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A static analysis of quadruped biomechanics, combined with observations of longitudinal postural movement, has revealed important functional attributes of the postural control system. Since posture is an outward expression of central nervous system (CNS) behavior, these results may contribute to an understanding of integrative functions of the CNS.

Beginning from a simple biomechanical model of the dog, the properties of the legs are examined to show how the end-reaction forces on a given foot can be controlled by the muscles in the corresponding leg. During quiet standing, the distribution of effort among the muscles can be modified by small body movements or by pushing horizontally with equal force at the anterior and posterior feet. A measured "bias force" of about 1/2 kg per foot indicates that the dog attempts to spread his feet longitudinally and thereby achieves a comfortable distribution of the effort required to stand. When the legs are

used for horizontal thrusting the muscle tensions must be adjusted so that a coordinated movement will result. Certain problems of mechanical stability are reduced to a simple mathematical condition and a method is given to determine effective muscle action for producing horizontal thrusts without losing stability.

Postural reactions of several trained dogs have been observed during and following abrupt longitudinal displacements of the supporting surface. The initial force response, which appeared to arise from sensory stimuli in each foot, was pulsatile and occurred before voluntary action could have developed. The "reflex like" character of this response lends support to current theory regarding "program" responses in motor control processes.

The functional properties of the anterior and posterior limbs are separately examined in terms of the anatomical structure. The anterior limbs are clearly very stable and well suited for supporting weight whereas the less stable posterior limbs are highly agile and adapted for horizontal thrusting.

Analysis of Postural Dynamics in the Dog

by

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ACKNOWLEDGMENT

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LIST OF SYMBOLS

F_h	kg	Longitudinal bias force
F_{ha}	kg	Longitudinal force at the anterior feet
F_{hp}	kg	Longitudinal force at the posterior feet
F_{va}	kg	Vertical force at the anterior feet
F_{vp}	kg	Vertical force at the posterior feet
L_a	cm	Effective length of the anterior leg
L_{1a}	cm	Effective length of the humerus
L_{2a}	cm	Effective length of the radius and forepaw
L_{3a}	cm	Effective length of the forepaw
L_p	cm	Effective length of the posterior leg
L_{1p}	cm	Effective length of the femur
L_{2p}	cm	Effective length of the tibia and hindpaw
L_{3p}	cm	Effective length of the hindpaw
T_{1a}	kg-m	Torque at the shoulder
T_{2a}	kg-m	Torque at the elbow
T_{3a}	kg-m	Torque at the wrist
T_{1p}	kg-m	Torque at the hip
T_{2p}	kg-m	Torque at the knee
T_{3p}	kg-m	Torque at the ankle
y	cm	Body position
y_a	cm	Horizontal distance between the shoulder pivot and respective foot contact

y_p	cm	Horizontal distance between the hip pivot and respective foot contact
W	kg	Body weight
δ_a		A determinant
δ_p		A determinant
θ_{1a}	deg	Effective inclination of the humerus
θ_{2a}	deg	Effective inclination of the radius and forepaw
θ_{3a}	deg	Effective inclination of the forepaw
θ_{1p}	deg	Effective inclination of the femur
θ_{2p}	deg	Effective inclination of the tibia and hindpaw
θ_{3p}	deg	Effective inclination of the hindpaw
φ_a	deg	Effective inclination of the anterior leg
φ_p	deg	Effective inclination of the posterior leg

ANALYSIS OF POSTURAL DYNAMICS IN THE DOG

I. INTRODUCTION

Postural Control

Stable posture in a quadruped results from the continuous, coordinated adjustment of muscle tensions affecting the position of all four limbs; it does not represent any form of static rigidity. Hence, quiet standing is a dynamic process which involves the regulated migration of the body center of gravity within confined limits established by the individual animal (Brookhart et al., 1965). Whenever external influences force the body out of its nominal posture or a major change in posture is desired, a more intense effort may be required to maintain or regain acceptable posture. Regardless of intensity, the basic mechanisms employed to effect postural movements are very similar to those observed during quiet standing.

In any postural task, whether it be the maintenance of a specific stance, the correction of a postural distortion or some form of locomotion, the central nervous system (CNS) must be continuously active to facilitate proper adjustments of muscle tensions. Thus, the posture is an outward expression of the dynamic, coordinated (integrated) functioning of the CNS. Observations of postural activities may afford a useful framework for studies of the integrative processes

occurring within the CNS.

Concisely stated, the objective of this work is to analyze the mechanical interaction between a quadruped body and the external world in a way which will expose characteristics of the neuromuscular mechanisms involved in coordinated physical movement. The process of engineering analysis which has been followed to reach this objective can be viewed as an essential step toward a suitable model of the postural control system. Although the complete analysis must include thorough discussions of postural mechanics and controlled experiments, certain results of the postural experiments may be presented in summary form before the extended analysis of postural mechanics is undertaken.

A Postural Experiment

The general aspects of postural movement can be easily treated with only a few simple notions. In all postural experiments which will be reported, the only mechanical interactions between the dog and his environment were the vertical and horizontal forces at each foot. The collective effect of these forces is to support the body weight and to thrust the body horizontally when movement is required. We will always consider that these forces are acting from the environment (supporting surface) to the dog. A positive force will be directed upward for the vertical component and headward for the horizontal

component. Thus, a positive force will tend to accelerate some part of the body either upward or headward, respectively.

Movement of the body can occur only when the forces at the feet are somehow coupled to the body through the legs. Clearly, if the muscles in a leg are relaxed and limp, a force acting on the foot will accelerate the leg itself with very little effect on the body or other limbs. If the leg becomes stiff because of muscle action, it may act both as a supporting strut under the body and as a lever between the foot contact and the body, thus coupling a sizeable force from the support surface to the body. These forces can exist only when the action of a muscle stiffens the leg in opposition to either friction or contact pressure at the foot.

Although the conventions chosen are intuitive for considering mechanical dynamics, they are somewhat confusing when viewing the dog as the active agent in determining the nature of various forces being applied to his feet. For general purposes, it is sufficient to consider each leg as a combination of jointed strut and lever whose elastic parameters are controlled by CNS commands. The CNS can exert an indirect control over all forces acting from the environment to the dog by continuous modification of the elastic parameters in response to the sensory inputs.

Our concern in conducting a postural experiment is to induce the dog to move his body in some regular fashion without lifting his feet.

The fact that a dog can indeed control his posture quite accurately and with uniform success has been established by Brookhart et al. (1965), Mori and Brookhart (1968) and Brookhart, Mori and Reynolds (1970). The first of these reports establishes the character of quiet standing while the remaining two deal with the recovery of correct posture following a rapid movement of the support surface. The dogs used in these studies and in the current experiments were selected only on the basis of temperament and size. In general, any medium sized dog of a mild nature will perform acceptably after a relatively short training period.

The basic facility used for the above experiments as well as those which are reported here has been a hydraulically actuated platform capable of abrupt horizontal movement in the longitudinal direction. Figure 1 is a schematic diagram showing the table system with the dog standing in a typical quiet posture. In this condition, the sum of horizontal forces at the feet is nearly zero and the sum of the vertical forces is equal to the body weight. When the table is moved abruptly under the body, the force equilibrium is destroyed and both horizontal and vertical movements must occur to return the body to its preferred posture. The central hypothesis of these experiments has been that the behavior of the dog during this recovery period is an expression of the integrated function of the CNS. The exact nature of the movement is determined by the combined biomechanical and

neuromuscular efforts of the dog.
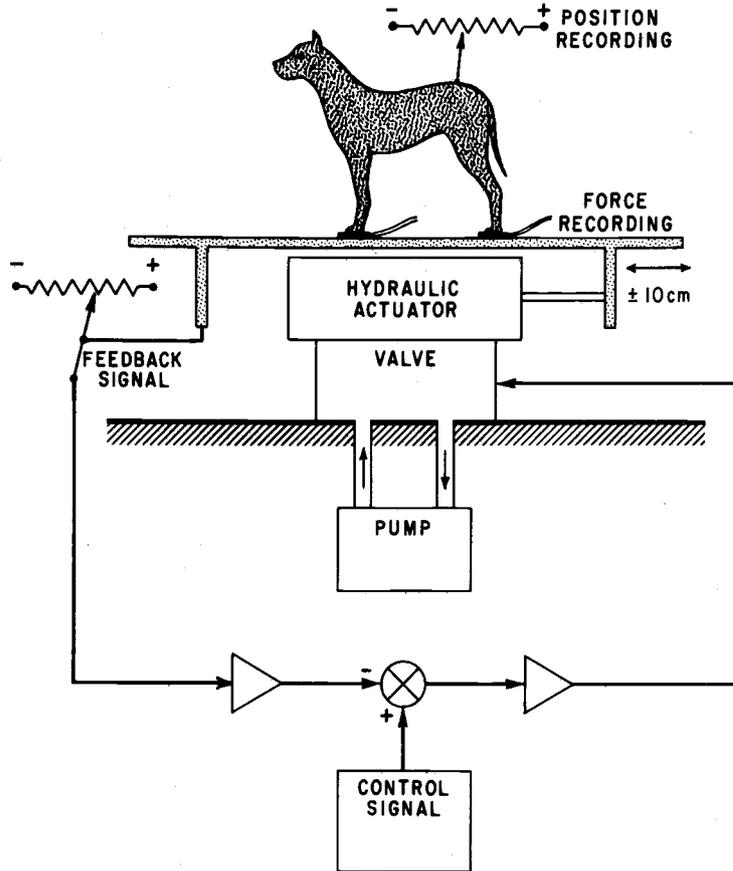
Figure 1. Schematic representation of the table system. The plat-
form which supports the animal is shown in sectional view.
Control of the platform position was achieved with a
hydraulic servo system.

To investigate the range of behavior which the dog can produce,

table movements of a wide variety were used. Those which yielded

the most significant results can be divided into two groups identified

as short and long ramps. The short ramps used were under 100 ms in

duration and less than 5 cm in magnitude. A typical long ramp was 180 ms in duration and 10 cm in magnitude. The peak acceleration of the table was limited by slipping of the dog's feet rather than the hydraulic capacity of the system. Generally speaking, an acceleration of 30 m/s^2 during short movements could be tolerated without losing contact on one or more feet.

A block diagram of the data acquisition and processing systems is shown in Figure 2. During a recording session with a dog, the movements of the table were controlled with a prerecorded signal which was reproduced by the FM recorder while the force and position signals were simultaneously recorded for time periods which ranged from 8 to 20 minutes. After a recording session was complete, the data were reduced by digitizing the recorded responses over a period of about 2.5 seconds at each table movement, starting from a prerecorded trigger signal which slightly preceded the onset of the recorded table movement. The signals were all digitized at a rate of 100 samples per second so that a maximum frequency component of 20 Hz could be very well reproduced. The behavior of the dog between the digitized sections could be determined by visual inspection of the strip-chart records which were originally used to monitor each recording session. The data acquisition equipment is further described in Appendix A. The numerical method used to calculate the body velocity of the dog is discussed in Appendix B.

Experiment Site

| Position and Force Transducers and Table Control as per Figure 1 |

Table Control Signal

Data Channels

Data Recording

| Analog FM Recorder |

| Strip-Chart Monitor |

A.   Data Acquisition

Playback

| Analog FM Recorder |

Digitization; Reduction

| EAI 690 Hybrid Computing System |

Bulk Storage

| Digital Magnetic Tape |

Data Retrieval

| Digital Magnetic Tape |

Processing

| EAI 690 or CDC 3300 |

Plotting

| Graphical Output |

B.   Data Processing

Figure 2.   Block diagram of the data handling system.

Before introducing several examples of typical response curves, we should observe that a quantitative description of the force responses has not been necessary to establish any of the major conclusions which are presented. The most important results follow either from the timing of various force manifestations or from the general shape of the force curves. For this reason, it has not been necessary to average large numbers of responses in order to establish the characteristics of the data which have been examined and no arguments have been based on the accuracy of the measurement equipment. There is no attempt to say that the quantitative characteristics of the data are unimportant. At this time, however, the analysis which is given in Chapter II has not raised any questions which require a quantitative answer.

Survey of Response Data

The first data records to be considered are the responses to a headward-tailward pair of 3.6 cm, 100 ms ramps which are shown in Figure 3. During the period of table movement, the legs pivoted quite freely around the hip and shoulder joints without any sign of significant muscular resistance and only minor body movements. The records of longitudinal horizontal force first show pulses which were associated with the starting and stopping accelerations experienced by the feet and legs. At about 100-130 ms after the onset of table movement, a
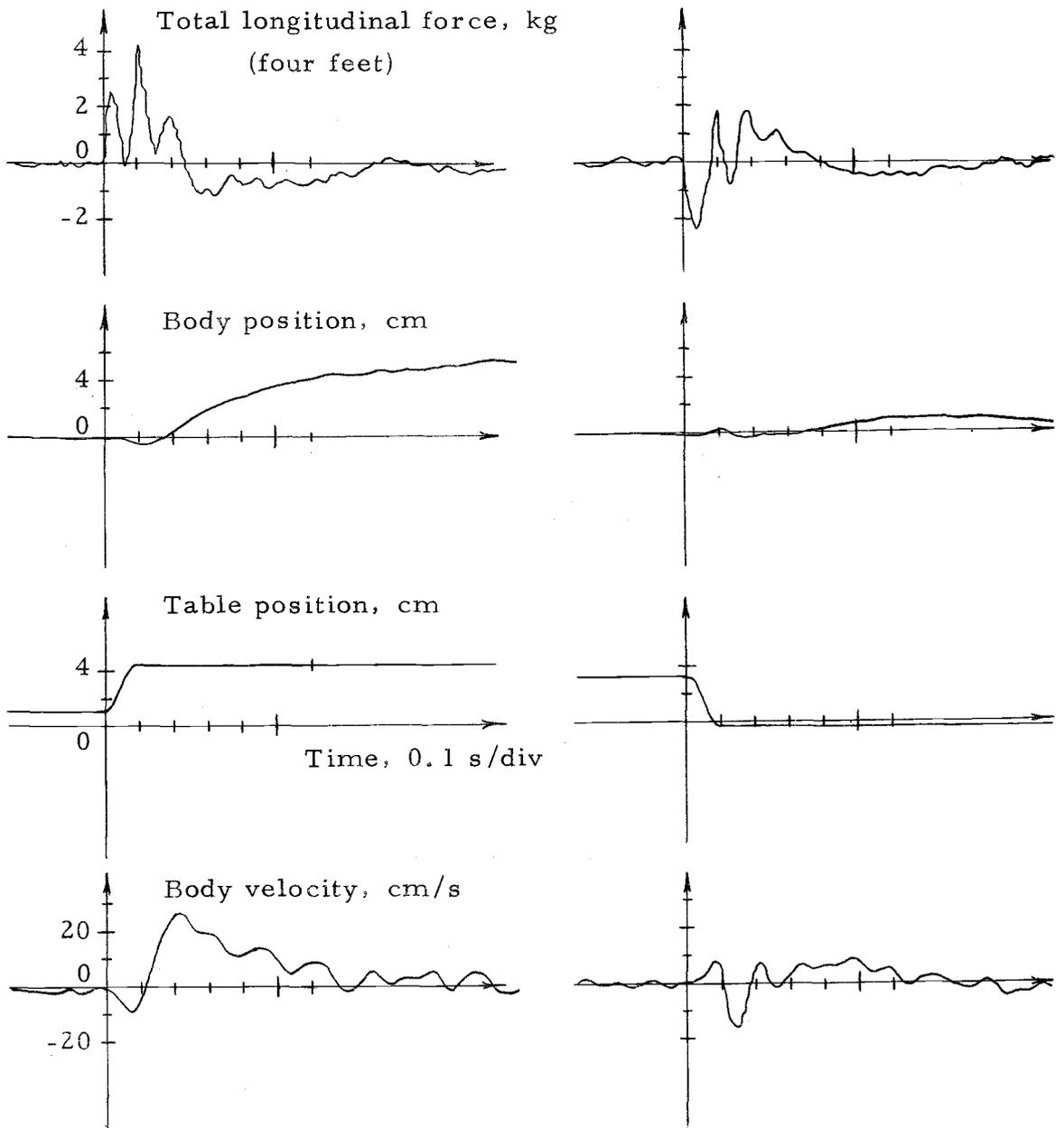
Figure 3. Typical position and force responses to a short ramp
displacement for Dog 8450. The 6 Hz (approximate) ripple
in the force curves is caused by panting.

force pulse in the direction of the initial acceleration generally appeared. Although the appearance and magnitude of this pulse depended on the particular dog and unidentified factors, it was always directed so as to cause the body to follow the table for both headward and tailward movements. Forces appearing in the range of 150-500 ms were much less regular than those appearing earlier. In the case of headward movements with highly experienced animals, a forward acting force generally occurred at about 200 ms. Tailward movements also stimulated a forward acting force in the same time period. The function of forces acting during this time period was to speed the recovery from a headward displacement and to slow the recovery from tailward displacement. For tailward movements, the body velocity at the time of this pulse was tailward and increasing; the force would often reverse the direction of movement. Recovery of desired posture following headward movements was generally more rapid than for tailward and sometimes involved considerable overshoot. After about 500 ms, all force manifestations subsided to low levels typically observed during quiet standing even though the body might still be far from its nominally "correct" position relative to the feet.

