have been due to unidirectionality of the variations within the trials. Since each animal was assigned a common starting point for all four conditions, the variations due to error in establishing a proper starting point should be eliminated when the data are processed as repeated measures.

The records for the "LB" condition in Figure 5 suggest a broadening

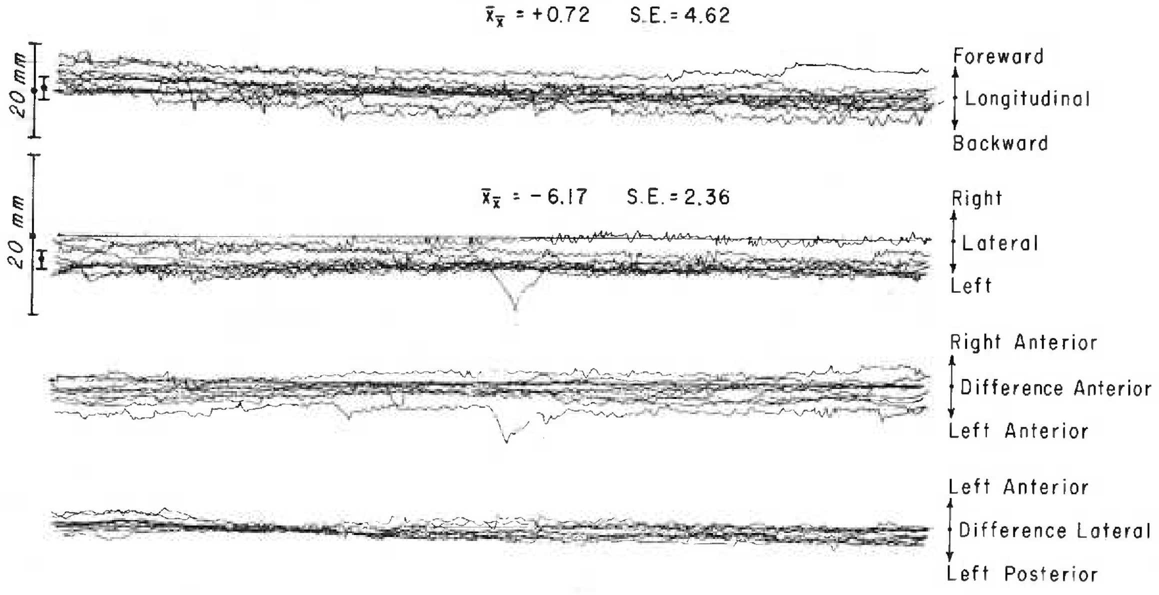
Figure 5. Illustrations of the method of summarizing recordings of all trials in a given condition. The records of individual trials were retraced in superimposed fashion after justification of calibration factors and baselines. The general features of the display are the same as those used in Figure 4. The straight horizontal lines represent the center baseline of the recording system. The means of all trial means ($\bar{X}_{\bar{x}}$) and the standard errors (S.E.) are indicated above each fascicle and represented at the left end of each fascicle.

COMPOSITES OF 10 TRIAL RUNS

DOG C-1 CONTROL



DOG C-1 LABYRINTHECTOMIZED and BLINDFOLDED



of the fasicles in both the longitudinal and lateral displacements of the center of weight distribution. This broadening of the fasicles was observed in four of the five animals. The broadening of the fascicles in the lateral displacements appear to be due to increased magnitude of the long term variations, but this appearance was not consistent in the other experimental animals. There was no observable peculiarity of the tracings in the "LB" condition which distinguished them from the tracings in other conditions, and which were consistent in each animal. Therefore, statistical tests were utilized for further evaluation.

SUMMARIZATION OF THE DATA

General. There are several different questions which may be asked and answered by the recorded data. The first of these may be phrased as follows: for each condition, is there evidence that the animals adopted a mean center of weight distribution that was different from that exhibited by the normal animals? If a specific feedback deprivation resulted in a persistent distortion of output, such a distortion would be reflected by a change in value of the mean center of weight distribution as represented by the mean of all trial means for a given condition. A second question could be raised about the degree to which any trial mean center of weight distribution remained constant over the ten trials within a condition. Given a mean center of weight distribution characterizing that condition, how much variation in the trial means appeared about this value from trial to trial? If a specific feedback deprivation resulted in a deterioration of the animal's ability to replicate a given trial mean center of weight distribution within a condition, the deterioration of that animal's performance would appear as an increase in the standard error of the ten trial means. Finally, during any trial, there were variations about the mean for that trial. Was the magnitude of these random variations within a trial influenced by the feedback deprivations? If a specific feedback deprivation resulted in a reduction in the capability of the system to respond to "noise" or to temporary disturbance during the trial, evidence of this reduced capability should appear as an increase in the mean of the standard deviations for a condition.

The tracings on the graph were read in millimeters of displacement from the center baseline at 30 second intervals for a sample of ten in each trial. The raw scores were multiplied by the correction factor to read actual millimeter displacement of the center of weight distribution. These corrected scores were then used to compute the mean center of weight distribution and standard deviations for each trial.

<u>The Mean of Means ($\bar{X}_{\bar{x}}$)</u>. The mean of the trial means within a condition was assumed to be the best estimate of the mean center of weight distribution for that condition. This mean of means, $\bar{X}_{\bar{x}}$, was calculated for each condition in each of the five experimental animals and the results tabulated in Tables 1 and 2.

Table 1. The means of means, $\bar{X}_{\bar{x}}$, of the longitudinal displacements of the center of weight distribution.

Dogs	Conditions			
	"C"	"B"	"L"	"LB"
C-1	+0.46 mm.	-0.08	-7.59	+0.72
C-2	+6.25	+1.48	+9.28	+11.56
C-3	+5.33	+11.74	+10.20	+12.87
C-4	+5.08	+0.53	+4.75	+5.14
C-5	+6.98	-3.61	-7.24	+13.82

Table 2. The means of means, $\bar{X}_{\bar{x}}$, of the lateral displacements of the center of weight distribution.

Dogs	Conditions			
	"C"	"B"	"L"	"LB"
C-1	-8.25 mm.	-7.59	-5.75	-6.17
C-2	+7.35	+0.32	-0.68	+3.02
C-3	+3.72	+1.63	-0.88	+5.50
C-4	+4.22	+1.04	+6.08	+6.17
C-5	-1.26	-0.98	+1.43	+1.90

The analysis of variance techniques were utilized in evaluating the assumption that the mean center of weight distribution remained fixed between conditions for the group of experimental animals. Preliminary testing for homogeneity of variances between conditions with the T-test method (17) indicated that a parametric analysis of variance test was required in testing the $\bar{X}_{\bar{x}}$ of the lateral displacements of the center of weight distribution between conditions, and that a non-paramentric analysis of variance test was required for testing the $\bar{X}_{\bar{x}}$ of the longitudinal displacements between conditions. Table 3 contains the tabulated results of the Single Classification Analysis of Variance for Repeated Measures (18), and indicates no significant differences of $\bar{X}_{\bar{x}}$, lateral displacements, between conditions for the group of experimental animals. Table 4 contains the tabulated results of the Friedman Two-way Analysis of Variance Test by Ranks (19) and indicates a significant difference between at least the maximum and minimum rank sums at the 5% level of confidence.