Figure 4 shows responses for both headward and tailward long ramps of about 10 cm magnitude and 180 ms duration. In these records the accelerating forces which swing the legs under the body peaked at about 40 ms. The acceleration peaks are rapidly followed by forces in
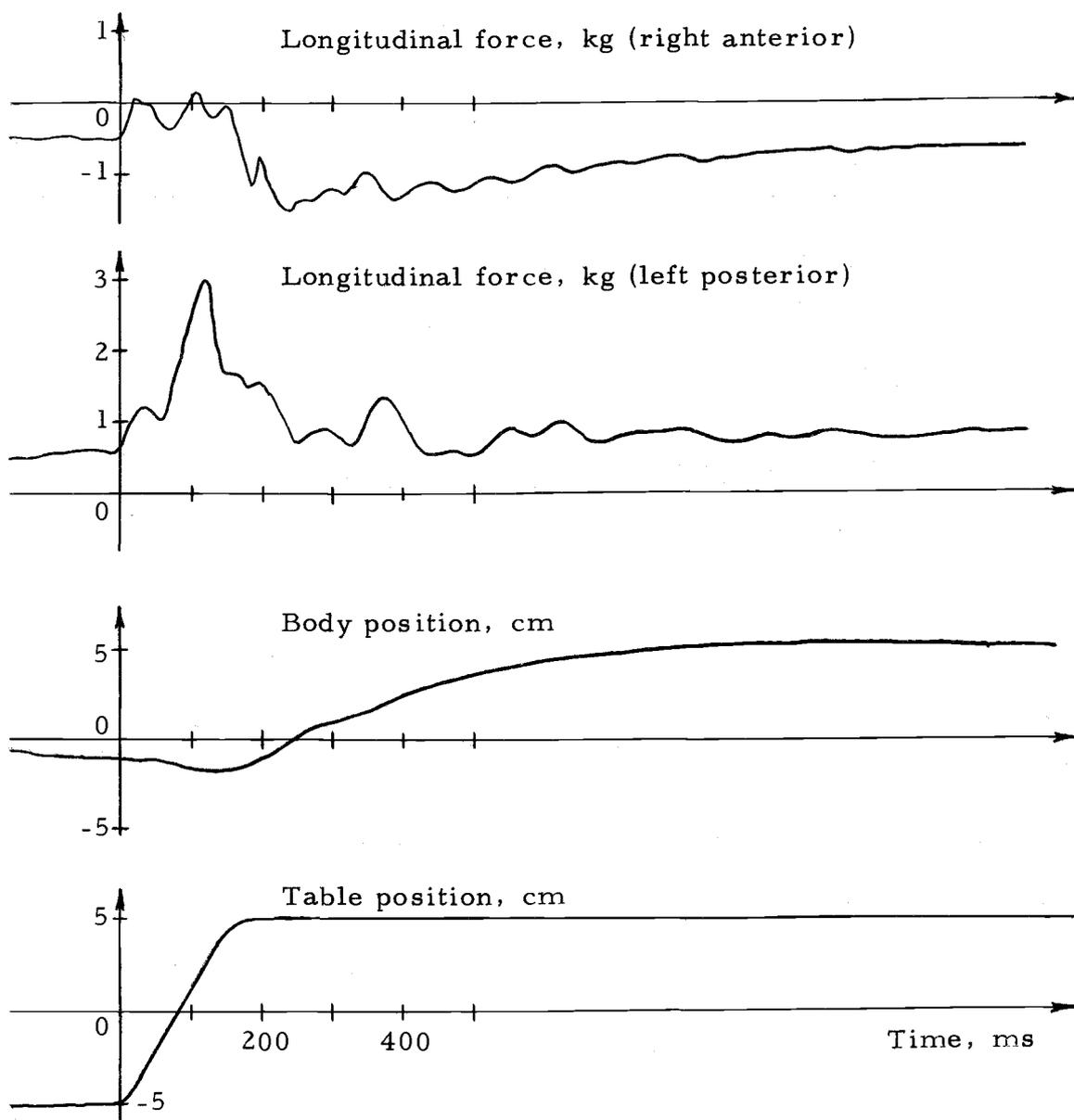
A. Headward movement, Dog 8450

Figure 4. Typical position and force responses to long ramp displacements for Dog 8450.

Longitudinal force, kg (right anterior)

Longitudinal force, kg (left posterior)

Body position, cm

Table position, cm

Time, ms
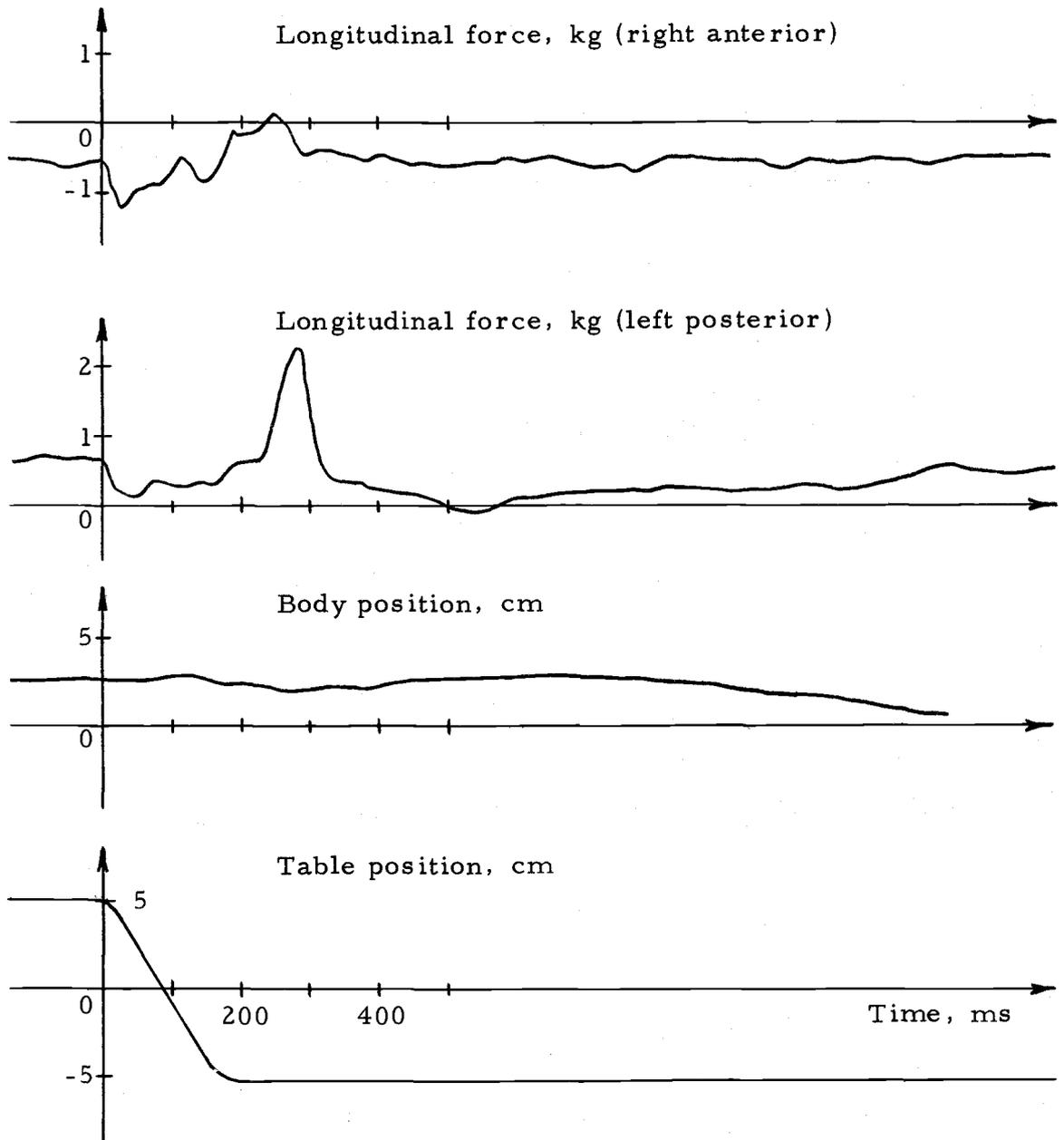
B.   Tailward movement, Dog 8450

Figure 4.   Continued.

the direction of the table movement which again peak at about 100-130 ms. When the table stopped at end of a headward movement, the forces decreased rapidly, coming close to resting levels after about 100 ms. The quiet period lasted for another 100 ms and was terminated by a forward force pulse which peaked about 200 ms after cessation of the table movement. Tailward ramps followed a similar pattern until the cessation of table movement. About 100 ms after the table stopped, there was a major forward acting force pulse which arrested the body's tendency to follow the table in a tailward direction.

At this point we can extract some generalizations from what has been given above. The most elementary result is that mechanical inertia forces are always associated with the starting and stopping of the legs as they conform to the table movement. Although the foot pads doubtlessly allow rocking and elastic stretch, the mechanical coupling properties between the foot and its support are suitably represented by a frictionless pivot at the center of pressure for each foot. (The center of pressure will usually be called the contact point.)

Following the initial acceleration forces, the second class of forces are those which peak in the range of 100-130 ms after the onset of table movement. The magnitude of these forces is irregular for unknown reasons, but the direction is consistently the same as the table movement. These forces are of physiological origin and may result from a reflex-like behavior, possibly corresponding to what has

been called the "functional stretch reflex" in man (Melvill Jones and

Watt, 1971). Forces occurring later than 200 ms seem dependent on a

number of conditions which suggest that they can be attributed to

voluntary actions originating in higher centers of the CNS as the dog is

able to assess his current postural condition.

These results are somewhat different from what might have been

expected in several important ways. There is no evidence of a signifi-

cant contribution from the classical stretch reflex. (This reflex

causes a muscle to contract forcefully in response to stretching. A

common manifestation is the knee-jerk test often included in a physical

examination. See Mountcastle [1968, p. 1733ff] .) Dog 7772 seemed

not to produce any noticeable muscle action following the virtual step

displacements, resulting in force records that are almost completely

attributable to starting and stopping forces which move the legs in a

passive swing under the body. The highly experienced dogs moved

more slowly than the newer animals and were particularly unwilling to

develop a rearward velocity. Rearward movements of the body were

often resisted to the point of overcorrection, thus producing much

slower corrections after rearward table movements. Body movements

were initiated by pulses of force rather than sustained effort. In

quiet standing, there was a significant forward directed force on each

posterior foot which was opposed by equal rearward acting forces on

the anterior feet. Quiet standing and slow body movements were

controlled by continuous adjustment of these forces.

Definition of Terms

Because every reader has had extensive experience with the
postural behavior of his own body, there are many facts concerning
body movement which are well known but not often expressed. The
terms defined below have been particularly useful when analyzing the
nature of a postural system (a dog on the table as in Figure 1) or when
examining the stimulus-response behavior of the different animals
used. Although many of these terms will not be used until Chapter
III, they have been included here for tutorial purposes in the hope that
the reader can describe his own intuitive concepts about body move-
ment in more precise terms than would normally be encountered.

Foot contact point--the center of pressure of the foot on a supporting
surface

Body--the collected weight (mass) of the dog supported at the shoulders
and hips with a center of gravity located behind the shoulders
about one-third the distance to the hips

Body position--the location of the body center of gravity relative to
the foot contacts

Body movement--longitudinal displacement of the body center of
gravity

Posture--the current description of animal stance as specified by

    selected joint angles

Command posture--an erect posture which the dog is trained to repli-

    cate and sustain under command

Postural movement--changes in posture

Stimulus--an action which causes directly or induces a rapid change in

    posture

Postural response--the pattern of postural movements which follow an

    external stimulus

Postural distortion--a deviation from the nominal command posture

Physiological response--force (tension) patterns in assorted muscles

    resulting from CNS activity following an external stimulus

Force response--the pattern of force changes at each foot which

    results from a particular combination of postural and physiologi-

    cal responses

Reaction force--any external force which acts on the dog, particularly

    at the foot contacts

Horizontal bias force--the sum of horizontal reaction forces on the

    anterior feet which is opposed by an equal and opposite sum of

    forces on the posterior feet

Force of physiological origin (FPO)--reaction forces whose magnitude

    and direction are determined by muscle activity at each joint of

    a leg

Class 1 force--reaction force perturbations attributed to the effects

    of linear and/or rotational inertia or the effects of friction

Class 2 force--reaction force perturbations which occur between

    70-150 ms after an identifiable external stimulus, also called an

    early FPO (EFPO)

Class 3 force--reaction force perturbations which occur at least 150

    ms after an identifiable external stimulus, also called a late

    FPO (LFPO)

II. POSTURAL MECHANICS

Introduction

The mechanical analysis of a dog standing erect on a plane sur-
face can begin from the basic notions of a postural task and a postural
system. After restricting the tasks to be performed and specifying
the system, the dog will be reduced to a mechanical model suitable
for conceptual discussion of limited postural movement.

The Postural Task

For our purposes, postural tasks may be divided into two groups:
1) those accomplished while all four feet are contacting the support
plane and 2) various forms of locomotion which require movement of
the feet. In all tasks accomplished without changes in foot placement,
the body center of gravity, when projected onto the support plane
(parallel to the acceleration vector), must not move outside the
quadrangle obtained by connecting the contact points of adjacent feet.
Whenever the center of gravity is to be moved outside this region,
locomotion is required. Normal locomotion may be described as the
rhythmic movement of the feet from one earth contact to another while
supporting the body in horizontal motion. In many respects, the
mechanisms employed during locomotion are essentially the same as
those required to produce any kind of physical movement. Since

locomotion would introduce experimental complications, it is excluded

from further consideration.

The fixed-foot tasks performed by the dog clearly must be

restricted to those which can be accomplished without slipping on the

support surface and without lifting a foot from its respective force

measurement device. The general task chosen was to regain the

"command" posture whenever this posture was distorted by a longi-

tudinal movement of the support surface. The particular movements

selected were virtual steps, ramps and sinusoids or combinations

thereof.

The Postural System

A postural system for considering any postural task may be

divided into four subsystems as follows: 1) the external environment

as described by spatial relationships, mechanical interaction forces at

foot contact points and gravitational forces, 2) the animal's mechani-

cal structure and body weight, 3) the mechanical actuators or muscles

and 4) the muscle control system as a subsystem of the CNS. The

first two items are generally classed as biomechanical and the second

two are neuromuscular. The functional properties of these subsystems

are considered below.

The external environment (a moveable table surface) is simply

an unyielding surface which will resist any reasonable force applied to

it. As explained in Chapter I, forces are considered positive when acting from the table to the dog's foot in a forward (or upward) direction.

The legs are the truly interesting part of the biomechanical system. Each leg consists of three essentially rigid members (bones) connected by two flexible joints which may be approximated by frictionless pivots. At each joint, a component of the axial force in one bone can be transmitted to the others as a function of the joint geometry. We will assume that forces may be applied to a bone only at joints or at the foot contact points.

A simplified dog skeleton (in lateral symmetry) and certain muscles are shown in Figure 5. The stance of the skeleton is believed to be approximately the same as the command posture. Since most of the leg bones are significantly inclined to the vertical, axial forces in adjacent bones are not efficiently transmitted across any of the joints. Therefore, quiet standing can be accomplished only through significant muscular effort.

To determine a geometrical model of the skeleton we need to locate the centers of rotation and pressure for each of the joints and for the contact points of the feet. Any hope of doing this very accurately seems unreal, since the distribution of stresses at a joint cannot be known. It is also not clear that the center of pressure and the center of rotation will ever coincide, since this is certainly not a
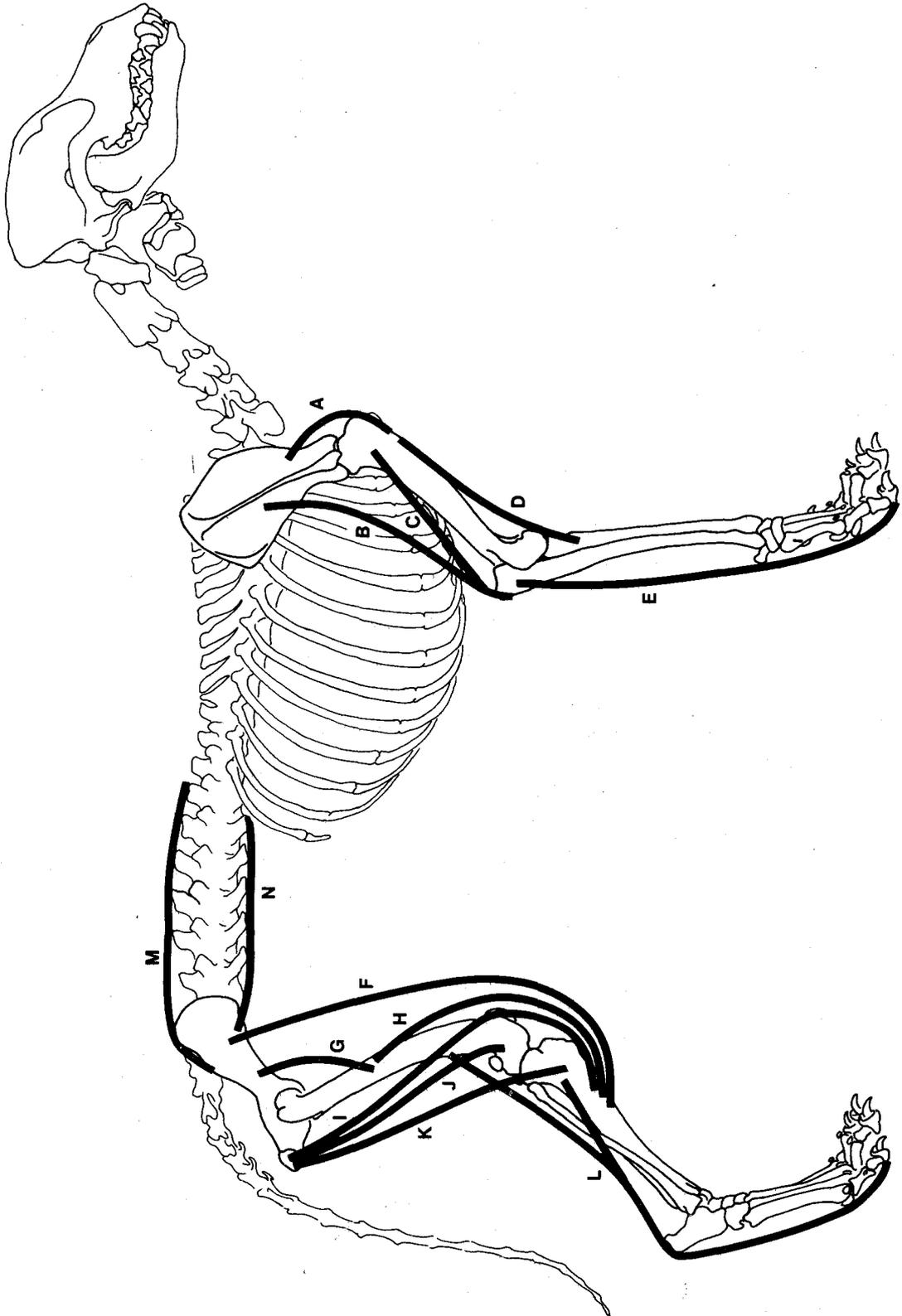
requirement for smooth joint movements. Using a combination of

X-rays and palpation on one of the experimental animals, the required

points may have been located within ±0.5 cm at the foot contacts and

±1.0 cm otherwise. Because of this handicap, any results which are

based on this model must be viewed as primarily qualitative rather

than quantitative.

Figure 6 shows the skeletal geometry as it was determined by

the above method. For convenience, the contact points of the feet

have been located directly under the supposed contact of the respective

leg and the body. From measurements between the estimated shoulder

pivot and the estimated foot contact points, it seems reasonable to

speculate that, when in the command posture, the body is 1 or 2 cm

forward, leaving the legs slightly inclined. As will be discussed

later, a slight forward lean may produce a desireable redistribution of

the effort required to stand.

The somatic musculature is so highly complex that we must

begin our analysis with a simple model having only limited anatomical

significance. Figure 5 provides examples of certain muscles which

are known to be important for resisting gravity and producing longi-

tudinal motion in the dog. The action of each of these muscles is to

produce tension between the regions where its opposite extremities

are connected to the different bones. When a muscle contracts, it will

pull adjacent bones tightly together while simultaneously producing a
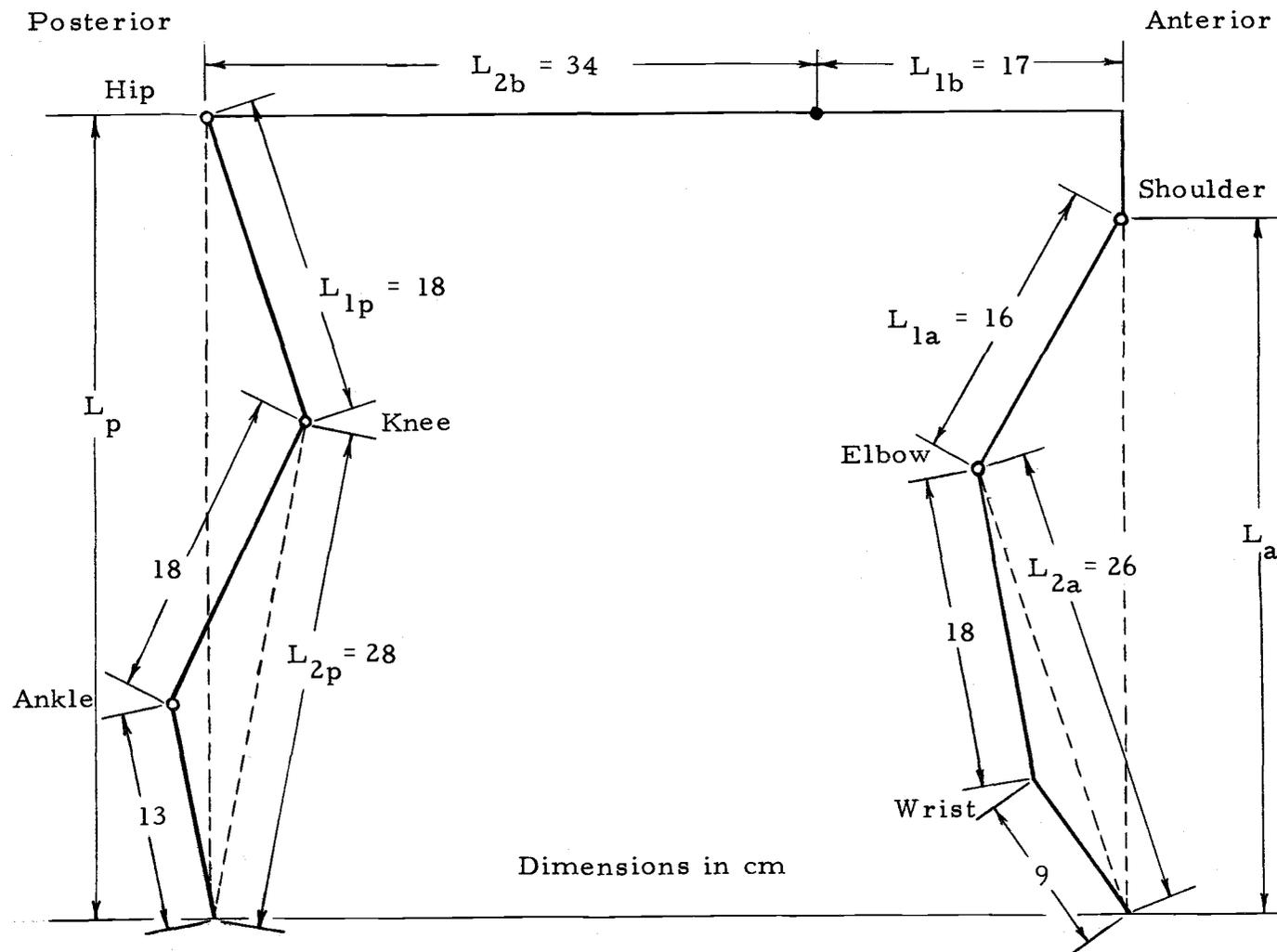
Figure 6.   A geometrical model of the skeleton.   The dimensions of this model were determined by external measurements and X-rays for Dog 7772.

turning about each joint which is between the extremes of the muscle.
When analyzing the interaction between a limb and its external
environment, we can exclude the internal forces holding the bones
together and consider only the moment about each joint and the forces
of external origin. All internal forces between the bones and tissues
are balanced by equal and opposite forces from adjacent bones or
tissues (Moffatt et al., 1969).

Because the prime action of a muscle has been limited to pro-
ducing rotation or stabilization of the various joints, we can replace
each muscle of the dog's anatomy with a moment generator at the
joints which the muscle spanned. The turning moment which is
transmitted between adjacent bones at a joint will be the sum of the
moments contributed by each muscle covering that joint. Thus, at
each joint of the skeletal model, one moment generator will represent
the combined effects of all muscles which spanned that joint. In what
follows, it will become clear that quiet standing and longitudinal
motion can be completely controlled by adjusting the turning moments
at appropriate joints of the model.

Beyond the complexity of muscle anatomy, the nerves which
control each muscle again defy any attempt to achieve a detailed model
which might preserve significant aspects of neuroanatomy. The
essential function of both nerves and muscles may be modeled by con-
sidering the nerves as control inputs to a moment generating servo

actuator located at a joint. The subsystem of the CNS which generates the muscle control signals is represented as a massive logic system capable of reducing sensory data to muscle control signals in a way which produces mechanical coordination of all body parts. The contribution of these models is strictly conceptual since they have only a very slight resemblance to actual anatomy.

Static Analysis

We now consider the mechanics of quiet standing using the skeletal model of Figure 6 which, as qualified above, is an approximate geometrical equivalent of the simplified skeleton shown in Figure 5. Although quiet standing has been described earlier as a dynamic process when considering CNS and muscle activity, the movements and accelerations of the body parts are so small that mechanical equilibrium can be assumed and a static analysis of the mechanics can be given. Since the general aspects of this subject have received considerable attention by earlier authors such as Gray (1944) and Manter (1938), we will treat primarily those portions which find unique application in this work.

With reference to the geometry of an inclined limb as shown in Figure 7 and the free body diagrams of Figure 8, the equations of static equilibrium can be written. This results in one set of linear, time-variant equations for each limb, each set containing three
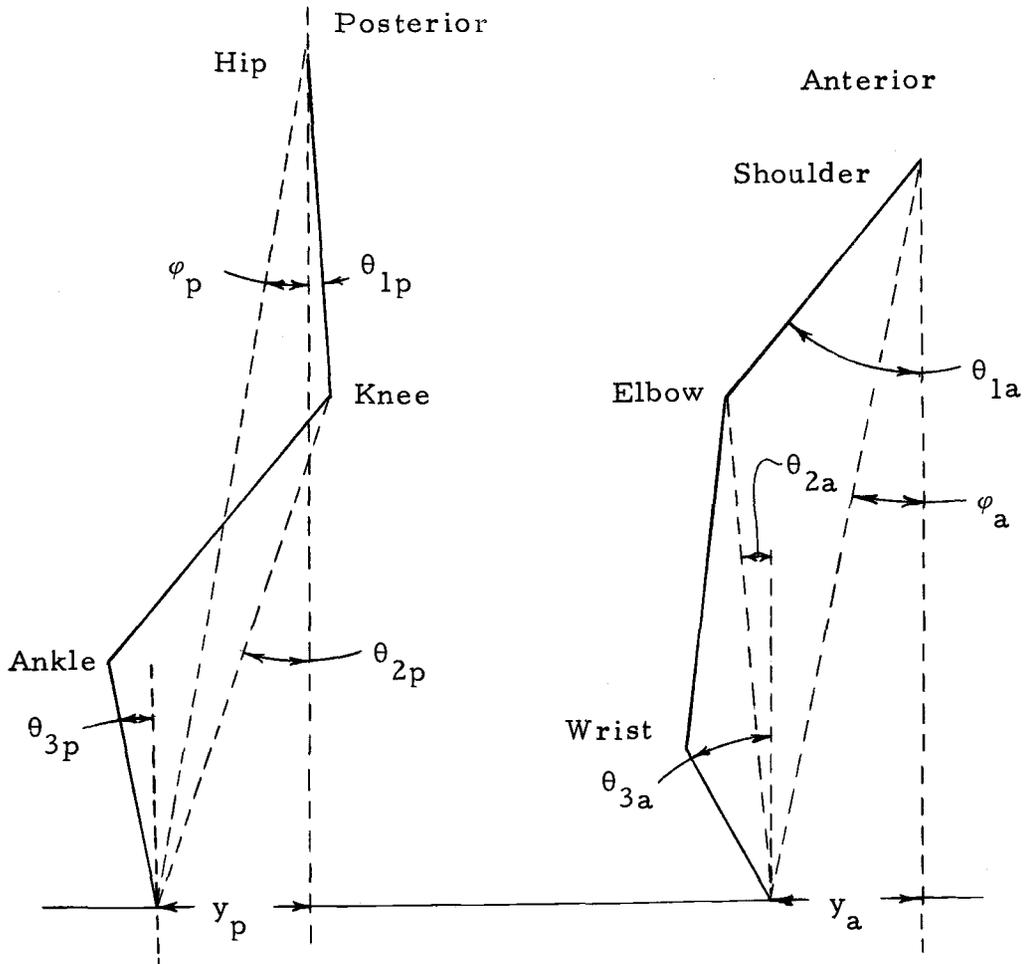
Figure 7. Geometry of the inclined limbs. Each limb contains three segments which are connected at the joints. The effective length of the leg is the distance from the body contact point to the foot contact point. The effective inclination angle is the inclination of this line segment.
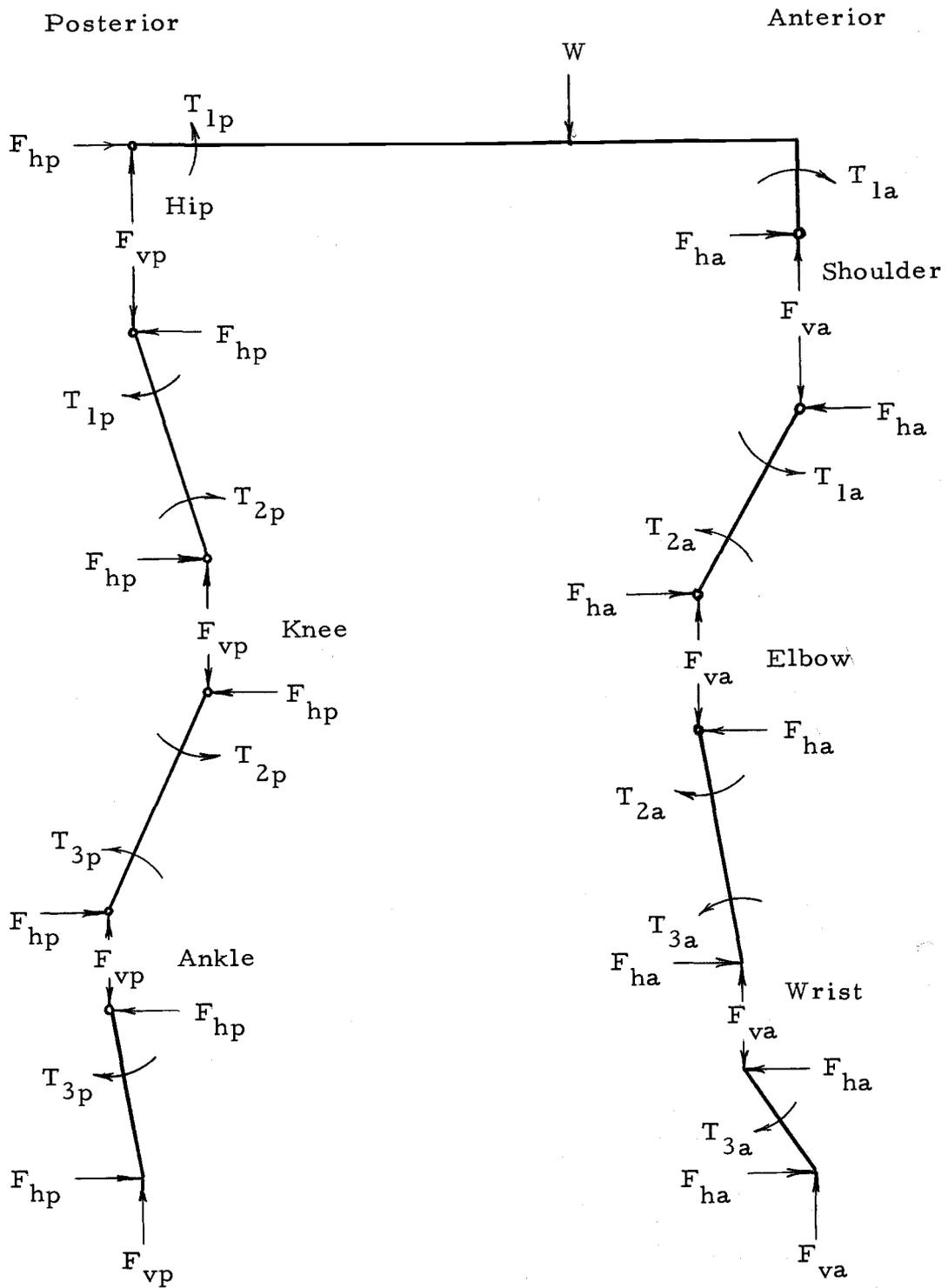
Figure 8. Free body diagrams for leg segments and the body.

$$F_{va} y_a - F_{ha} L_a \cos \varphi_a = T_{1a} \tag{1}$$

$$F_{va} L_{2a} \sin \theta_{2a} + F_{ha} L_{2a} \cos \theta_{2a} = T_{2a} \tag{2}$$

$$F_{va} L_{3a} \sin \theta_{3a} + F_{ha} L_{3a} \cos \theta_{3a} = T_{3a} \tag{3}$$

$$-F_{vp} y_p + F_{hp} L_p \cos \varphi_p = T_{1p} \tag{4}$$

$$F_{vp} L_{2p} \sin \theta_{2p} - F_{hp} L_{2p} \cos \theta_{2p} = T_{2p} \tag{5}$$

$$F_{vp} L_{3p} \sin \theta_{3p} + F_{hp} L_{3p} \cos \theta_{3p} = T_{3p} \tag{6}$$

$$F_{va} = \frac{W(L_{2b} + y_p)}{(L_{2b} + L_{1b} + y_p - y_a)} \tag{7}$$

$$F_{vp} = W - F_{va} \tag{8}$$

(Symbols are defined in Figures 6-8.)

equations. Because lateral symmetry has been assumed, the equa-
tions for the anterior limbs are identical and can be reduced to one
set of three equations representing the combined contribution of the
two limbs. The posterior limbs are treated similarly in the model.

If y_a and the forelimb geometry are specified, the unknowns
in the first three equations are F_{ha}, T_{1a}, T_{2a} and T_{3a}. Clearly,
for any fixed geometry of the anterior limb, an infinite number of
solutions to the equations will exist. This means that the dog can,
without moving, continually adjust the joint moments T_{1a}, T_{2a} and
T_{3a} at the expense of changing F_{ha}. If we now specify y_p with a

fixed geometry for the posterior limb and set $F_{hp} = -F_{ha} = F_h$ to preserve equilibrium, the torques T_{1p}, T_{2p} and T_{3p} must satisfy the second triple of equations, but this time the solution is unique.