Table 3. Summary of the Single Classification Analysis of Variance in testing the $\bar{X}_{\bar{x}}$ of the lateral displacements of the center of weight distribution between conditions.

Source	SS	df	MS	F
Between	327.02	4		
Within	81.60	15		
Treatments	23.66	3	7.89	1.63
Residuals	57.94	12	4.83	
Total	408.62	19		

Table 4. Summary of the Friedman's test in evaluating the $\bar{X}_{\bar{x}}$ of the longitudinal displacements of the center of weight distribution between conditions.

Dogs	Conditions			
	"C"	"B"	"L"	"LB"
C-1	3	2	1	4
C-2	2	1	3	4
C-3	1	3	2	4
C-4	3	1	2	4
C-5	3	2	1	4
Rank Sums	12	9	9	20
$X_r^2 = 9.72$*	*Significant at the 5% level of confidence			

This difference occurred between "B" and "LB", and between "L" and "LB" conditions. It may be concluded that no other differences were significant since the maximum range of the rank sums barely reached the 5% level of confidence.

The Standard Error (S.E.) The standard error is a measure of the variability of the trial means about the mean of means, and reflects the ability of the animal to replicate any given trial mean center of weight distribution within a condition. The S.E. for each condition was computed as the standard deviation of the ten trial means in each condition, and the results tabulated in Tables 5 and 6.

Table 5. The standard errors, S.E., of the longitudinal displacements of the center of weight distribution.

Dogs	Conditions			
	"C"	"B"	"L"	"LB"
C-1	2.92 mm.	2.54	3.41	4.62
C-2	2.15	2.47	1.77	5.07
C-3	1.76	2.63	2.20	3.64
C-4	1.93	4.40	1.84	4.26
C-5	3.58	5.09	2.24	3.95

[illegible]

Table 6. The standard errors, S.E., of the lateral displacements of the center of weight distribution.

Dogs	Conditions			
	"C"	"B"	"L"	"LB"
C-1	1.75 mm.	1.92	1.48	2.36
C-2	2.17	4.41	3.18	5.15
C-3	2.46	2.81	1.87	6.06
C-4	3.87	3.13	1.56	1.26
C-5	1.26	2.46	1.67	6.08

[illegible] $p > 0.05$

The analysis of variance techniques were again used to evaluate the effects of labyrinthine and visual deprivation on the animal's ability to replicate a given trial mean center of weight distribution within a condition. The variances between the conditions were not found to be homogeneous in both the longitudinal and the lateral displacements of the center of weight distribution. However, inspection of the tracings indicated that three of the trial means of the longitudinal displacements in the "L" condition of dog C-5 were clustered closely together far beyond the range of the remaining seven trials. Since they were run on the same day and were far beyond the expected range of variation, the three trials were not considered random for that condition and were thus eliminated. The most likely cause of such spurious trials was probably an undetected paronychia, an infection of the foot which causes the animal to unload weight from the involved foot. These foot infections occurred several times in different animals during the experimental trials, but were generally easy to detect when the animals limped. After the elimination of the three aberrant trials, the $\bar{X}_{\bar{x}}$, S.E. and $\bar{X}_{S.D.}$ were recalculated and new tests were carried out on the data. With the elimination of the three trials the variances of the longitudinal displacements were homogeneous, but the variances of the lateral displacements remained unchanged. The results of the Friedman's test of the S.E. for the lateral displacements are tabulated in Table 7 and indicate a difference between "C" and "LB" conditions at the 10% level of confidence.

Table 7. Summary of the Friedman's test in evaluating the standard errors of the lateral displacements between conditions.

Dogs	Conditions			
	"C"	"B"	"L"	"LB"
C-1	2	3	1	4
C-2	1	3	2	4
C-3	2	3	1	4
C-4	4	3	2	1
Rank Sums	10	15	8	17

$$X_r^2 = \frac{12}{Nk(k+1)} \mathop{}_{j=1}^{k} (R_j)^2 - 3N(k+1)$$

$= 6.36$ Significant at the 10% level of confidence

The results of the Single Factor Analysis of Variance for testing the S.E. of the longitudinal displacements are tabulated in Table 8, and indicate a significant difference at the 1% level of significance. The Neuman-Keuls Test (18) was utilized to locate the significant differences. Table 9 summarizes the results for the Neuman-Keuls Test and indicates that significant differences exist between "C" and "LB", and between "L" and "LB" conditions.

Table 8. Summary of the Single Classification Analysis of Variance in testing the Standard errors of the longitudinal displacements of the center of weight distribution between conditions.

Source	SS	df	MS	F
Between	3.20	4		
Within	21.24	15		
Treatments	13.08	3	4.36	6.41**
Residuals	8.16	12	0.68	
Totals	24.44	19		

Table 9. Summary of the Neuman-Keuls Test for the S.E. of the longitudinal displacements of the center of weight distribution.

Conditions		"L"	"C"	"B"	"LB"
Ordered S.E.		2.29 mm.	2.47	3.43	4.31
Differences between pairs	"L"	-	.18	1.14	2.02**
	"C"		-	.96	1.84**
	"B"			-	.88
	"LB"				-

** Significant at the 1% level of confidence

The Mean Standard Deviation ($\bar{X}_{S.D.}$). The mean standard deviation, $\bar{X}_{S.D.}$, is a measure of the within trial variability of the center of weight distribution about the trial mean, $\bar{X}$, and is assumed to indicate the magnitude of the variations within each trial with respect of $\bar{X}$.

The $\bar{X}_{S.D.}$ was computed by averaging the standard deviations for the ten trials within a condition, and the results were tabulated for the longitudinal and lateral displacements in Tables 10 and 11, respectively.

Table 10. The mean standard deviations, $\bar{X}_{S.D.}$, of the longitudinal displacements of the center of weight distribution.

Dogs	Conditions			
	"C"	"B"	"L"	"LB"
C-1	1.68	1.90	2.79	2.82
C-2	1.63	0.91	1.61	2.26
C-3	2.85	2.05	1.89	3.41
C-4	3.55	4.77	4.04	2.58
C-5	2.95	1.61	2.37	2.25

Table 11. The mean standard deviations, $\bar{X}_{S.D.}$, of the lateral displacements of the center of weight distribution.

Dogs	Conditions			
	"C"	"B"	"L"	"LB"
C-1	1.46	1.90	2.30	1.15
C-2	1.14	0.73	2.21	1.45
C-3	2.26	1.97	1.56	3.21
C-4	2.43	2.09	1.99	2.43
C-5	1.28	1.66	4.89	1.28

Preliminary testing with the T-test indicated homogeneity of variances in both the longitudinal and lateral displacements of the center of weight distribution. Tables 12 and 13 contain the tabulated results of the Single Factor Analysis of Variance for Repeated Measures for the longitudinal and lateral displacements, respectively, and indicate that visual and labyrinthine deprivation have no significant effect upon the magnitude of the variations within trials.

Table 12. Summary of the Single Classification Analysis of Variance in testing the mean standard deviations of the longitudinal displacements of the center of weight distribution between conditions.

Source	SS	df	MS	F
Between	9.66	4		
Within	6.93	15		
Treatments	0.46	3	0.153	0.283
Residuals	6.47	12	0.539	
Totals	16.59	19		

Table 13. Summary of the Single Classification Analysis of Variance in testing the mean standard deviations of the lateral displacements of the center of weight distribution between conditions.

Source	SS	df	MS	F
Between	2.63	4		
Within	12.77	15		
Treatments	2.72	3	0.91	1.09
Residuals	10.05	12	0.84	
Totals	15.40	19		

DISCUSSION

General

The effects of visual and labyrinthine deprivation on postural stability were examined by statistically testing the changes in the mean of means ($\bar{X}_{\bar{x}}$), standard error (S.E.), and the average standard deviation ($\bar{X}_{S.D.}$) of the center of weight distribution for each condition: control ("C"), blindfolded ("B"), labyrinth-deprived ("L"), and combined labyrinth-deprived and blindfolded ("LB").

In the longitudinal displacements of the center of weight distribution, the lack of significant differences of the $\bar{X}_{\bar{x}}$ between the "C" and "B", and between the "C" and "L" conditions indicates that deprivation of either the visual or labyrinthine channel alone did not significantly alter the position of the mean center of weight distribution. Although the data from the "C" and "LB" conditions were not significantly different, the presence of significant differences between the "B" and "LB" (5% level), and between "L" and "LB" (5% level) conditions suggest that simultaneous deprivations of both channels significantly altered the mean center of weight distribution in the forward direction. The lack of significant differences of the S.E. between the "C" and "B", and between the "C" and "L" conditions suggests that the lack of information over each channel by itself did not compromise the ability of the animal to replicate the <u>trial</u> mean center of weight distribution. The significant differences between "C" and "LB" (1% level), and between the "L" and "LB" (1% level) conditions indicate that simultaneous deprivations compromised this ability. The lack of information conveyed over visual and labyrinthine channels had no significant influences upon the random variations of the center of weight distribution within trials. A more detailed consideration of each of these observations is given in the following paragraphs.

In the lateral displacements of the center of weight distribution, there were no significant differences of the $\bar{X}_{\bar{x}}$, S.E. and $\bar{X}_{S.D.}$ between conditions.

The Mean of Means

We have earlier defined the ideal center of weight distribution as that position which requires the minimum expenditure of muscular force and metabolic energy. It is assumed that the actual center of weight distribution will vary randomly about this ideal position but that the control system operates to keep the discrepancy small. On these grounds, it seems reasonable to regard the mean of the ten trial means ($\bar{X}_{\bar{x}}$) in the control condition as the best estimate of this ideal center of weight distribution. In conditions other than the control, any significant departure of $\bar{X}_{\bar{x}}$ from the control $\bar{X}_{\bar{x}}$ permits the inference that the animal does not vary about his ideal center of weight distribution, and that the line connecting his center of gravity with the ideal center of weight distribution is not parallel to the lines of gravitational force. This unparallelism due to departure of $\bar{X}_{\bar{x}}$ from the control $\bar{X}_{\bar{x}}$ is maintained by persistent distortion of the error signal.

For a given setpoint, the correction of any deviation from the ideal center of weight distribution commences upon the development of an error signal, and ceases upon the reduction of this signal to zero. Therefore, in order for an animal to match the setpoint, the error signal should accurately reflect the deviation in position. In such a case, deviations in position caused by external displacing forces would be accurately counteracted by the control system. Similarly, disturbances which have their sources in the controlled elements and in the neural networks traversed by the error and actuating signals produce deviations in position that are also corrected. The error signal, however, may be altered by disturbances in the sensor and feedback pathways in such a way that it no longer reflects the deviation in position accurately. The response of the control system which brings this altered error signal to zero results in an unstable position which does not match the setpoint, and deviations from the ideal center of weight distribution are not accurately corrected. It should be noted that, in the presence of a persistent alteration in the error signal, the control system continues to function with the same degree of accuracy and efficiency in correcting deviations in position with respect to the new unstable position. Since the error signal is generated by the detection of a difference between the setpoint and the feedback signals, any alteration in the error signal should have its source in these two signals. The setpoint for the command posture was assumed to remain fixed and unaltered; therefore, sources of alteration in the error signal are assumed to be limited to the feedback channels.

The alteration of the error signal may also be steady-state in nature, associated with a change in the quality of information being transmitted through the feedback channels. Thus, the selective alteration of information from non-adaptive receptors without influence on information from rate-sensitive receptors would introduce a persistent change in the error signal. In order to bring this changed error signal back to zero, the animal would have to adopt a steady-state deviation of his center of weight distribution so that it would not match his ideal.

The data indicate that the visual and labyrinthine channels normally exerted some steady-state influence upon the error signal, and that upon deprivation the tonically altered error signal moved the mean center of weight distribution anteriorly. Although the data indicate that labyrinthine deprivation alone did not significantly alter the error signal, it is to be recalled that the "L" condition represents a chronic condition, and that compensation by the remaining channels may have occurred to attenuate the labyrinthine steady-state influence. The significant difference between the "B" and "BL" conditions implies two different things. First, since the compensated labyrinth-deprived animal shows functional changes upon acute blindfolding, some of the compensation must have involved a change in the treatment of visual feedback signals. Second, since the deviation noted in the "LB" animals was a steady-state deviation, the original, normal labyrinthine input must have been exerting a tonic or steady-state influence on the error signal. Observations of the animals in the postoperative period also suggest that the labyrinthine deprivation alone is capable of producing a persistent distortion of output in the form of decreased muscle tonus, and that the magnitude of this distortion decreased over time. The inabilities of the animals to maintain stance in the immediate postoperative period and to decelerate themselves were probably due to failure to exert sufficient extensor tonus. Decrease in extensor tonus, although not observable during the trials of the "L" condition, may have been sufficiently present to produce movement of the center of weight distribution anteriorly. Davis and Pollock (20) have demonstrated persistent decrease in extensor tonus of antigravity muscles in decerebrate animals upon labyrinthectomy. Fulton, Liddel, and Rioch (21) produced hypotonia in the homolateral limbs upon unilateral vestibular lesions in normal cats. It may be hypothesized that the labyrinth normally exerted a significant amount of steady-state influence upon the error signal, and that after labyrinthine deprivation the visual channel partially compensated for the change in steady-state influence. The significant difference between the "L" and "LB" conditions indicates that significant change in the mean center of weight distribution occurred as a result of acute visual deprivations in a previously labyrinthectomized animal. However, the lack of significant differences between "C" and "B" indicates that no significant change occurred as a result of acute visual deprivation in a previously normal animal. The difference in response to acute visual deprivation suggests that the visual channel had partially compensated for the loss of labyrinthine steady-state influence.