A more general picture of the interactions being discussed appears in Figure 9 where the curves of the joint moments versus horizontal force are given under the assumption that $y_a = y_p = y$, a constant, and that L_a and L_p were constant, i.e., the knee, ankle, elbow and wrist angles were constant. As is clear from the equations, each moment is a linear function of F_h if there is no body movement. It is now somewhat more evident how, for any given posture, the dog can redistribute the effort of standing among the various joints without moving.

One interesting point is that in normal quiet standing, F_h is not zero. The values of F_h corresponded closely to a linear function of body position as is shown in Figure 10. The dotted line in the figure determines the linear function $F_h = f(y)$, where y is an estimated value corresponding to the horizontal distance between the shoulder pivot and the foot contact. F_h is usually called the horizontal bias force and the value of y was estimated to be about 2 cm (Dog 7772 only) when the dog was in his preferred posture. The function $f(y)$ given by the dotted line will be used to determine appropriate values of F_h for many of the calculations which will follow.
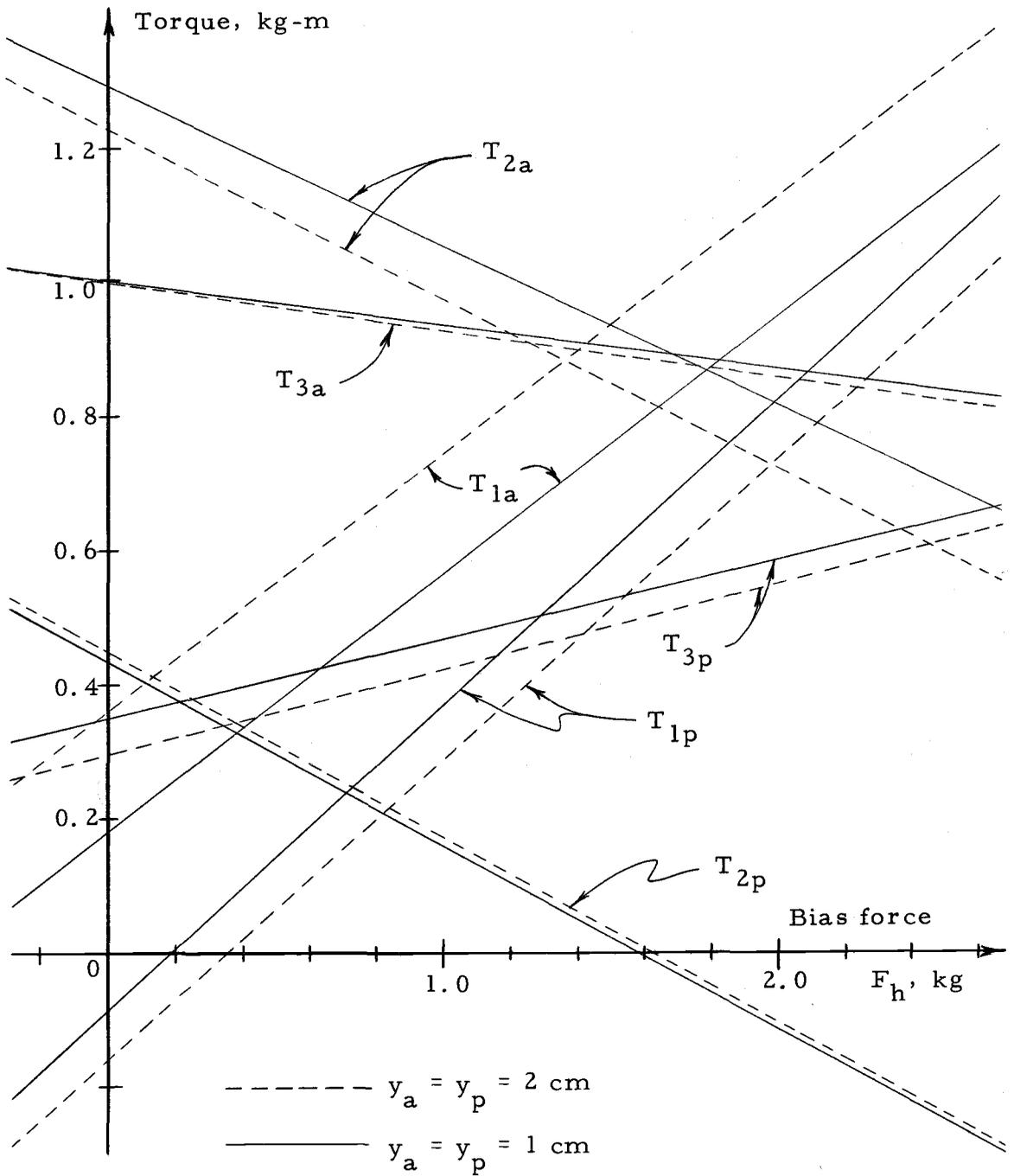
Figure 9. Joint torques vs. horizontal bias force. Each joint torque is a linear function of the horizontal bias force for fixed leg geometry. See Equations (1)-(6).
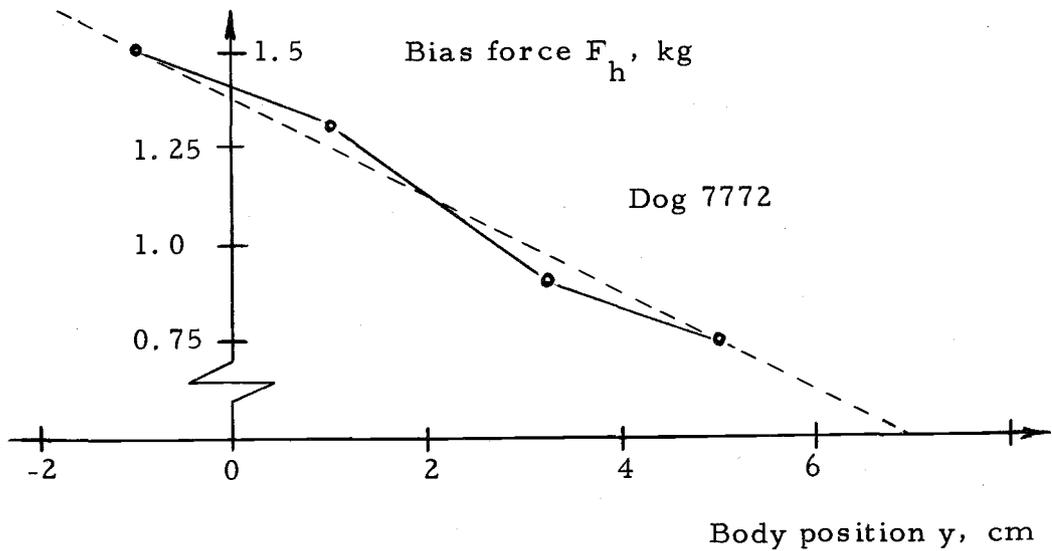
Figure 10. Measured horizontal bias force vs. estimated body posi-
tion. These data were obtained by inducing the dog to
lean forward and backward from his preferred posture.
The values of y were estimated from external measure-
ments of the leg inclinations.

In Figure 11 the curves for joint moments versus relative body

position are drawn for $F_h = 1.0$ kg (solid lines) and for $F_h = f(y)$

(dotted lines), assuming the lower joint angles to be constant. These

curves suggest that the joint moments of the front limb can be nearly

equalized by leaning forward with $F_h = 1.0$ and that when

$T_{1a} = T_{2a} \approx T_{3a}$, the moments are also nearly equalized in the

joints of the posterior limb. Without anatomical evidence and physical

measurements, it is not really clear that such equalization would be

preferred by the dog, but speculations to that effect are irrepressible.

It is clear, however, that the difference between T_{1a} and T_{2a} is

less when $F_h = f(y)$ as given by Figure 10.
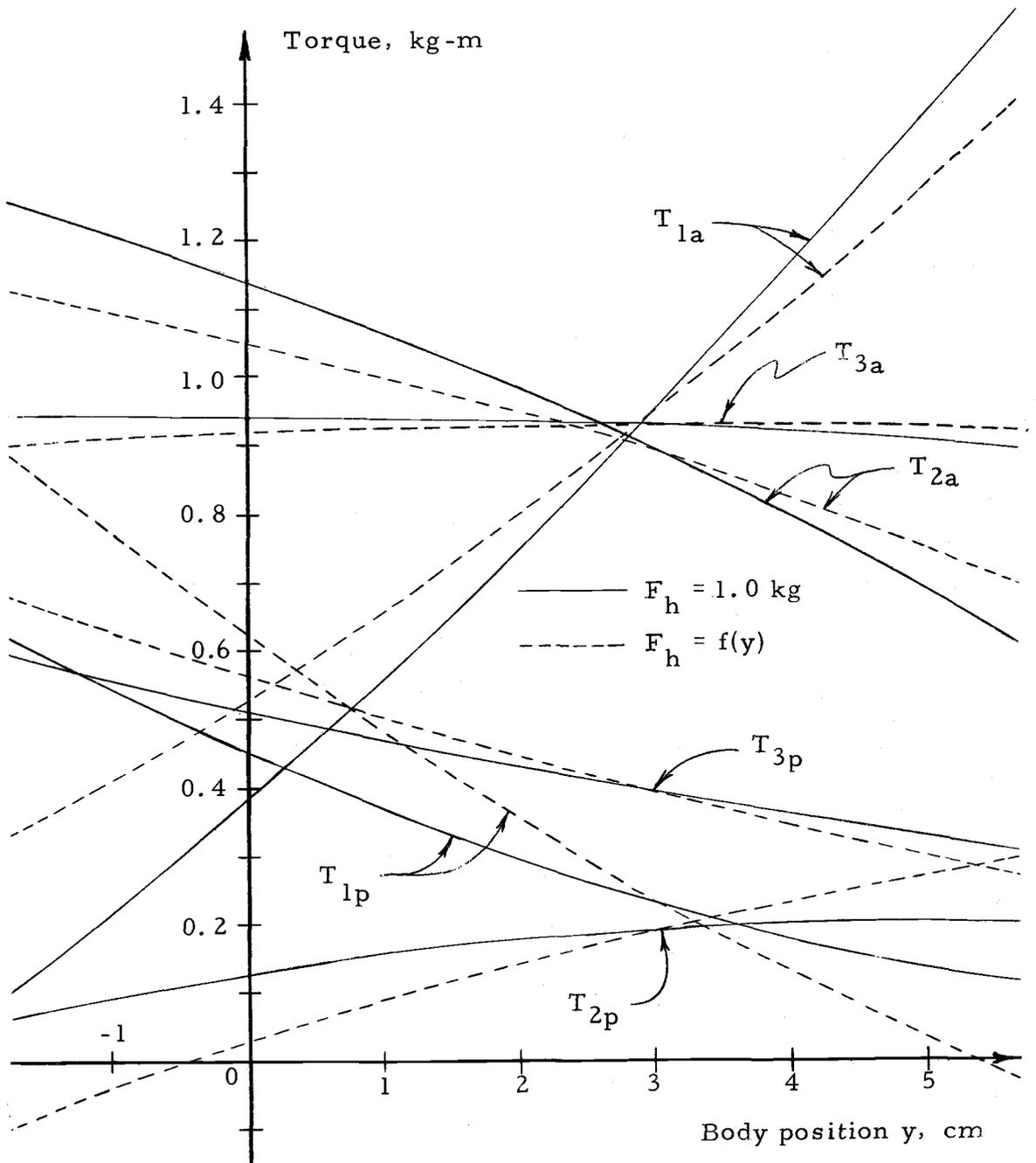
Figure 11. Joint torques vs. body position. For the solid lines, F_h was equal to 1.0 kg. The dotted lines were calculated for $F_h = f(y)$ as given in Figure 10.

Because at least 60 percent of the body weight is supported by the front legs, it is likely that front leg effort and geometry are of primary importance in the maintenance of correct posture. This idea is supported by an experiment in which the spacing between the anterior and posterior foot contacts was varied over a considerable distance. When moving the posterior feet forward of their normal position, the body moved forward about half the distance that the feet were moved. The body did not follow proportionately when the posterior feet were moved rearward. This condition was met by extending the hind legs considerably and increasing the horizontal force magnitude. The net effect of this action was to maintain stability without major changes in the joint moments of the front legs.

If we define mechanical effort to be proportional to torque magnitudes, then the total effort which is required for quiet standing is the summation of the absolute values of all joint torques which are given in Equations (1)-(6). It is clear from these equations and Figure 9 that, except for special cases of anterior-posterior symmetry, the effort of standing will be a non-constant, piecewise-linear function of F_h. The function is continuous and its first derivative has a step discontinuity at each value of F_h where the torque at a given joint changes sign. As seen in Figure 12, the minimum mechanical effort given by this function is realized when F_h is about 0.2 kg for $y = 1$ cm and about 0.33 kg for $y = 2$ cm. Since it may be presumed

that the dog would try to stand with minimum effort, we might expect

the above values of F_h to agree with the values presented in Figure

10. For the above two values of y the values of F_h from Figure

10 are 1.25 and 1.125 kg, respectively, which are significantly

greater than predicted. In resolving this discrepancy, the following

three points should be considered. First, the dog will clearly want to

minimize his biological or muscular effort and not necessarily the

mechanical effort which has been defined. If certain muscles may be

used at greater mechanical advantage than others, these muscles and

the associated joints will probably carry a greater burden of effort

without discomfort. Muscles may also function as antagonists so that

biological efforts would produce canceling mechanical efforts. Sec-

ond, the geometry chosen to represent the skeleton is the product of

gross estimation and may not be properly representative. Third, it is

very likely that the stability of a particular stance is improved by

standing with F_h greater than its minimum-effort value. Hence, a

balance between stability and effort could result in greater than mini-

mum effort at the desired posture.

If we consider a single leg, the effort required to produce given

vertical and horizontal forces at the foot contact will vary according to

the angles of the leg joints. Particularly in the posterior limbs, the

inclination angles of the thigh, shank and foot can vary over a con-

siderable range without changing the effective length or inclination of

the leg. If we specify effective leg length and inclination and the desired vertical and horizontal forces, the resulting effort can be calculated as a function of femur inclination. This calculation leads to the curves which are shown in Figure 13. It is interesting that the observed inclination of the femur is about 15 degrees and that this angle gives reasonable equalization of effort among the joints.

Mechanical effort, kg-m

4.0

y = 2 cm

y = 1 cm

3.0

-0.5   0   0.5   1.0   1.5   2.0
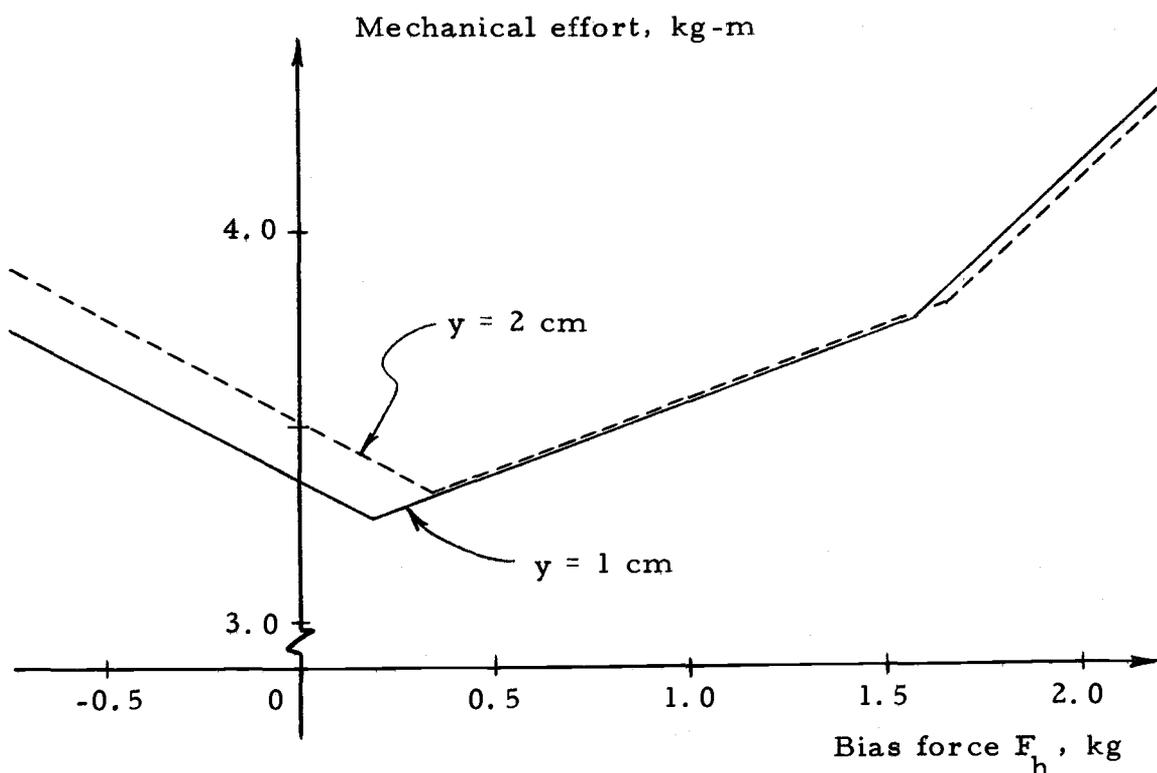
Bias force F_h, kg