The visual channel alone did not seem to exert a steady-state influence upon the error signal in a normal animal, but did seem to exert an influence in a previously labyrinth-deprived animal. However, it is to be pointed out that the visual deprivation was achieved through elimination of environmental cues, as opposed to labyrinthine deprivation which was achieved through ablation of the receptors. It may be that steady-state influence is normally exerted by the activity emanating from the intact retinal network independently of its function relative to pattern vision. The experimental design is inadequate to evaluate this possibility. Certainly, labyrinthine deprivation achieved through elimination of the environmental cue, such as in a state of weightlessness in space, does not seem to cause the same degree of incapacitation as that experienced by dogs after labyrinthine ablation.

Although the setpoint was assumed to remain fixed, there are certain identifiable situations in which the setpoint is believed to change. It has been mentioned that one source of deviation of center of weight distribution was due to volitional alterations in stance in an attempt to relieve discomfort from long standing. These brief volitional movements are assumed to occur through alterations in the command setpoint. When these variations were associated with grossly observable movements of the animal, they were of short duration and did not cause a persistent distortion of the output. The setpoint may also change under conditions of apprehension, as was observed during the early phase of training and blindfolding. During the training period, it was observed that the animals responded to reprimand by becoming apprehensive and assuming a crouching position that resulted in the movement of the center of weight distribution forward. The minimal observable crouching moved the center of weight distribution approximately 10 mm. anteriorly. The success to which elimination of apprehension can be achieved through training is demonstrated by the absence of any tendency for the $\bar{X}_{\bar{x}}$ to move forward between conditions "C" and "B". Training and avoidance of reprimand eliminated any observable tendency to assume this crouching position. The crouching was also observed as an initial reaction to the blindfolds, and was probably due to apprehension as a result of a new experience. Apprehension may also occur in response to increased disorientation caused by the combined visual and labyrinthine deprivations, and thus cause a persistent distortion in output. Since one cannot be certain that this apprehension can be eliminated with training, this source of persistent distortion in output, though remote, cannot be totally ignored.

The lack of significant changes in the $\bar{X}_{\bar{x}}$ of the lateral displacements of the center of weight distribution between conditions indicates that the steady-state influence upon the error signal did not produce a unilateral distortion of position. It should be pointed out that these results alone do not reflect the completeness of the bilateral labyrinthine deprivations. Since the analysis of variance techniques test differences between conditions for the animals as a group, random lateralization as a result of incomplete bilateral labyrinthectomy would not be reflected in the changes of the $\bar{X}_{\bar{x}}$. Inspection of the data for changes in $\bar{X}_{\bar{x}}$ for each individual animal indicate no marked tendency for lateralization, even in dog C-4 which was suspected on the basis of caloric testing to be only partially labyrinth-deprived.

The Standard Error

The standard error, S.E., is a measure of the variability of the trial mean about the mean center of weight distribution, $\bar{X}_{\bar{x}}$, and is a reflection of the animal's ability to replicate a given trial mean. If the animal were able to replicate a given trial mean over the ten trials within a condition, all trial means would obviously coincide with the $\bar{X}_{\bar{x}}$ and the variations within any one trial would be randomly and symmetrically dispersed about the $\bar{X}_{\bar{x}}$. The deviation of any trial mean from a given $\bar{X}_{\bar{x}}$ then occurs with the appearance within the trial of superimposed variations which by themselves are not symmetrically dispersed about the $\bar{X}_{\bar{x}}$. These variations may have a wide range of magnitude and duration; for a given magnitude of trial mean, they may be of short duration and large magnitude or may be of long duration and small magnitude. These variations are a component of the normal variations observed in all animals as indicated by the S.E. values for the normal condition.

The data therefore indicate that combined visual and labyrinthine deprivations significantly compromised the animal's ability to adequately correct the variations which increase the magnitude of S.E., and consequently the animal's ability to replicate a given trial mean. It may be hypothesized that the combined deprivations produced a significant loss of information concerning body position relative to the environment, and resulted in the inability of the control system to detect and correct these variations in position. There is no reason to believe that the animals have changed setpoint from trial to trial, or that the degree of apprehension varied between trials.

The significant differences between the "L" and "LB" conditions considered with the non-significant difference between the "C" and "B" conditions suggest that the visual channel may have compensated for the labyrinthine deprivation to a certain extent.

It may be argued that the increase in S.E. of the "LB" condition reinforces the conclusion based on the changes in $\bar{X}_{\bar{x}}$. The changes in $\bar{X}_{\bar{x}}$ between conditions were attributed to some alteration in the error signal produced by a steady-state distortion of the feedback signal such that the animals exhibited a new mean center of weight distribution which deviated from the ideal ($\bar{X}_{\bar{x}}$ control). The increase in the S.E. implies that the "LB" animals also exhibited a degradation of their ability to arrive at their new $\bar{X}_{\bar{x}}$, and persisted in holding a deviated position over the entire duration of each trial. This persistent adoption of a position different from the $\bar{X}_{\bar{x}}$ of the "LB" condition during the length of the trial also hints at a distortion of the steady-state feedback signal or in the manner in which it is processed by the control system. Thus, both the $\bar{X}_{\bar{x}}$ values and the S.E. values point toward the conclusion that the acutely blindfolded and labyrinth-deprived animal behaves as though steady-state influences in his control system have been degraded.

The changes of the S.E. (lateral) between the "C" and "LB" conditions were statistically significant at the 10% level, and tend to agree with and support the results of the changes in the S.E. for longitudinal displacement.

The Mean Standard Deviation

The mean standard deviation, $\bar{X}_{S.D.}$, was assumed to be a measure of the magnitude of within trial variations with respect to the trial mean. The $\bar{X}_{S.D.}$ is probably the most difficult of the three measures of postural stability to interpret reliably. Unlike the $\bar{X}_{\bar{x}}$ and the S.E., the $\bar{X}_{S.D.}$ is influenced by the presence of drifts due to error in selection of the proper initial stance and to unidirectionality of variations within a trial. Thus, the sensitivity of the $\bar{X}_{S.D.}$ in detecting within-trial variations is inversely proportional to the magnitudes of these drifts. Dogs C-1 and C-2 had no observable drifts of position in the longitudinal direction in the control condition; they also had the smallest $\bar{X}_{S.D.}$ values of the five animals. The values of $\bar{X}_{S.D.}$ in dogs C-3, C-4, and C-5 were approximately half the magnitudes of the drifts, and appeared to correlate better with the magnitudes of the drifts than with the within-trial variations. Therefore, the interpretation of the data should be made with the reservation that the $\bar{X}_{S.D.}$ is a measure of the magnitude of within-trial variations which are possibly contaminated by improper selection of initial stance which do not constitute evidence of control instability.

The measurements of the $\bar{X}_{S.D.}$ failed to reveal any significant differences between conditons, suggesting that the within-trial variation was not influenced by the sensory deprivations. The actual measurements are consistent with the visual appearance of the composite tracings of groups of trials with one exception. In the case of dog C-4, the control records exhibit a clear, unidirectional drift of longitudinal position in all trials. For the same animal in the "LB" condition, there is little if any drift apparent in the composite tracings; however, the impression of increased, rapid, variability is unmistakeable. Careful visual inspection will not permit a decision as to whether this appearance of greater instability results from a higher frequency of variations only, or whether greater amplitude of variations is also a factor in generation of changes in visible appearance.

It deserves to be pointed out that the insecurity of interpretation enforced by the presence of drifts applies only to the data for the longitudinal displacements of the center of weight distribution. Lateral drifts did not occur with the same frequency and regularity as did the longitudinal drifts. The fact that the $\bar{X}_{S.D.}$ for the lateral displacements of the center of weight distribution was the same for all conditions increases confidence in the interpretation of this measure as an index of control system instability within trials.

If it be accepted that the within-trial variability was not affected by sensory deprivations, certain implications relative to the control system operation are justified. It has already been pointed out that the combined sensory deficits revealed that a steady-state influence on the error signal probably characterizes normal labyrinthine input. If the sensory deprivations also degraded the facility with which the system senses and corrects for errors based on the derivatives of position, one would expect that the variability around a trial mean would increase, with resultant increase in $\bar{X}_{S.D.}$. Since this did not occur, it seems reasonable to conclude that the sensory deprivations used in this study influenced neither the feedback signals from "velocity or acceleration receptors", nor the manner in which they were utilized by the central nervous system portions of the control mechanism.

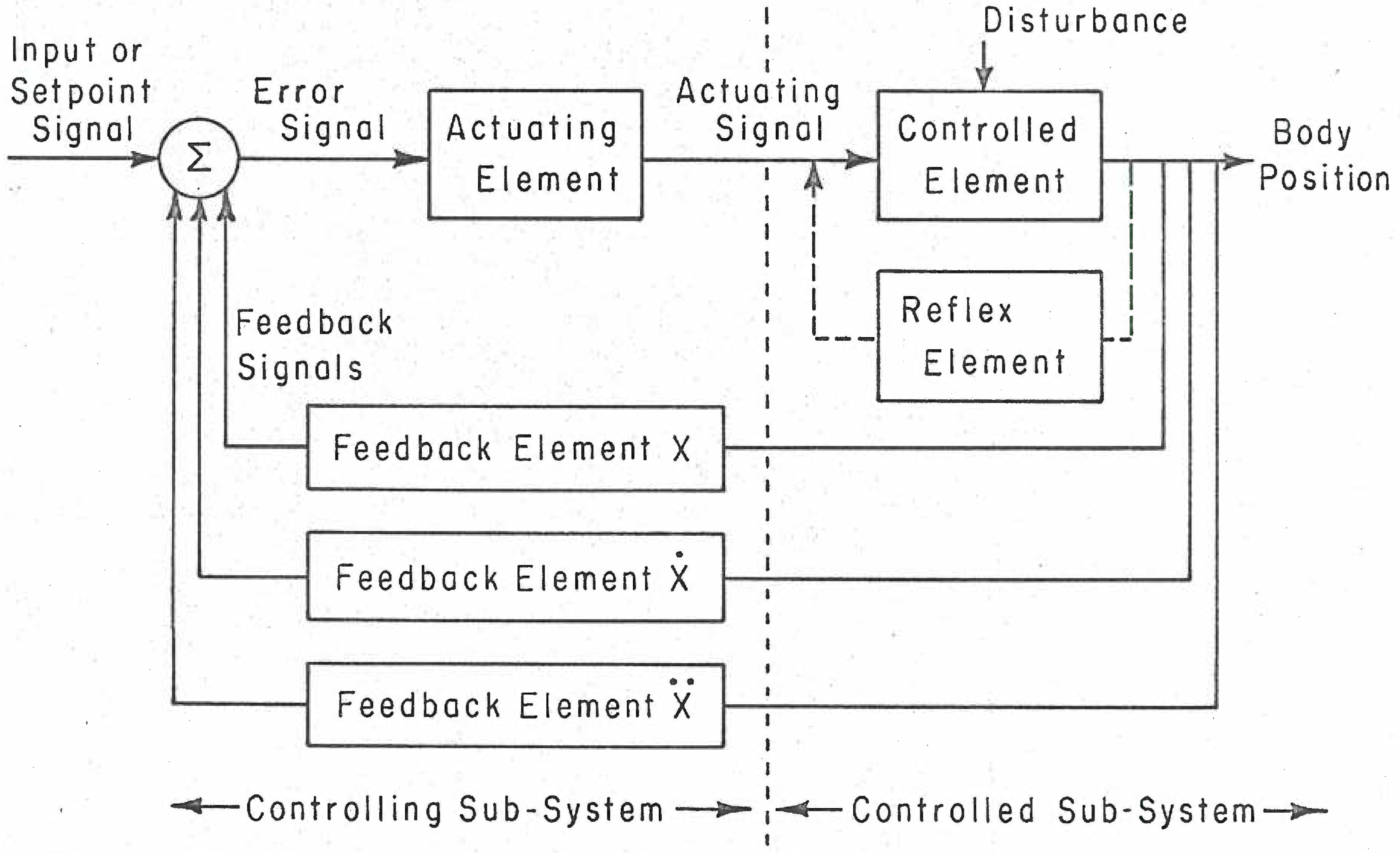
Implications of the Control System Operation

These data may be considered from two different points of view in relation to the normal operations of the postural control system. From the point of view of the block diagram of the control system (Figure 1), the data suggest slight modifications to reflect the observations made here. The other point of view suggests a perspective view of the postural control mechanism as seen operating in the quietly standing animal.

As a part of the introduction to this problem, a block diagram was presented to illustrate one way in which the postural control mechanisms could be conceived. In Figure 1, the varieties of feedback channels were not subdivided into functional or anatomical units, but were lumped into a single element. It is already known from previous work that this is an oversimplification and that, on anatomicofunctional grounds, at least three feedback channels should be shown in such diagrams. The results of this study suggest still another manner for classifying feedback influences using a functional subdivision without anatomical implications. The data imply that steady-state distortions of feedback information were produced by the combined visual and labyrinthine deprivations, but give no evidence of disturbance of feedback signals related to change of position. On these grounds, it seems reasonable to propose that the total feedback operations should be subdivided into three channels on the basis of the type of information processed by the individual channels. Thus, Figure 1 has been modified and presented again as Figure 6. The feedback pathway, in the remodelled form, affords a channel for information pertinent to steady-state position (x), a channel for information related to the rate of change of position ($\dot{x}$, velocity), and a channel for information related to the second derivative of position ($\ddot{x}$, acceleration). The observations reported here indicate that the double sensory deprivations affected only the first of these channels. It is not physiologically inconsistent to suppose that each of the channels identified on anatomicofunctional grounds (somesthetic, visual, and labyrinthine) might be similarly subdivided according to type of information.