Figure 12. Total mechanical effort vs. horizontal bias force. The curves in this figure were obtained by summing the absolute values of each joint torque which is plotted in Figure 9.
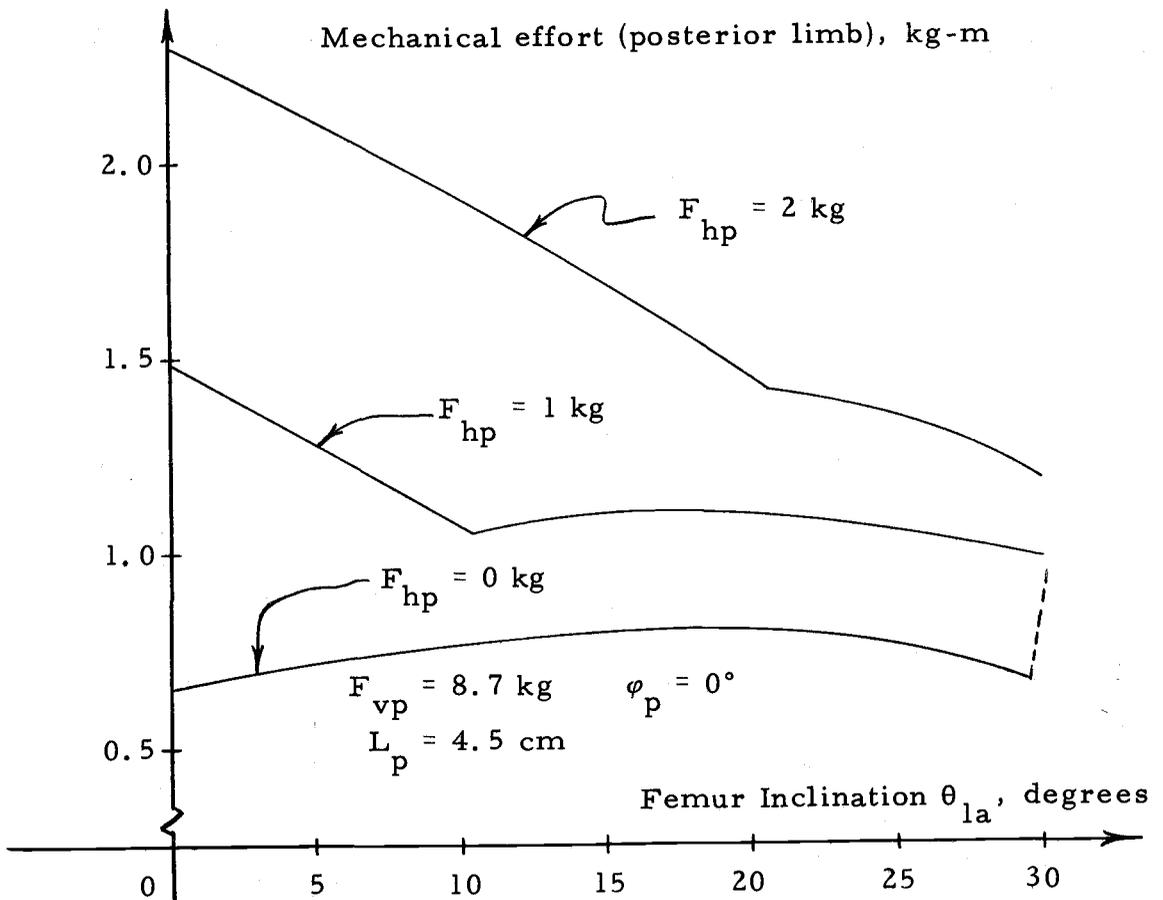
Figure 13. Mechanical effort in the posterior limb vs. femur inclina-
tion. The effective length of the limb and the external
forces were held constant at the values shown.

For several reasons this computation is not repeated for the
anterior limbs. The primary reason is that the wrist joint is almost
fully extended when in normal position and is held in that position
unless the foot is lifted. Second, because the wrist is extended
nearly to the limit of its movement, the torque at the joint pivot may
result partly from non-muscle tissues which bind the bones together.
Any torques not originating from muscle effort are not a true indica-
tion of biological effort. Other curves of mechanical effort have

included the wrist torque only because it was nearly constant over the range of investigation and did not change the qualitative features of the display.

We can also consider how the total effort of standing might change with respect to body position. Figure 14 presents two curves for the total mechanical effort of standing versus body position, one for F_h = 1.0 kg and another for F_h = f(y) as defined by Figure 10. It is again apparent that the dog does not necessarily stand with minimum mechanical effort. Other factors, such as the equalization of effort among joints, could logically explain the differing properties of these two curves.
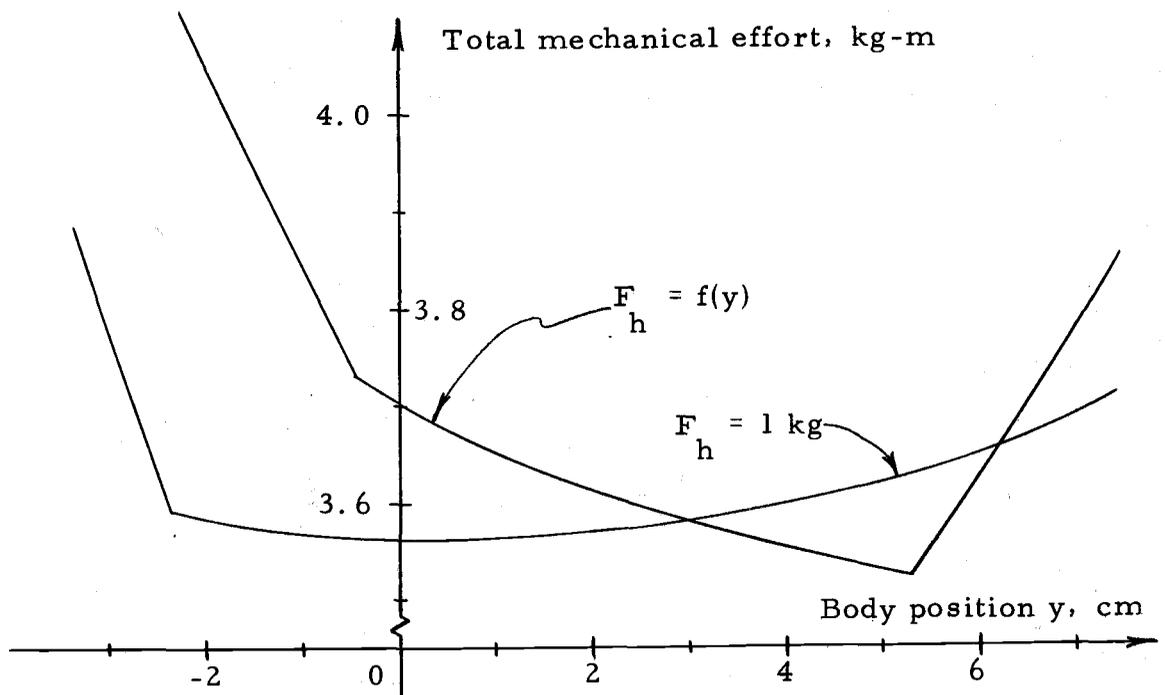
Figure 14. Total mechanical effort vs. body position. These curves were obtained by summing the absolute values of each joint torque which is plotted in Figure 11.

Previous authors have emphasized that the maintenance or modification of posture must involve the entire somatic musculature as a single functional unit (Gray, 1944). The present analysis of static posture shows full agreement with this concept. Any adjustment in the position or moment of a particular joint must be accompanied by compensating adjustments at all other joints. With this principle in mind, we now consider how postural movement might be accomplished.

Mechanics of Thrusting

The first principle of mechanical dynamics to be considered is Newton's third law, which states that a body or group of bodies can change momentum only when influenced by an external force. When analyzing the postural model given in Figure 6, the practical result of this law is that changes in posture, i. e., longitudinal movement of the center of gravity, can occur only when the horizontal forces F_{ha} and F_{hp} which act on the anterior and posterior feet, respectively, are of unequal magnitude. Because there is normally a bias force present, a headward movement could be started both by increasing the horizontal component magnitude at the posterior foot contacts and by decreasing the corresponding anterior component magnitude. These changes, as well as those required for tailward movement, can theoretically be accomplished without producing vertical movement by causing the elbow joint moment to vary inversely with the shoulder

moment and similarly with the knee and hip. We deviate briefly to show that these conditions for torque control are not observed in the dog.

A previous study of the dog when responding to table displacements (Mori and Brookhart, 1968; Brookhart et al., 1970) presented the vertical forces exerted by each of the posterior feet for ramp displacements of the table. These forces represented the weight of the dog currently supported by the given foot plus the forces associated with vertical acceleration of certain body parts. For a 2 cm headward displacement lasting 58 ms, a peak force of about 8 kg with respect to a 6 kg quiescent value occurred about 140 ms after the onset of table movement. This means that the posterior portion of the body could have experienced a vertical acceleration of 1.33 g. Although it is theoretically possible to accelerate the body horizontally but not vertically, we must conclude that the dog does not respond in this manner. One plausible explanation of this behavior is offered below.

Because the table movement is very rapid, the legs of the dog are significantly displaced under his body before any corrective action can occur in the muscles. This leaves the body without adequate support to resist gravity for a short time during which it will pivot on the legs in the direction opposite to foot displacement. This action occurs simultaneously with a lowering of the body mass. Hence, the corrective action from the legs should be to reverse the downward motion by

lifting the body at the same time a horizontal thrust is developed to propel it. The process of lifting and thrusting simultaneously is obviously a fundamental mechanism of locomotion.

Regardless of the coupling between vertical and horizontal force changes, the fact remains that longitudinal movement can result only when there is a condition of force imbalance between the anterior and posterior horizontal components acting at the feet. After considering certain aspects of leg geometry and mechanical freedom for each leg, we will attempt to show how the joint moments might be controlled to produce desired changes in the forces acting on the feet.

As mentioned earlier, the wrist joint appears to be extended to the mechanical limit of rotation during normal standing. If we assume that only small changes in the wrist angle occur, the lower front leg can be replaced with a single rigid member. This implies that negligible muscle action is required to stabilize the wrist joint, hence, Equation (3) can be discarded. It is now possible to solve Equations (1) and (2) to obtain F_{va} and F_{ha} as functions of the two independent variables T_{1a} and T_{2a}, provided that the determinant of the coefficients is non-zero. (This condition is guaranteed whenever the elbow angle is unequal to 180 degrees. See Equation (9) and Figure 7.) After obtaining these functions in explicit form, the partial derivatives of end reaction force with respect to joint moment can be calculated for each possible combination. These derivatives, which

$$\frac{\partial F_{va}}{\partial T_{1a}} = \frac{L_{2a} \cos \theta_{2a}}{\delta_a} \qquad \frac{\partial F_{va}}{\partial T_{2a}} = \frac{L_a \cos \varphi_a}{\delta_a}$$

$$\frac{\partial F_{ha}}{\partial T_{1a}} = \frac{-L_{2a} \sin \theta_{2a}}{\delta_a} \qquad \frac{\partial F_{ha}}{\partial T_{2a}} = \frac{y_a}{\delta_a}$$

$$\delta_a = y_a L_{2a} \cos \theta_{2a} + L_a L_{2a} \cos \varphi_a \sin \theta_{2a} \qquad (9)$$

$$= L_a L_{2a} (\sin \varphi_a \cos \theta_{2a} + \cos \varphi_a \sin \theta_{2a})$$

$$= L_a L_{2a} \sin(\varphi_a + \theta_{2a})$$

appear as Equations (9) and are plotted in Figure 15 (solid lines), give

a measure of the effectiveness of each joint for producing horizontal

or vertical force changes at the foot contacts. We can now consider

what changes in joint torques will be required to produce given

changes in the end-reaction forces.

Suppose that the present values of joint torques are $T_{1a} = t_{1a}$

and $T_{2a} = t_{2a}$. This defines a point P in the $T_{1a}-T_{2a}$ plane

given by $P = (t_{1a}, t_{2a})$. For all such points, there are unique values

of F_{va} and F_{ha} which are determined by the coordinates of the

points. Suppose further that for the point P, the value of F_{va} is

f_{va} and that we desire to find a second point P' where

$F_{va} = f'_{va} > f_{va}$. Although there are an infinite number of points along

a straight line which could be chosen, we desire to find the point P'

which is closest to P, since this point will be reached with minimal

changes in the values of T_{1a} and T_{2a}. It is clear that we should
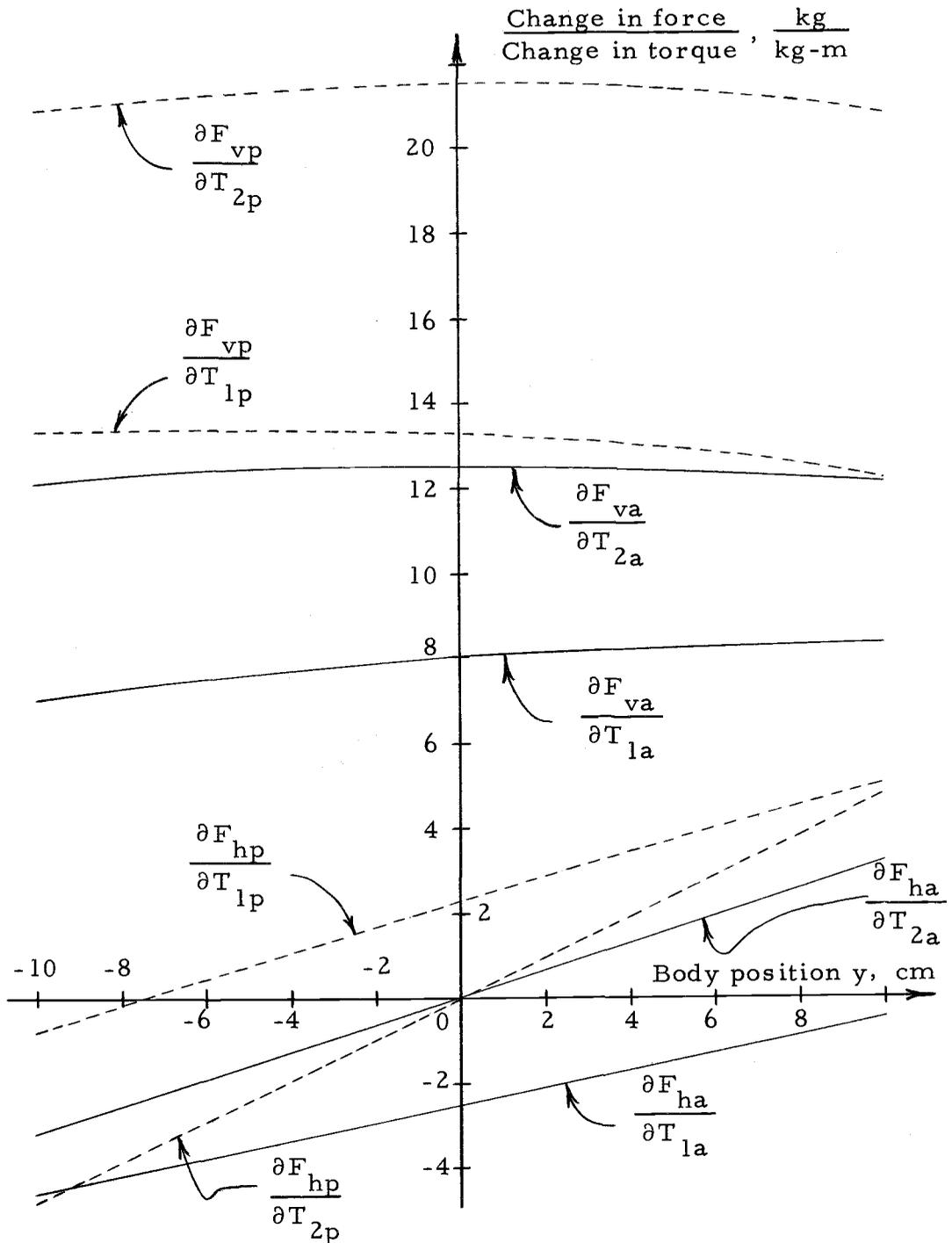
Figure 15. Partial derivatives of end-reaction forces vs. body position. These curves give a measure of the effectiveness of each joint torque for producing changes in the end reaction forces. In the posterior limb, the hip torque T_{1p} and the knee torque T_{2p} have been chosen as the independent variables.

choose the coordinates of P' such that the vector from P' to P

is parallel to the gradient vector for F_{va}. The magnitude of the

desired change in F_{va} will determine the minimum distance

between the two points. If we do not move parallel to the gradient of

F_{va}, then the change in F_{va} will be proportional to the distance

between the lines which pass through the points P and P' and

are perpendicular to the gradient vector. We shall call this distance

the projection of the vector P' - P onto the gradient of F_{va}. If we

now define Δt_{1a} and Δt_{2a} as the respective changes in T_{1a} and

T_{2a} along the projection, we can find the changes in force Δf_{va} and

Δf_{ha} which are associated with moving between the two points.

Equations (10), which specify the force changes, are clearly the

$$\Delta f_{ha} = \frac{\partial F_{ha}}{\partial T_{1a}} \Delta t_{1a} + \frac{\partial F_{ha}}{\partial T_{2a}} \Delta t_{2a}$$

$$\tag{10}$$

$$\Delta f_{va} = \frac{\partial F_{va}}{\partial T_{1a}} \Delta t_{1a} + \frac{\partial F_{va}}{\partial T_{2a}} \Delta t_{2a}$$

inner products of the gradient and the projections of P' - P for

each force function. We should perhaps note that since F_{va} and

F_{ha} are linear functions for a fixed body position y,   the gradients

are constant for a specific value of y. The extent to which each

gradient varies with y is determined by the leg geometry.