From the second point of view, the data, along with direct observations of the animal, indicate that combined visual and labyrinthine deprivations produce very little change in postural stability. The change was so small that it could not be detected by direct observations, but only through the use of statistical techniques. Even with the statistical treatment, the change was barely detectable at the 5% level

Figure 6. A conceptual presentation of the proposed modifications to the control system model illustrated in Figure 1. The feedback elements are functionally categorized to conform to the implications of the data. The data suggest that feedback operations related to position (x) are impaired by the combined sensory deprivation and that feedback operations related to velocity ($\dot{x}$) and acceleration ($\ddot{x}$) remain unchanged.



BLOCK DIAGRAM OF A MODIFIED REGULATORY SYSTEM of confidence, and was manifested in the longitudinal displacements of the center of weight distribution but not in the lateral displacements. Either of two conclusions may be made based upon the fact that the observed change in postural stability was so small. The first conclusion could be that the somesthetic channel is the most important and overriding of the three feedback channels. It was indicated earlier that whereas labyrinthine and visual inputs are important for the control of head position, information from these sources alone could not be expected to reflect accurately the position of other body parts with respect to the supporting surface. Thus, a priori, there is reason for expecting that the experimental design used here might be productive of only minimal alterations in postural stability. This expectation, however, could not be accepted without actual testing. Furthermore, the data do not permit the establishment of a priority rating of the three types of input on the basis of importance. The data only indicate that, in the absence of the two other inputs, the somesthetic channel is capable of maintaining postural stability at near-normal values.

The alternative conclusion could be that the problems presented by the task of quiet standing are so simple as to permit them to be solved without taxing the capacity of the central integrating mechanisms. As mentioned in the introduction and as suggested by the data, each channel has associated with it certain capacities to compensate for the loss of one or two channels. The small change in stability as reflected in the data is a reflection of the capacity associated with the somesthetic channel to handle the instability of posture in the absence of visual and labyrinthine channels. The experimental design of this investigation does not permit further investigation into the nature of these capacities.

These conclusions suggest the necessity for utilizing more serious challenges upon the control system to evaluate the capacity of the integrating system with respect to the feedback channels. Observations of humans (~~3~~2) along with observations of the animals in this experiment suggest that instability caused by feedback deprivations would become more obvious during dynamic testing procedures. Stressing the control system may reveal information about the magnitude of the capacity associated with each channel and help us make a choice between the latter two conclusions.

SUMMARY AND CONCLUSION

The effects of bilateral visual and labyrinthine deprivations on the postural stability of quietly standing dogs have been examined in this study. The animals were required to stand quietly on force plates which provided voltage outputs to enable the recording system to compute and record the longitudinal and lateral displacements of the center of weight distribution as separate indices of stability. Ten trials of five minutes duration were recorded for each of five animals in each of four conditions: normal, blindfolded, labyrinth-deprived, and combined labyrinth-deprived and blindfolded. Recordings of the longitudinal and lateral displacements were sampled for magnitude of deviation from the center baseline. The means of the ten trial means of the center of weight distribution for each condition ($\bar{X}_{\bar{x}}$), variations of the ten trial means within a condition (S.E.), and the average variation of the recording within each trial in a condition ($\bar{X}_{S.D.}$) were computed and tested for differences. The results indicate a very small significant change in $\bar{X}_{\bar{x}}$ and S.E. (longitudinal) after combined visual and labyrinthine deprivations, but no significant increase after single deprivations. There were no significant differences in $\bar{X}_{S.D.}$ (longitudinal or lateral), S.E. (lateral), or $\bar{X}_{\bar{x}}$ (lateral) after single or combined sensory deprivations.

The results have been interpreted on the assumption that quiet standing is achieved through the operations of a feedback regulated control system using the various sensory channels as feedback pathways. The results imply that a steady-state distortion of the feedback information was produced by combined deprivations, but gave no evidence of disturbance of information related to the change of position. It was therefore proposed that the feedback operations be classified functionally on the basis of the type of information processed, namely, position, velocity, and acceleration. The results also suggest that each feedback channel is able to compensate for the loss of one or two other channels.

The minimal changes in stability produced by these deprivations suggest either (1) that for the purpose of the control of quiet standing the somesthetic feedback paths are used to the almost complete exclusion of the visual and labyrinthine inputs, or (2) the problems presented to the control system during quiet standing are too simple to tax the capacity of the system to a significant degree even in the absence of two sources of feedback information.

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Appendix A. Correction Factors for the Longitudinal and Lateral Displacements of the center of gravity.

Because of the difficulty of obtaining equal sensitivities on all four preamplifiers, correction factors were computed for each animal to convert the recorded displacements of the center of weight distribution to actual millimeter displacements. The recorded displacemnts were multiplied by these factors to yield the actual results.

$$\text{Correction factor for longitudinal displacements} = \frac{(PD)\ (CW)}{2\ (WD)\ CD)}$$

PD = longitudinal distance between plates in millimeters

CW = calibration weight in kilograms

WD = weight of dog in kilograms

CD = average calibration deflection in millimeters

$$\text{Correction factor for lateral displacements} = \frac{(PD)\ (CW)}{2\ (WD)\ (CD)}$$

PD = lateral distance between plates in millimeters

CW = calibration weight in kilograms

WD = weight of dog in kilograms

CD = average calibration deflection in millimeters.

Appendix B. Mean and Standard Deviation in Millimeters for Each Trial and the $\bar{X}_{\bar{x}}$, $\bar{X}_{S.D.}$ and S.E. for Each Condition of Dog C-1

	"C"				"B"			
	Longitudinal Displacement		Lateral Displacement		Longitudinal Displacement		Lateral Displacement	
Trials	Means	S.D.	Means	S.D.	Means	S.D.	Means	S.D.
1.	+4.05	2.32	-7.15	1.90	+1.15	2.34	-6.40	2.09
2.	+1.45	3.48	-9.25	0.98	-3.60	2.21	-7.85	1.40
3.	+3.10	1.90	-7.25	0.83	+2.40	1.90	-10.55	2.15
4.	-2.60	1.28	-6.75	1.93	-2.75	2.45	-6.60	2.67
5.	+1.45	1.64	-5.15	2.27	-1.25	2.08	-4.55	1.34
6.	-0.10	1.63	-7.80	2.51	+4.10	1.73	-7.85	1.36
7.	+1.00	1.22	-10.55	1.07	+0.10	1.10	-8.70	2.34
8.	+3.65	1.68	-10.70	0.53	-1.30	1.83	-5.45	1.48
9.	-3.90	1.12	-8.75	1.67	-2.15	1.41	-10.20	2.37
10.	-3.50	0.53	-9.10	0.94	+2.45	1.96	-7.75	1.81
X_{x}	+0.46		-8.25		-0.08		-7.59	
$X_{S.D.}$		1.68		1.46		1.90		1.90
S.E.	2.92		1.75		2.54		1.92	