In Figure 16, the gradients of F_{va} and F_{ha} are shown as

radius vectors in the T_{1a}-T_{2a} plane. The coordinates of point P_0 represent typical values of T_{1a} and T_{2a} during quiet standing. The coordinates of points P_1 and P_2 specify joint torques which were encountered during maximum effort in typical headward and tailward body movements, respectively. We can notice that the projection of $P_1 - P_0$ on Grad F_{ha} is in the direction of increased horizontal force and conversely for the projection of $P_2 - P_0$. Both projections on Grad F_{va} are in the direction of decreased vertical force, a point which will be considered further in Chapter III.
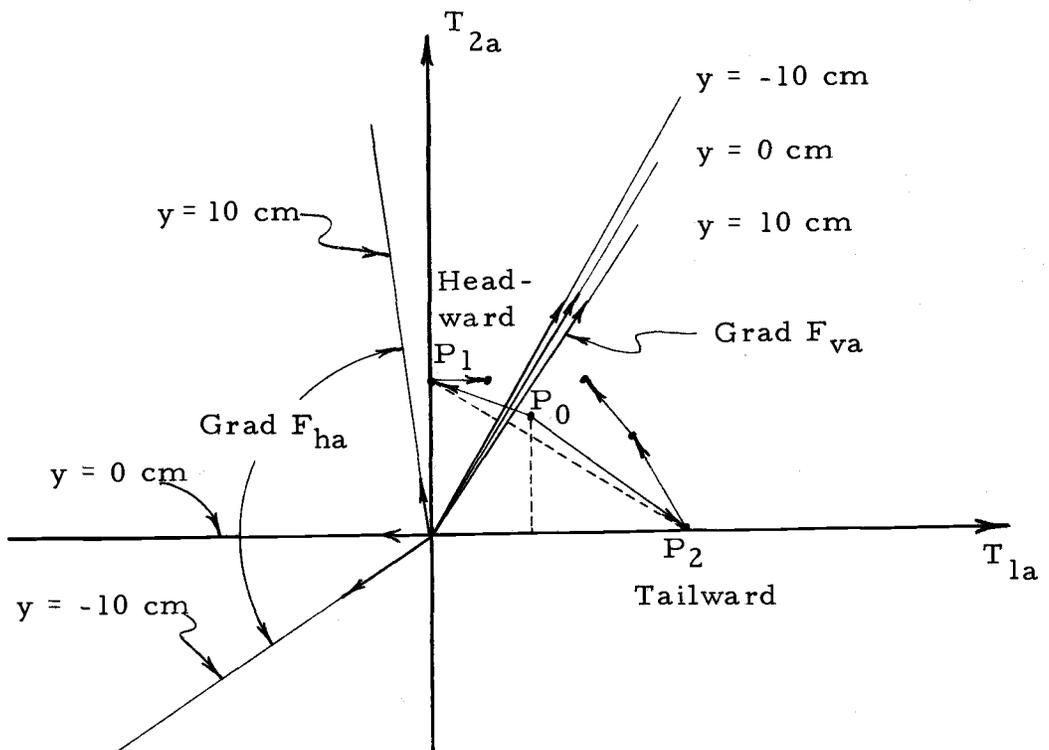
Figure 16. Gradient vectors for the anterior limb.

In the posterior limb, the ankle is normally within its range of free motion and therefore must be stabilized by muscle action rather than by ligaments and other non-muscle tissue. Because the ankle and knee are on opposite sides of a straight line between the hip and foot contact, there is an inherent potential for instability in the mechanical structure of the leg, a fact which may explain why the more nervous dogs showed a tremor in the hind legs during some experiments. In a functional sense, the posterior leg is much more agile than is the highly stable anterior leg. If we notice that the anterior limbs are primarily to support the body and the posterior limbs are for thrusting and movement, the above properties of the legs seem well suited to their respective tasks.

Because the ankle torque is controlled primarily by muscle action, we cannot discard the corresponding equation (Equation (6)) as was possible with the wrist in the front leg. Retaining the third equation gives rise to mathematical properties which deserve extended consideration.

Equations (4)-(6) have been copied with generalized coefficients and appear as Equations (11). Note that each coefficient is a function

$$c_{11}F_{vp} + c_{12}F_{hp} = T_{1p}$$
$$c_{21}F_{vp} + c_{22}F_{hp} = T_{2p} \tag{11}$$
$$c_{31}F_{vp} + c_{32}F_{hp} = T_{3p}$$

of leg geometry and inclination. Basically, these equations say that if

we pick F_{vp} and F_{hp}, there are unique values of T_{1p}, T_{2p} and

T_{3p} which will produce static equilibrium in the leg. This means

that we can write each torque as a function of F_{vp} and F_{hp}. How-

ever, when we consider the problem of controlling the limbs, it is

more natural to identify the joint torques as inputs and the end-

reaction forces as outputs. Therefore, we would like to express F_{vp}

and F_{hp} as functions of the joint moments as we did above for the

two-joint anterior limb. If we pick any two equations, we may solve

for the forces as functions of the two joint torques included in the

chosen equations. When these functions are substituted into the third

equation, we obtain a relationship among the joint moments which is

given as Equation (12). This is the equation of a plane in three-space

$$(c_{21}c_{32}-c_{31}c_{22})T_{1p} + (c_{31}c_{12}-c_{11}c_{32})T_{2p}$$
$$+ (c_{11}c_{22}-c_{12}c_{21})T_{3p} = 0 \qquad (12)$$

and simply means that the domain of the force functions is restricted

to those points which lie on the plane. It is clear that only two of the

three torques may be considered as independent. Hence, the third

must be a function of the other two. The implications of this restric-

tion will be examined below.

Equations (11) were developed to describe the condition of

mechanical equilibrium in the leg. If this condition is not met, the torque imbalance on each physical leg segment will cause rotational acceleration of that segment. The center of mass for the leg will accelerate whenever the end-reaction forces at the hip and the foot are unbalanced. Such accelerations are clearly required during movement of the body since the leg must also move. Hence, in a physical leg, movement can not occur unless Equation (12) is violated. If we model the leg using hypothetical massless members, then we must again impose the strict conditions of equilibrium, i.e., Equation (12) must be satisfied. Because the linear and rotational inertias of the leg segments are small compared to the body inertia, the acceleration forces acting on these segments are small compared with the end-reaction forces at the foot and the assumption of massless members is quite realistic. Therefore, the equations of static and dynamic equilibrium are the same and the need to exactly satisfy Equation (12) arises because of the assumptions made to obtain a model. If we pick T_{1p} and T_{2p} as independent control variables (inputs) and then pick T_{3p} to satisfy Equation (12), the result is equivalent to assuming that the ankle is rigid. This is the same assumption used when considering the wrist, but there is no longer an anatomical basis. Choosing T_{1p} and T_{2p} as the independent inputs is intuitively sound because the musculature and lever arms associated with these joints make them much more effective for generating changes in end-reaction forces.

The ankle appears to be stabilized in response to hip and knee action during most movements which are to be considered.

Having established T_{1p} and T_{2p} as independent inputs, it is again possible to analyze the posterior limb in the same manner as was employed for the anterior limb. The desired partial derivatives are given in Equations (13) and are plotted as dotted lines in Figure 15.

$$\frac{\partial F_{vp}}{\partial T_{1p}} = \frac{-L_{2p} \cos \theta_{2p}}{\delta_p} \qquad \frac{\partial F_{vp}}{\partial T_{2p}} = \frac{-L_p \cos \varphi_p}{\delta_p}$$

$$\frac{\partial F_{hp}}{\partial T_{1p}} = \frac{-L_{2p} \cos \theta_{2p}}{\delta_p} \qquad \frac{\partial F_{hp}}{\partial T_{2p}} = \frac{y_p}{\delta_p}$$

$$\delta_p = y_p L_{2p} \cos \theta_{2p} - L_p L_{2p} \cos \varphi_p \sin \theta_{2p} \qquad (13)$$

$$= L_p L_{2p} (\sin \varphi_p \cos \theta_{2p} - \cos \varphi_p \sin \theta_{2p})$$

$$= L_p L_{2p} \sin(\varphi_p - \theta_{2p})$$

The points P_0, P_1 and P_2 in Figure 17 specify the conditions (joint torques) in the posterior limb which correspond with the points given in Figure 16 for the anterior limb. Other aspects of Figure 17 are also analogous to the earlier presentation and therefore do not need further explanation here.

With regard to static posture, we again emphasize that a change in one joint moment will generally be accompanied by changes in most or all other joint moments. If the dog is in a stable posture, such

adjustments will be controlled to produce only minor movements and are likely intended to improve comfort by redistributing the effort of standing. This redistribution of effort can be so well coordinated that each part of the body will remain in mechanical equilibrium. Movement can be accomplished by changing a particular joint moment or group of moments without any compensating changes in other joints. When a joint moment is perturbed from its equilibrium level, the initial effect can be estimated by noting the changes in the horizontal and vertical end-reactions on each foot which are predicted by the partial derivative values plotted in Figure 15. As soon as significant movement occurs, every part of the body will be effected and each joint moment must be dynamically adjusted so that the external forces acting on the dog will move the body to its desired position smoothly.
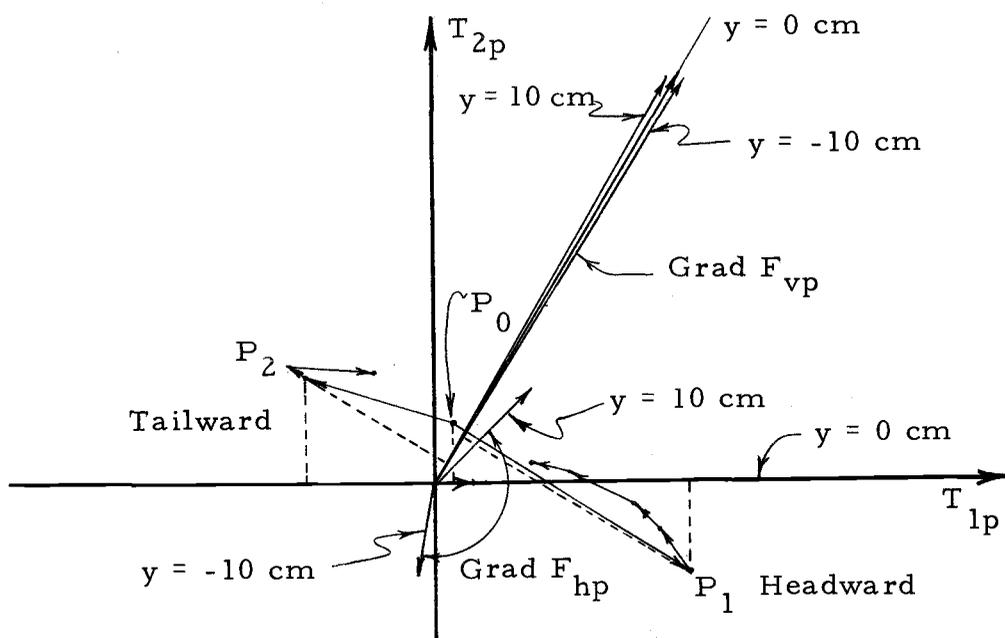
Figure 17. Gradient vectors for the posterior limb.

Figures 16 and 17 illustrate a method for determining what torque changes are necessary to produce specified changes in end-reaction forces. This method could be particularly useful for determining the pattern of torque changes needed to initiate a rapid body movement. Fine adjustments for the regulation of quiet standing would more logically be determined by considering the total effort of standing and the comfortable distribution of this effort.

While the model which has been given is clearly useful for analysis it contributes very little toward an understanding of controlled body movement during major excursions. The following chapter attempts to analyze observed movement of the dog with the aid of the concepts already discussed.

III. POSTURAL MOVEMENT

Introduction

The objective of this chapter is the description and analysis of postural movements and the illumination of the strategies which the dog used to maintain balance and coordination. Although a wide range of behavior was encountered from the six different dogs used as subjects, certain characteristics were uniform and can be presented as "typical" behavior. Other manifestations which seemed peculiar to a particular dog will be explained mostly through appeal to intuition since the sample of dogs employed was certainly not large enough for establishing behavioral norms.

Since the fixed-foot postural task has been described earlier, we can now consider the problem of conducting a controlled experiment using a dog as the subject. Earlier studies have established that a trained dog, when in a comfortable stance, can regulate the long term migration of the center of gravity to stay within ±1 cm of a given point (Brookhart et al., 1965). The initial effect of an event (any table movement) is to distort the posture by displacing the feet with respect to the body. Although the dog could elect to stand in the distorted posture provided the table movements were small, his training and comfort both call for a correction of posture. Hence, the fundamental concept of these experiments is that a trained dog will attempt

to accurately control his posture when under command to do so. Because each foot is supported by a force measurement device, this task must be accomplished in the "fixed-foot" fashion.

It is clear that behavior of a dog following an event is dependent both on the nature of the induced distortion and on the philosophy of correction employed by the animal. If the training process has instilled extreme sensitivity to body position, the correction of a distortion might logically be very rapid, perhaps nearly time-optimal subject to the restraints of physical ability. If, however, the training has taught the dog to hold still, he may elect to "sneak" back to a comfortable posture with very slow movements. The inability to ascertain the control strategy of each dog is a serious deficit which clearly limits the observer's ability to interpret a dog's behavior. In this work, we have generally assumed that the dogs place primary emphasis on the control of body position, thus tending to show rapid recovery from postural distortions. One dog, however, was particularly slow in his recoveries and may have been attempting to hold still. It is also conceivable that slow recoveries require less total exertion of effort, but this does not explain why only one dog behaved in this manner.

Experimental Methods

The group of experimental animals used included three pairs of

dogs described as follows: Dogs 8450 and 7772--large, highly experi-enced; Dogs 8531 and 8514--medium size, well trained but less experienced; Dogs 20933 and 20922--medium size, partly trained and completely inexperienced. Data from each of the dogs are distinctive and serves to demonstrate different aspects of animal behavior.

In any experiments involving higher animals, a subject can generally respond more effectively to some disturbance if he is able to anticipate either the timing or nature of the event. For this reason, the sequences of table movements used for most of the observations were a kind of constrained pseudorandom walk. The time between events conformed to a truncated exponential distribution (a Poisson process), the direction of movement was equally divided between headward and tailward and the magnitude of the displacement was uniform between two limits. These three parameters were independ-ently determined for each event by selecting three numbers from a set of uniform pseudorandom digits and then transforming them to obtain the desired distributions. A sequence of events might contain from 20 to 100 separate table movements over a maximum period of 20 min-utes.

Because the total excursion of the table was limited to about 14 cm, it is obvious that an unrestrained random walk was not physically possible. In our case, the actual statistical properties of any sequence of events was not really important provided that the dog

was unable to anticipate what would happen next. Therefore, any event which would have moved the table out of its range of travel was delayed until after a special corrective movement returned the table to a central position. In a sequence of about 100 events, this correction might have occurred 10-12 times, which means that each sequence actually consisted of short segments of a pseudorandom walk interrupted by position corrections. Since a segment could often include 10 or more events, the statistical quality of the sequence was undoubtedly adequate for removing the possibility of anticipation in the dog.

Each recording session produced data describing the table movement, body movement, and the horizontal forces at each foot. For certain experiments, measurement of vertical forces was included. One restriction in data acquisition was that vertical and horizontal force measurements involved two different transducers. During quiet standing, simultaneous measurement of vertical and horizontal forces was accomplished by "stacking" these devices under each foot. For mechanical reasons, this was not practical whenever rapid table movements were involved since the devices could upset or at least tip quite easily during acceleration of the table. Further information regarding the measurement devices is given in Appendix A and by Petersen, Brookhart and Stone (1965).

After the data records were digitized, three additional variables were derived from the measured quantities. These were body position

relative to the table, relative body velocity, and absolute body velocity.

Relative body position is obviously the body position minus the table

position. After suitable digital smoothing, the two velocities were

computed by the process described in Appendix B. Although the

velocity records are not often included in this presentation, they were

very useful in the early analysis of animal behavior.

Results of Experiments

When considering the results of a particular table movement,

we must realize that certain quantitative properties of the response

curves may be dependent on the body position and weight distribution

just before initiation of the displacement. Although these quantitative

characteristics sometimes varied considerably between movements,

the important qualitative attributes were very consistent. The exam-

ple responses which are presented were selected after visual compari-

son of several hundreds of responses from the different dogs. The

conclusions which have been derived from these responses are not

dependent on the quantitative properties of the examples or on the

particular selection which has been made.

At this point, we consider the three types of horizontal force

manifestations which were defined at the end of Chapter I. After

repeating the definition of each force, a discussion to support the

definition will be given. Throughout the remaining text, a perturbation

of force will be called a force. This usage should always be clear from the context.

Class 1 force: reaction forces attributed to the effects of linear
                and/or rotational inertia or the effects of friction

In earlier sections, it was claimed that significant horizontal forces were required to accelerate and decelerate the legs as they conformed to table movements. Because these forces arise from mechanical inertia, their appearance should be regular in both timing and magnitude. For a given level of table acceleration, the magnitude of these forces should depend only on the mass distribution and physical properties of the leg being accelerated. Confirmation of these predictions is supplied in Appendix C.

In most of the table movements used, there was an abrupt acceleration which started the table movement and a similar deceleration which stopped it. Therefore, manifestations of the inertia forces are limited to the times when these accelerations are at high levels. When the table movement started, there was a horizontal force peak at each foot which subsided within about 50 ms. The deceleration forces could not be clearly distinguished except when the table was stopped within less than 80 ms after being started. Otherwise, the forces resulting from muscle activity became of equal or greater magnitude.

Class 2 force: reaction forces which occur between 70 and 150 ms

after an identifiable external stimulus, also called an

early FPO (EFPO)

The identification of class 2 forces follows from a process which eliminates definitions other than the one given above. The peak of a class 2 force was generally observed about 110 ms after a pulse of table acceleration and its action was in the direction of acceleration. A class 2 peak came too late to be an inertial force and therefore must be considered as an FPO. Three of the four experienced dogs showed very regular manifestations of class 2 forces. In Dog 7772, class 2 forces were either weak or absent and the speed of recovery from postural distortion was much slower.

In the discussion regarding class 3 forces, it will become clear that a voluntary FPO can not develop within less than 150 ms after the application of some stimulus. The regularity of class 2 manifestations is reminiscent of reflex behavior, but there is no spinal reflex which suitably explains the occurrence of these forces. The occurrence is too late to arise from the classical stretch reflex. Class 2 forces were also observed after the cessation of prolonged table movements (see Figure 4) when the rotation of the legs under the body had just been stopped and the stretching of muscles had also ceased.

Melvill Jones and Watt (1971) have reported what they called a

"function stretch reflex" in the gastrocnemius muscle of man. The similarity between this so-called reflex and the class 2 forces will be further examined below.

Class 3 force: reaction forces which occur at least 150 ms after an identifiable external stimulus, also called a late FPO (LFPO)

Force manifestation which peaked after 150 ms following the onset of a table displacement were extremely variable between dogs and between different events with the same dog. Irregularity alone, however, is not a sufficient argument for the given definition. The primary evidence for this definition came from the "panic" behavior of relatively untrained animals.

After a few training periods an uninitiated dog would easily stand for the larger part of a minute without moving his feet from the measurement devices. Slight table movements induced a "startle" effect and ramp movements of the type normally used elicited an abrupt departure from the table along the shortest forward route. This departure was essentially the same regardless of the direction of the table excursion. Since two differing stimuli, i.e., oppositely directed table movements, elicited the same response, it is logical that the response originated in the higher centers of the brain where the sensory consequences of both stimuli could be interpreted as meaning

the same thing, i.e., "something is wrong." Generally, one or two

feet could be lifted between 150 and 250 ms after the initial movement

and substantial forward directed forces were clearly distinguishable in

the same time period.

Having given these definitions, it must be noted that the useful-

ness is unfortunately somewhat limited. If a table movement lasted

100 ms, the class 1 force associated with cessation of movement

occurred simultaneously with any class 2 force which followed the

onset of movement. Also, if the cessation of movement elicited a

class 2 force, it would occur in coincidence with the class 3 force

following initial movement.

The above difficulties clearly arise because a table movement

can not occur rapidly enough to really appear as a step function without

causing foot slippage. There will always be positive and negative

accelerations sufficiently separated in time to be discerned as two

distinct stimuli. For this reason, a table movement will be consid-

ered as presenting three stimuli to the dog as follows: Stimulus a,

starting acceleration; stimulus v, sustained velocity of displacement;

stimulus d, stopping acceleration (deceleration). Now a force pertur-

bation can be described as class 2 relative to stimulus a (class 2a) or

perhaps as class 2d/3a where both classifications fit equally well.

We now consider how to apply the above definitions to typical

force records. The basic method is to locate each distinguishable

stimulus in time and then mark off two successive time periods follow-
ing every stimulus according to the time intervals given for classes
2 and 3. A ramp movement contains stimuli a, v and d. Class 1
forces must occur simultaneously with either stimulus a or d. Class
2 and 3 forces can occur in response to any of the three stimuli.

In Figure 18, each of the time periods following the stimuli are
shown as a time line. From this diagram, each period of overlap can
be found. Since stimulus v does not appear to produce important
responses (this will be discussed later), the significant periods of
overlap reduce to those shown as I1 and I2. In these periods, the
force classification will be ambiguous on the basis of timing alone, and
some additional factors must be included. Fortunately, the periods of
overlap change whenever the duration of table movement is changed
and certain of the ambiguities can be resolved by comparing responses
from ramp movements of several different lengths. Figure 18 shows
the classification times for an 80 ms ramp where the overlap periods
I1 and I2 are 20 and 60 ms, respectively. For 100 ms ramps, I1
vanishes and I2 lengthens to 80 ms. Classification of forces in I2 will
be explained below.

To show how the classification method works, a pair of force
responses from Dog 8531 are separated and analyzed in Figure 19.
Class 1 forces can be readily discerned since the ramp duration is
rather short. In the tailward movement, the class 2a pulse is

typically distinct and is followed by a force which is either class 2d or class 3a. Since the force is in the direction of action for stimulus d, the class 2d specification is preferred and is denoted by class 2d(3a).
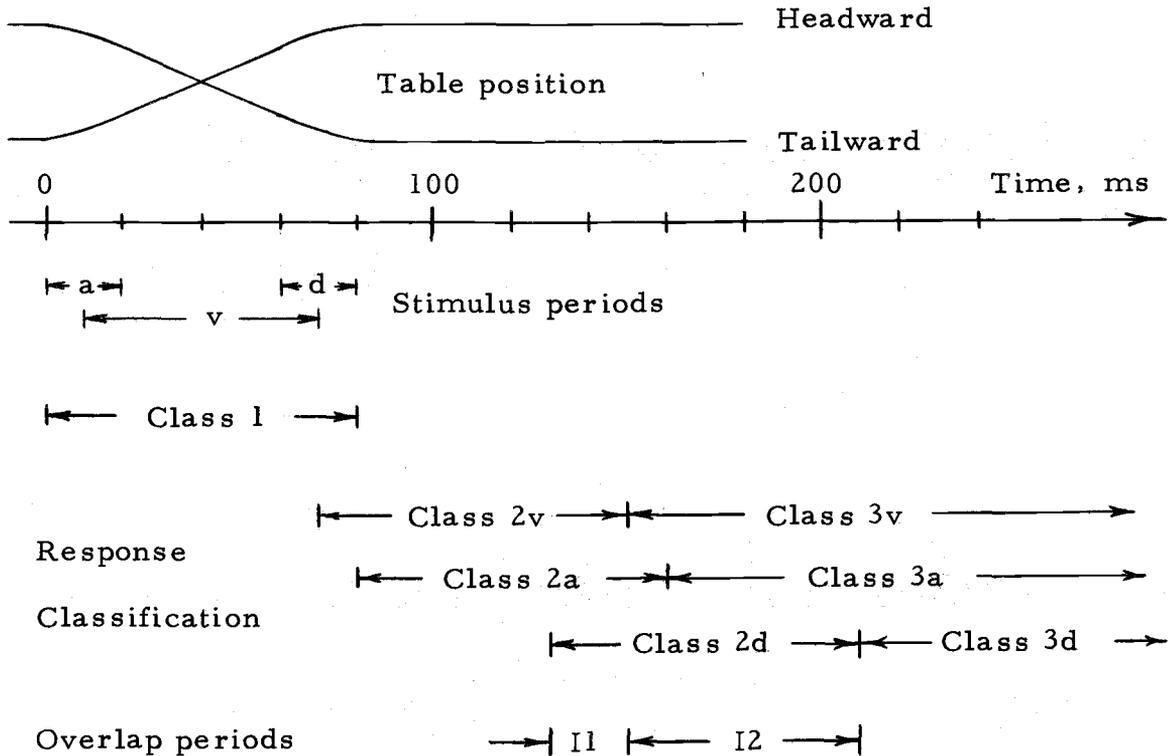
Figure 18. Timing diagram for force classification.

The headward movement shown in Figure 19 is essentially the same as above with regard to the class 1 and 2a forces. The last two forces appear to overlap enough that their time of occurrence and classification are less certain. The class 2d pulse seems to be wedged between the 2a and 3a peaks, an occurrence which was common

Total longitudinal force

Total longitudinal force

Class 1a, 1d

Class 1a, 1d

Class 2a

Class 2a

Class 2d

Class 2d(3a)

Class 3a

All forces are 1 kg/div

Table position, cm

4

Time, 100 ms/div

Time, 100 ms/div

Headward

Tailward

Figure 19. Separation of typical force responses. These responses
are the same as the 4 cm records for Dog 8531 which are
shown in Figure 20.

when rapid body movements were attempted.

Figures 20 and 21 contain examples of responses for Dogs 8531 and 8514, respectively. The 4 cm records in Figure 20 are the same as were classified in Figure 19. Each of the remaining responses can be similarly specified by the separation process which has been illustrated. These records, as well 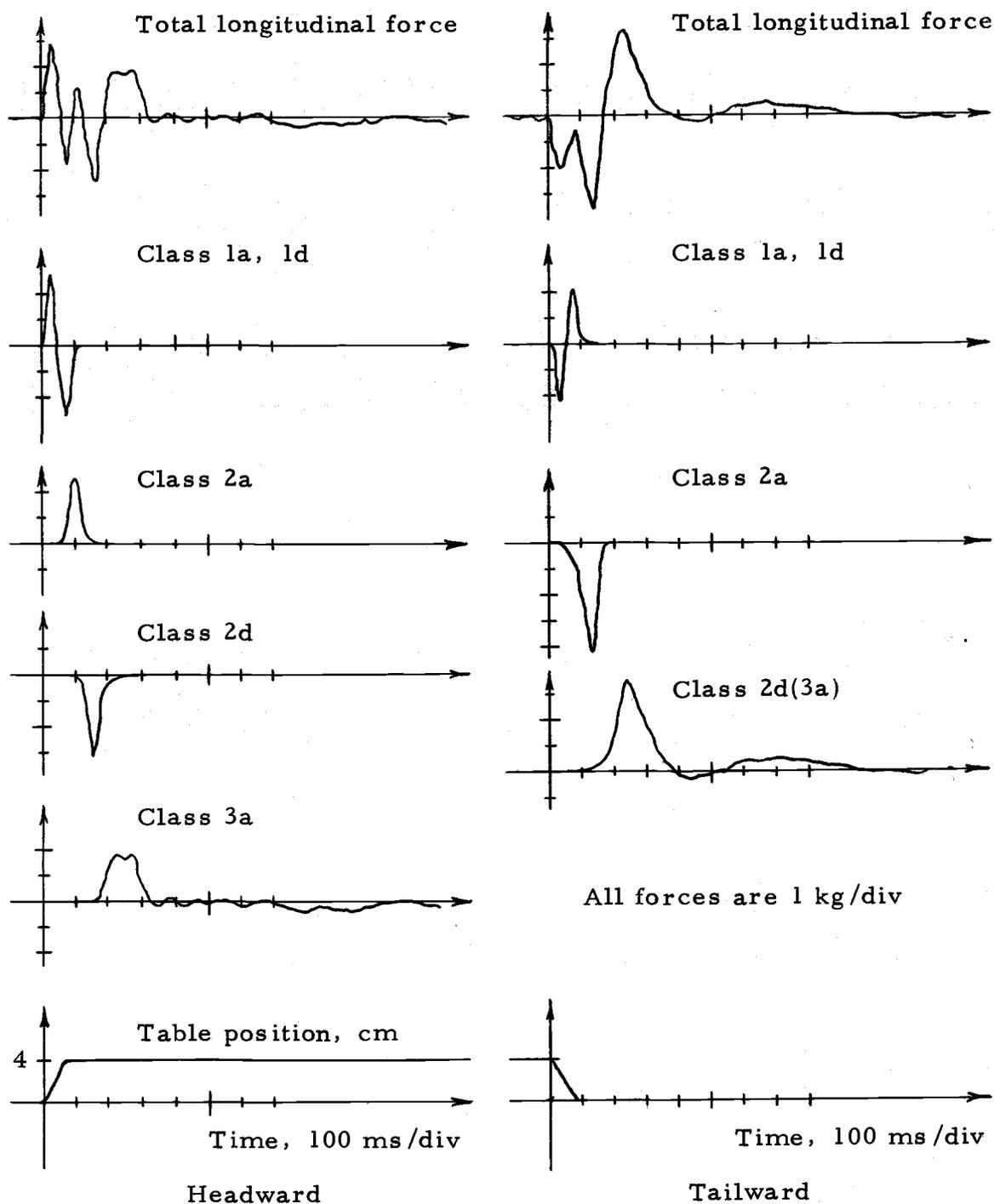as those which follow, show that the dogs produced body movement with short pulses or bursts of force rather than with sustained forces of lower level. Since a single burst is seldom adequate to reach the desired posture, there may be two or three FPO pulses before activity returns to typical quiescent levels. Because the force pulses seem to appear in a regular manner, it is natural to look for stimulus-response relationships which might be compatible with known facts regarding central nervous system and neuromuscular functions. The force classification scheme being applied is intended to assist in this process.

Dogs 8514 and 8531 were generally faster in body movements than were Dogs 8450 and 7772 which will be discussed next. This could be due partly to the fact that they were both somewhat smaller, perhaps 15 percent shorter at the shoulders. With shorter legs, a given displacement of the feet will obviously produce greater inclination of the legs. It is not possible to know whether this factor or the relative lack of experience accounted for the differences in speed of body movement during recovery from induced postural distortions.
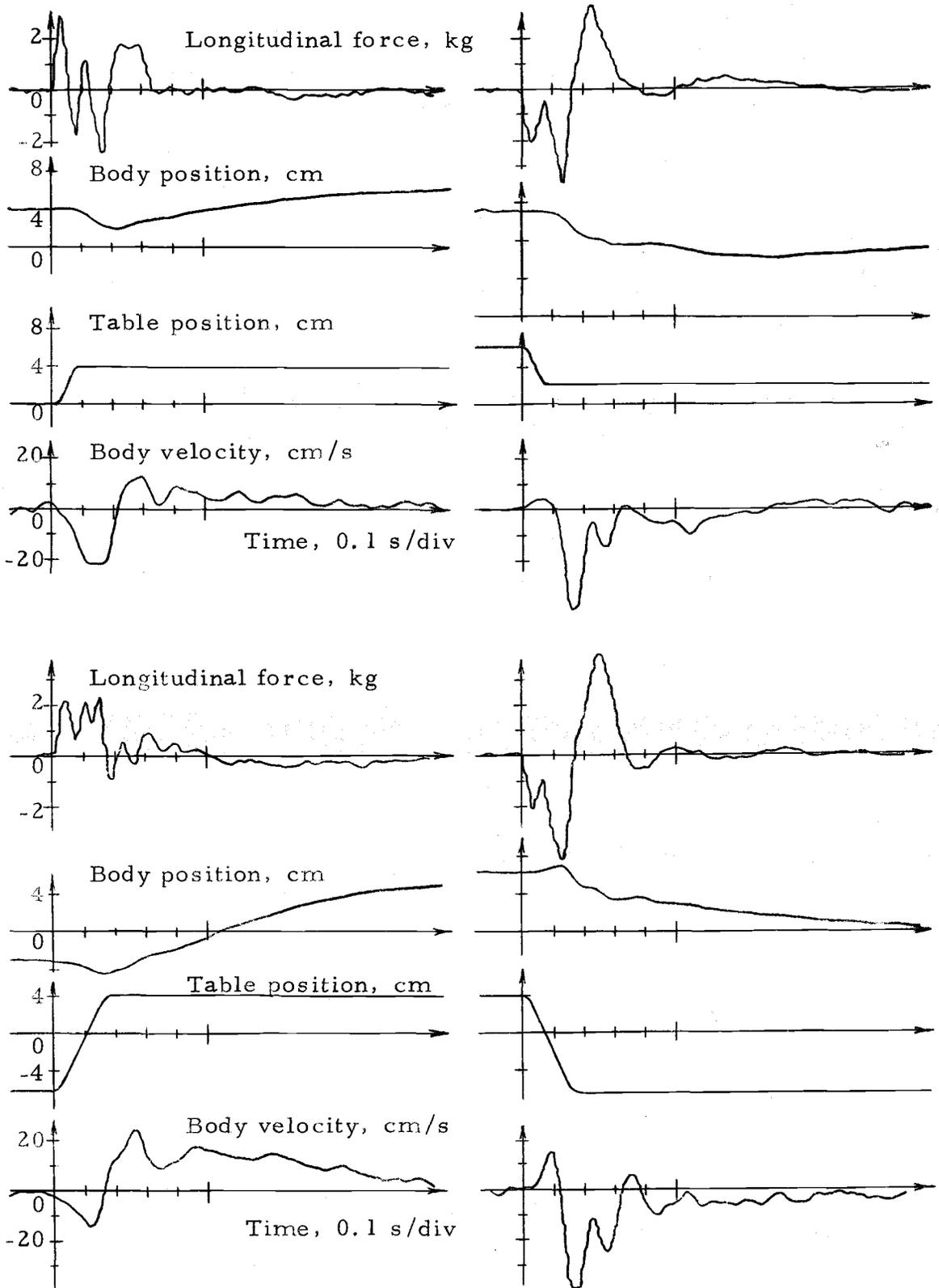
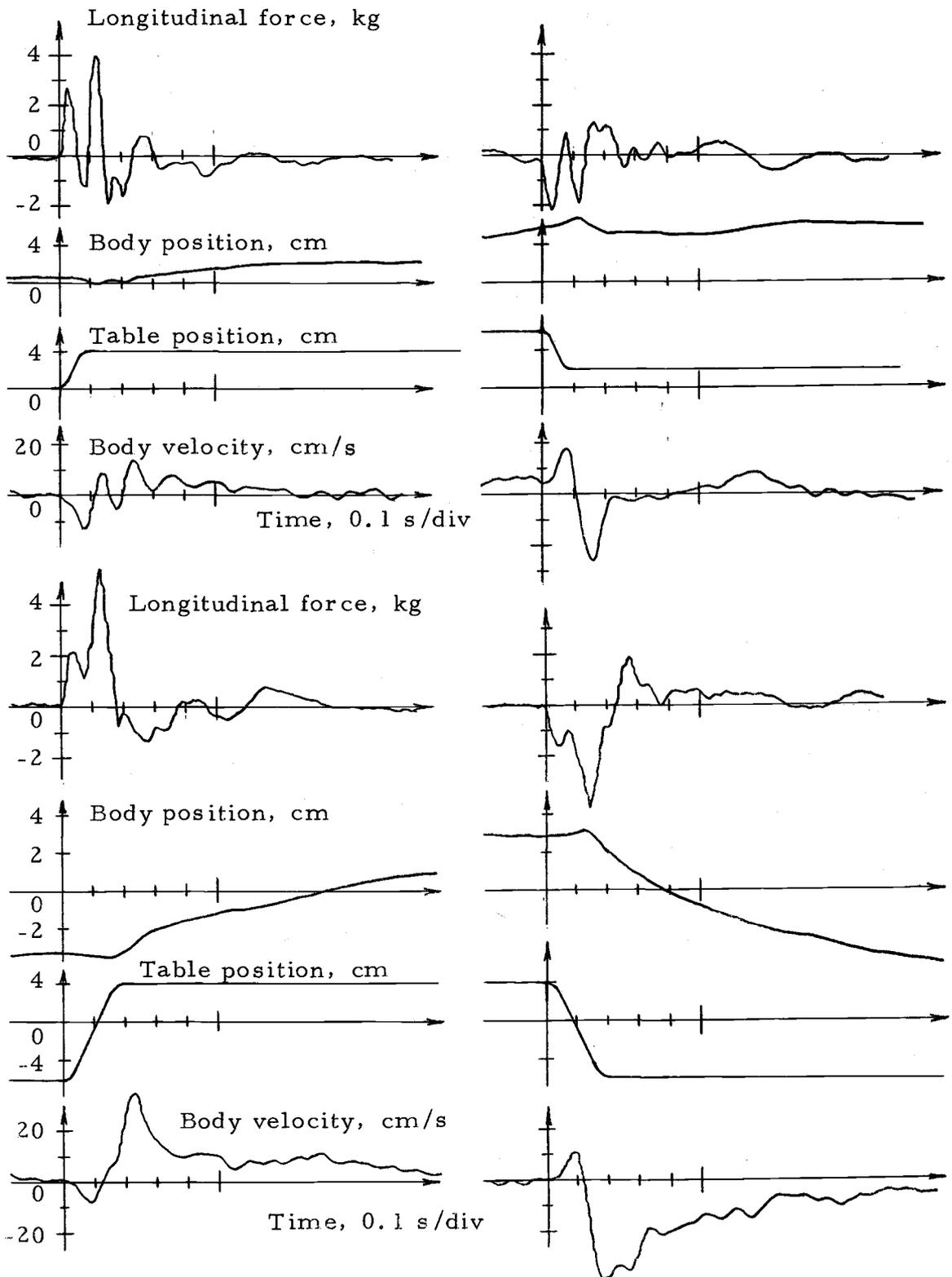Figure 20. Responses to short and long ramps for Dog 8531.