	"L"				"LB"			
	Longitudinal Displacement		Lateral Displacement		Longitudinal Displacement		Lateral Displacement	
Trials	Means	S.D.	Means	S.D.	Means	S.D.	Means	S.D.
1.	-1.40	4.25	-4.45	3.77	+10.30	2.36	-7.15	0.94
2.	-7.95	1.77	-5.05	2.79	-0.55	2.92	-8.10	0.77
3.	-3.90	4.26	-5.20	3.03	-1.75	4.46	-6.40	0.51
4.	-8.40	1.43	-5.90	0.77	+3.40	1.76	-5.40	3.06
5.	-9.15	1.78	-6.25	2.02	+5.15	4.45	-6.80	1.20
6.	-7.30	2.73	-5.05	1.94	+0.75	2.89	-7.25	1.23
7.	-8.15	2.27	-3.35	3.32	-0.50	1.51	-0.75	1.16
8.	-7.15	2.91	-7.75	2.07	0.00	2.98	-3.65	1.16
9.	-7.95	3.21	-8.30	0.89	-6.05	2.73	-8.30	0.54
10.	-14.60	3.33	-6.25	2.43	-3.60	2.14	-7.95	0.90
X_{x}	-7.59		-5.75		+0.72		-6.17	
$X_{S.D.}$		2.79		2.30		2.82		1.15
S.E.	3.41		1.48		4.62		2.36	

Appendix C. Mean and Standard Deviation in Millimeters for Each Trial and the $\bar{X}_{\bar{x}}$, $\bar{X}_{S.D.}$, and S.E. for Each Condition of Dog C-2

	"C"				"B"			
	Longitudinal Displacement		Lateral Displacement		Longitudinal Displacement		Lateral Displacement	
Trials	Means	S.D.	Means	S.D.	Means	S.D.	Means	S.D.
1.	+4.40	1.70	+5.10	1.37	+1.15	0.89	+6.75	0.59
2.	+4.55	1.36	+8.30	0.89	+4.65	0.92	+3.20	0.82
3.	+7.25	1.32	+7.60	0.32	-2.70	0.92	-3.75	0.98
4.	+2.25	0.92	+4.90	0.70	+2.40	0.40	-3.30	1.20
5.	+7.20	1.95	+10.80	1.58	+3.75	1.21	-2.80	1.42
6.	+4.95	2.55	+6.55	0.80	-0.80	0.75	+4.05	0.44
7.9	+8.95	0.64	+8.70	1.89	+1.60	0.32	+6.85	0.41
8.	+7.10	0.77	+10.05	0.83	+3.75	1.48	-3.70	0.35
9.	+6.95	2.90	+7.10	1.45	-1.65	1.76	-1.00	0.62
10.	+8.95	2.21	+4.40	1.58	+2.65	0.47	-3.10	0.46
$\bar{X}_{\bar{x}}$	+6.25		+7.35		+1.48		+0.32	
$\bar{X}_{S.D.}$		1.63		1.14		0.91		0.73
S.E.	2.15		2.17		2.47		4.41	

	"L"				"LB"			
	Longitudinal Displacement		Lateral Displacement		Longitudinal Displacement		Lateral Displacement	
Trials	Means	S.D.	Means	S.D.	Means	S.D.	Means	S.D.
1.	+6.80	1.18	-1.10	3.04	+9.85	1.83	+4.05	0.55
2.	+9.80	0.98	-1.35	2.53	+8.25	1.38	+1.30	3.35
3.	+8.40	0.65	-0.60	0.93	+12.50	2.64	+5.95	1.23
4.	+8.15	1.16	+3.95	5.56	+17.30	0.75	+4.55	0.83
5.	+10.60	1.26	+3.20	2.31	+13.55	2.53	-1.40	1.07
6.	+11.75	0.48	+0.95	1.21	+15.25	2.39	+6.15	0.91
7.	+8.25	3.39	+1.30	1.38	+14.25	1.48	+12.15	0.58
8.	+12.30	2.59	-5.20	0.93	+17.00	1.29	-2.50	2.31
9.	+8.70	3.47	-5.65	2.81	+1.60	3.54	-5.60	2.16
10.	+8.05	0.96	-2.25	1.36	+6.10	4.73	+5.55	1.54
$\bar{X}_{\bar{x}}$	+9.28		-0.68		+11.56		+3.02	
$\bar{X}_{S.D.}$		1.61		2.21		2.26		1.45
S.E.	1.77		3.18		5.07		5.15	

Appendix D. Means and Standard Deviations in Millimeters for Each Trial and the $\bar{X}_{\bar{x}}$, $\bar{X}_{S.D.}$, and S.E. for Each Condition of Dog C-3

	"C"				"B"			
	Longitudinal Displacement		Lateral Displacement		Longitudinal Displacement		Lateral Displacement	
Trials	Means	S.D.	Means	S.D.	Means	S.D.	Means	S.D.
1.	+8.60	2.73	+5.25	1.03	+11.35	2.19	+4.30	2.86
2.	+7.20	3.08	+2.80	3.42	+12.75	2.08	-2.55	2.57
3.	+5.05	2.02	+7.25	1.63	+12.20	2.48	-0.10	0.94
4.	+3.65	2.43	+1.25	2.09	+13.15	2.11	-0.25	2.97
5.	+3.75	3.87	+7.90	3.55	+11.75	1.96	-0.90	0.94
6.	+6.70	4.18	+2.45	3.30	+12.30	1.97	+3.75	1.75
7.	+4.90	2.89	+0.75	2.15	+11.35	2.89	+0.45	1.96
8.	+2.95	2.09	+3.95	1.14	+7.30	1.00	+5.85	2.74
9.	+4.70	3.22	+1.55	2.13	+16.50	1.47	+1.00	1.73
10.	+5.85	2.08	+4.05	2.16	+7.75	2.41	+4.75	1.25
$\bar{X}_{\bar{x}}$	+5.33		+3.72		+11.74		+1.63	
$\bar{X}_{S.D.}$		2.85		2.26		2.05		1.97
S.E.	1.76		2.46		2.63		2.81	

	"L"				"LB"			
	Longitudinal Displacement		Lateral Displacement		Longitudinal Displacement		Lateral Displacement	
Trials	Means	S.D.	Means	S.D.	Means	S.D.	Means	S.D.
1.	+10.75	1.35	-0.40	1.12	+7.55	2.97	+15.15	3.31
2.	+13.15	3.75	-1.15	1.99	+17.45	2.32	-3.90	2.80
3.	+7.40	4.39	+1.75	1.16	+14.20	2.43	-2.70	1.16
4.	+11.65	0.71	-1.75	1.23	+16.20	3.24	+3.45	3.50
5.	+10.75	0.68	+1.00	0.75	+9.45	2.23	+13.95	2.46
6.	+12.30	1.86	-2.95	0.68	+16.80	4.60	+5.65	4.52
7.	+6.15	0.78	-3.05	3.05	+7.40	3.56	+5.45	4.56
8.	+8.70	1.58	+0.70	3.03	+13.30	2.19	+7.65	5.20
9.	+11.30	2.92	-3.45	1.19	+12.75	5.35	+5.95	1.84
10.	+9.85	0.88	+0.45	1.36	+13.60	5.23	+4.40	2.84
$\bar{X}_{\bar{x}}$	+10.20		-0.88		+12.87		+5.50	
$\bar{X}_{S.D.}$		1.89		1.56		3.41		3.21
S.E.	2.20		1.87		3.64		6.06	

Appendix E. Mean and Standard Deviation in Millimeters for Each Trial, and the $\bar{X}_{\bar{x}}$, $\bar{X}_{S.D.}$, and S.E. for each Condition in Dog C-4

	"C"				"B"			
	Longitudinal Displacement		Lateral Displacement		Longitudinal Displacement		Lateral Displacement	
Trials	Means	S.D.	Means	S.D.	Means	S.D.	Means	S.D.
1.	+6.20	3.00	+6.70	1.65	+7.35	4.60	+4.35	1.89
2.	+8.25	3.71	+0.70	0.92	+2.90	4.48	-0.25	1.13
3.	+5.05	4.16	+9.00	2.98	+2.55	4.92	-5.30	2.00
4.	+2.05	2.25	+10.55	3.08	+2.55	2.92	-2.35	1.37
5.	+4.00	3.51	+0.60	1.05	+2.90	8.05	+3.60	1.54
6.	+4.35	3.23	+2.45	2.06	-0.30	5.24	+1.85	2.85
7.	+3.85	3.35	-1.60	3.08	-6.75	4.04	+0.70	1.43
8.	+3.30	2.87	+3.30	2.57	-3.65	3.51	+0.30	4.21
9.	+6.85	4.82	+5.70	2.31	+2.90	4.75	+4.55	2.89
10.	+6.95	4.63	+4.80	4.62	-5.15	5.25	+3.00	1.55
$\bar{X}_{\bar{x}}$	+5.08		+4.22		+0.53		+1.04	
$\bar{X}_{S.D.}$		3.55		2.43		4.77		2.09
S.E.	1.93		3.87		4.40		3.13	

	"L"				"LB"			
	Longitudinal Displacement		Lateral Displacement		Longitudinal Displacement		Lateral Displacement	
Trials	Means	S.D.	Means	S.D.	Means	S.D.	Means	S.D.
1.	+6.70	4.55	+5.65	2.41	+2.35	3.07	+4.25	1.45
2.	+4.65	3.95	+5.05	2.81	+10.10	2.42	+7.50	0.97
3.	+4.25	3.96	+4.85	1.16	+6.80	0.92	+6.20	2.97
4.	+3.55	4.09	+5.10	1.76	+8.45	3.48	+7.95	2.15
5.	+2.25	5.97	+7.05	2.12	-0.35	2.28	+7.65	1.73
6.	+2.70	3.41	+6.50	2.60	+3.45	3.38	+4.70	2.21
7.	+5.75	2.27	+9.75	1.32	+9.90	3.41	+5.00	3.65
8.	+3.50	5.94	+6.20	2.80	+8.00	2.79	+6.05	2.29
9.	+7.85	3.23	+4.20	1.06	-2.20	1.84	+6.25	4.05
10.	+6.30	3.02	+6.50	1.87	+4.85	2.16	+6.20	2.85
$\bar{X}_{\bar{x}}$	+4.75		+6.08		+5.14		+6.17	
$\bar{X}_{S.D.}$		4.04		1.99		2.58		2.43
S.E.	1.84		1.56		4.26		1.26	

Appendix F. Mean and Standard Deviation in Millimeters for Each Trial and the $\bar{X}_{\bar{x}}$, $\bar{X}_{S.D.}$ and S.E. for Each Condition of Dog C-5

	"C"				"B"			
	Longitudinal Displacement		Lateral Displacement		Longitudinal Displacement		Lateral Displacement	
Trials	Means	S.D.	Means	S.D.	Means	S.D.	Means	S.D.
1.	+3.60	1.88	-1.75	1.83	-4.10	1.10	-1.85	1.65
2.	+2.15	2.00	-1.50	1.33	-0.70	1.30	+4.45	2.18
3.	+8.60	4.14	-1.45	1.50	-0.80	1.37	+0.30	1.03
4.	+5.80	2.55	-2.55	2.38	-1.85	1.99	-2.05	2.02
5.	+10.05	2.30	+1.60	0.46	-2.50	1.87	-2.50	0.97
6.	+6.30	2.98	-2.30	1.16	-17.65	1.41	+1.95	1.14
7.	+6.05	5.80	-0.35	1.45	-1.10	1.26	-2.35	2.38
8.	+3.40	2.41	-0.90	0.77	-0.85	1.87	-3.30	2.24
9.	+13.40	1.79	-2.65	1.22	-2.50	2.20	-2.45	1.36
10.	+10.50	3.63	-0.80	0.68	-4.10	1.71	-2.05	1.62
$\bar{X}_{\bar{x}}$	+6.95		-1.26		-3.61		-0.98	
$\bar{X}_{S.D.}$		2.95		1.28		1.61		1.66
S.E.	3.58		1.26		5.09		2.46	

	"L"				"LB"			
	Longitudinal Displacement		Lateral Displacement		Longitudinal Displacement		Lateral Displacement	
Trials	Means	S.D.	Means	S.D.	Means	S.D.	Means	S.D.
1.	+16.55	1.70	+0.40	1.19	-10.20	3.34	+1.50	2.87
2.	+10.60	3.06	-0.70	1.87	-8.55	7.14	+2.55	3.85
3.	+10.30	2.75	-0.30	1.45	-8.35	6.23	+1.85	1.87
4.	+17.65	0.53	+2.35	0.97	-3.75	4.33	-1.60	2.15
5.	+16.80	3.08	-0.10	1.05	-5.05	5.11	+2.35	1.43
6.	+17.25	2.98	+1.75	0.95	-6.55	4.58	+3.30	1.84
7.	+14.15	3.17	+19.00	2.87	-8.25	3.53	+0.05	2.63
8.	+6.90	1.76	-1.20	0.97				
9.	+10.35	1.76	+0.45	0.95				
10.	+17.70	1.75	-0.75	0.59				
$\bar{X}_{\bar{x}}$	+13.82		+1.90		-7.24		+1.43	
$\bar{X}_{S.D.}$		2.25		1.28		4.89		2.37
S.E.	3.95		6.08		2.24		1.67	