Figure 21.   Responses to short and long ramps for Dog 8514.

Responses from Dogs 7772 and 8450 are shown in Figure 22. Because Dog 7772 produced almost no FPO, the class 1 forces are distinct at both a and d. The first headward movement for this dog in Figure 22 shows a weak class 2a force, whereas it is completely absent in the second. The tailward movement again shows the distinct class 1a and 1d forces followed by a class 2a force, which is typical for tailward movements. The momentum imparted to the body by the class 2a pulse is quickly negated by the third force which is class 2d(3a) and in opposition to the direction of body movement.

Dog 8450 characteristically overcorrected postural distortions induced by headward displacements but was rather slow in responding to the tailward movements. The more rapid headward movement, sometimes equivalent with the two inexperienced dogs, is obvious in the first movement shown in Figure 22. In the horizontal force record, the class 1a force is as distinct as before but the class 1d force is superimposed on either a class 1v (arising from viscous friction or damping in the muscles) or the rising edge of a class 2a pulse which is fully developed at the second peak. The third force peak is classified as class 3a because it is in the wrong direction for a class 2d force. The record of tailward movement is quite similar to Dog 7772 and there is again a question regarding the classification of the third force.

From the second headward movement, we see that the magnitude
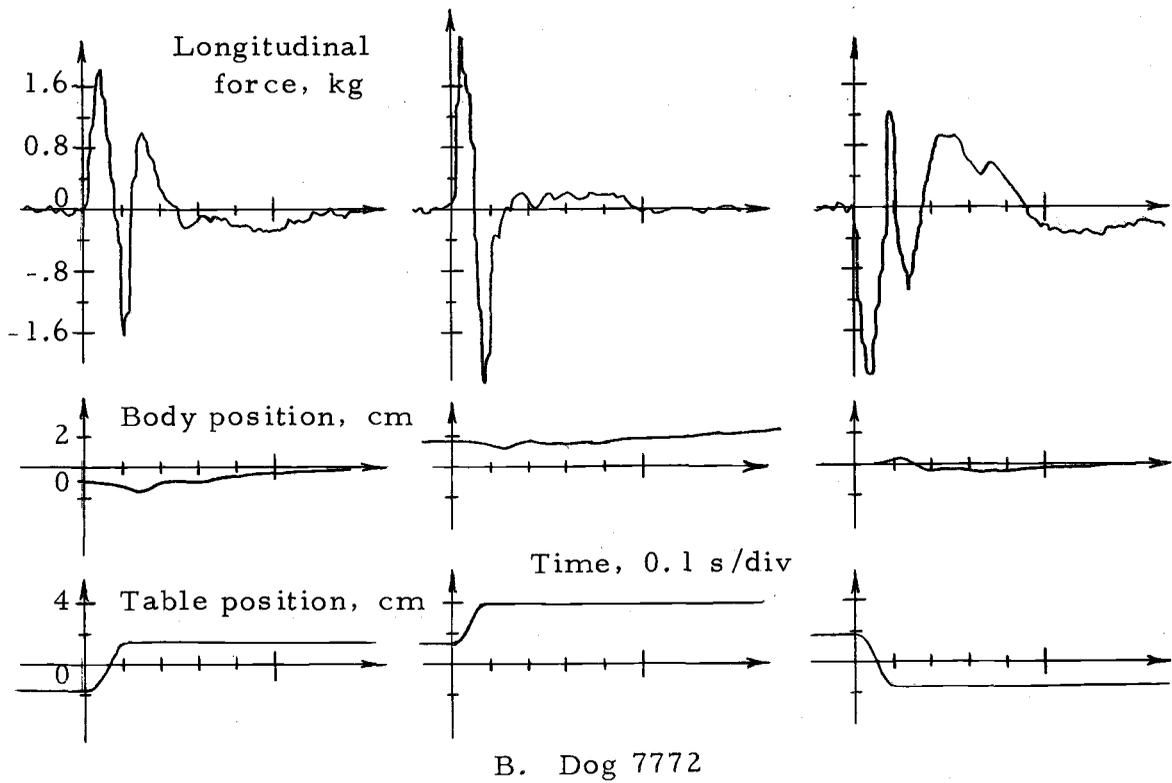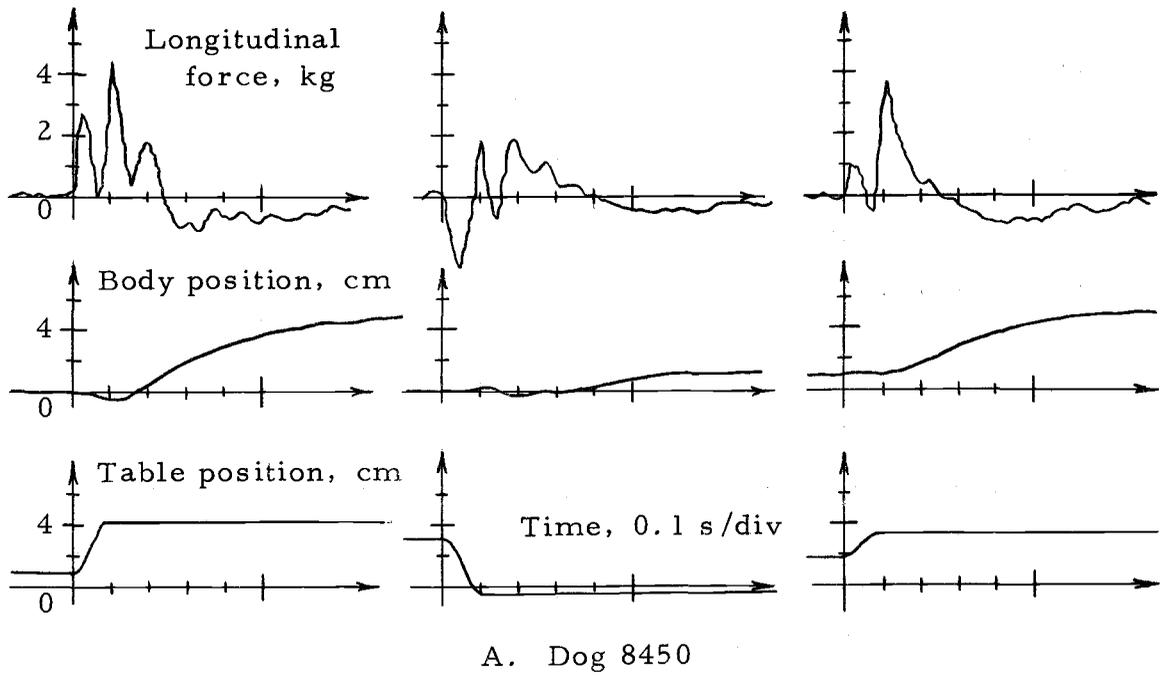
A. Dog 8450

B. Dog 7772

Figure 22. Assorted short ramp responses for two dogs.

of a class 2a force is not always dependent on the magnitude of the table displacement as might be expected. Since the position of the body was about the same for the two headward movements shown, there is no certain way to explain what determines the magnitude of a class 2a force. If this force originates in the higher centers of the brain stem as suggested by Melvill Jones and Watt (1971), it may be that the level of muscle excitation is preset according to what the dog would be expecting, or at a level which would be acceptable for most possible table movements. In this example, the force pulse produced more than twice the required movement, indicating that it was much larger than necessary. A third force peak is absent and the level subsided to low values typical of very slow corrections of position error, thus compensating for the initial overexertion.

Now that a number of force response patterns have been examined, we can reconsider the identification of the class 2a forces. Several properties of these forces deserve rather extended consideration.

If the class 2a forces are really manifestation of the functional stretch reflex, then they should probably be classified as class 2v, since the functional stretch reflex allegedly arises from stretch rather than acceleration or external forces. Because table velocity and the corresponding stretching of leg muscles would develop more slowly than the acceleration peak at stimulus a, the timing of the class 2a

force peaks makes them somewhat questionable as class 2v forces.

Another evidence favoring the classification as it has been given is found in the work of Mori, Reynolds and Brookhart (1970), who reported that animals which were deprived of certain sensory afferents by a condition of pedal anesthesia were considerably slower in their initial response to table movement. At the time of those investigations, there was no way to measure horizontal forces, but it seems apparent that removal of the class 2a force pulses could result in slower movements such as were observed during the pedal anesthesia. If this is the case, the class 2a forces are most likely stimulated by receptors in the pads of each foot. These receptors would report the presence of a shear force whenever the legs were experiencing acceleration and also when the legs were coupling forces between the body and the table. Since the first indication that an event is occurring is the shear force developed during stimulus a, it is logical to expect that these forces would elicit some observable response. In the experiments of Melvill Jones and Watt (1971), a forceful contraction of the gastrocnemious was observed about 150 ms after the muscle was stretched by dorsiflexion of the foot. (This contraction appears to be analogous to the class 2a force. The timing difference arises because of longer neural pathways in the human.) Although the authors attributed this contraction to the stretching of the gastrocnemious , there is no apparent way to exclude the possibility that the

observed force was really a response to the external force applied to dorsiflex the foot rather than muscle stretch.

Another argument supporting the idea that acceleration (shear force on the foot pads) does indeed elicit a direct response is that other sensory data seems to provide less explicit information about current or future movement of the legs and feet. Because the external force is applied directly to the feet, sensory signals arising from the feet are the most direct consequence of these forces. Other mani- festations of the external force would appear as rotation of the joints and stretching of many different muscles. To determine the current behavior of the entire leg, a large amount of sensory data from the muscles and tissues (particularly the tissue near joints) would have to be evaluated by a potentially time-consuming process of sensory integration.

The importance of shear force detection during stimulus a or d is further emphasized by arguments which suggest that joint angle sensory processes are not suitable for immediate assessment of changes in leg and body positions. One evidence supporting this speculation is that during and immediately following periods of table movement, large errors in body position are tolerated without cor- rective action. Ramp movements often produce a response overshoot of 200 percent. If the amount of table movement could be rapidly determined from the changes in leg inclination (joint angles), these

overshoots should be better controlled.

The behavior of the dog's body during sinusoidal table movement has also raised questions regarding the effectiveness of joint angle sensory processes. During these movements, the body position contained a distinct component at the table frequency which was superimposed on a slow, quasi-random drift between two fairly distinct limits. The sharpness of the turn-around when the limit is reached suggests that sudden torque changes have been triggered by some sensory process which was previously either inactive or ineffective. Since muscle and skin sensory receptors must be continuously active during sustained sinusoidal movements, it follows that their input to the postural control mechanism is inadequate to eliminate the drifting behavior. Hence, there is reason for suspecting that their contribution to the determination of body position is of less importance than might have been supposed.

Both ramp and sinusoidal responses give evidence that position control is highly pulsatile. In the ramp response it is the class 2a pulse which produces the initial rapid movement. The sinusoidal responses suggest that a corrective pulse is triggered whenever the balance of stability of the body is endangered by having drifted away from a central position on the moving table. The notion that motor activities can be directed by neural networks which generate stereotyped behavioral "programs" upon receipt of a command signal (such

as shear force detection) is commonly accepted by neurophysiologists. Hence, it is not surprising that the initial force response following a ramp displacement of the table would be pulsatile and specified only by direction, having been triggered by output from shear force sensors in the foot pads.

In summary regarding the shear-force stimulus at a foot pad, we might say that the pattern of force responses from the dog are similar to what would be expected if an engineer designed a position control system where the primary sensor gave gross measurements of external force application. It would be intuitively practical to control this system by responding with large pulsatile efforts when external forces were encountered and then to make further corrections whenever the position of the system could be accurately determined from the secondary sensors. By responding directly to force, control action could be initiated before velocity and position data would reveal much change in the system state.

Changes in horizontal force during postural movement are the most direct external manifestations of neuromuscular activity in the dog; hence, we have devoted considerable space to describing the features which were observed. If both vertical and horizontal forces at a foot are known, then the analysis of Chapter II provides a method for obtaining the torques at each joint of a leg. These joint torques are the direct result of interactions between muscles and skeletal

members and therefore are even more closely related to muscle
activity than are the end-reaction forces. Realizing that changes in
muscle behavior are a direct consequence of CNS activity, we will
next examine the patterns of torque change associated with a pair of
table displacements.

The table movements used for this example were 80 ms ramps
of 2 cm magnitude. Because vertical and horizontal forces could not
be measured simultaneously at the same foot during table movements,
it was necessary to use records of vertical forces from the left feet
and horizontal forces from the right feet. These data give a reason-
able account of torque changes in the right legs because there is little
difference between the patterns of force perturbation seen on adjacent
feet. Equations (1)-(6) have been repeated as Equations (14) and (15)

$$0.020 \, F_{va} - 0.385 \, F_{ha} = T_{1a}$$

$$0.067 \, F_{va} + 0.251 \, F_{ha} = T_{2a} \tag{14}$$

$$0.054 \, F_{va} + 0.072 \, F_{ha} = T_{3a}$$

$$-0.020 \, F_{vp} + 0.449 \, F_{hp} = T_{1p}$$

$$0.059 \, F_{vp} - 0.274 \, F_{hp} = T_{2p} \tag{15}$$

$$0.040 \, F_{vp} + 0.124 \, F_{hp} = T_{3p}$$

with numerical values of the coefficients for a body position $y = 2$ cm

(forward lean) and the geometry of Figure 6. The force and position

records used as data appear in Figure 23 and the calculated torque

patterns are plotted in Figures 24 and 25. The torque curves begin

75 ms after onset of table movement when inertia (class 1) forces

were becoming negligible. This point coincides with the initiation of

muscle activity and is therefore the first point of interest regarding

torque changes caused by muscle effort.

The first observations from these figures is that adjacent joints

(excluding the wrist) show inverse changes in torque during horizontal

force changes. If the posterior limb is to thrust forward, the most

effective action is to increase the torque at the hip. (See Figures 15

and 17.) The ankle torque must next be increased to avoid collapsing

the joint. These combined actions would elevate the body unless the

moment at the knee is reduced.

Equation (16) specifies the equilibrium relationship among the

joint moments of the posterior limb which was first given as Equation

$$-0.018T_{1p} - 0.021T_{2p} + 0.021T_{3p} = 0 \qquad (16)$$

(12). By observing the signs and magnitudes of each coefficient, we

see that an increase in T_{1p} can be offset by decreasing T_{2p}

and/or increasing T_{3p}. In this way, a forward thrust can be devel-

oped without greatly distorting the mechanical configuration of the leg

as would result from violation of Equation (16). A reverse thrust in

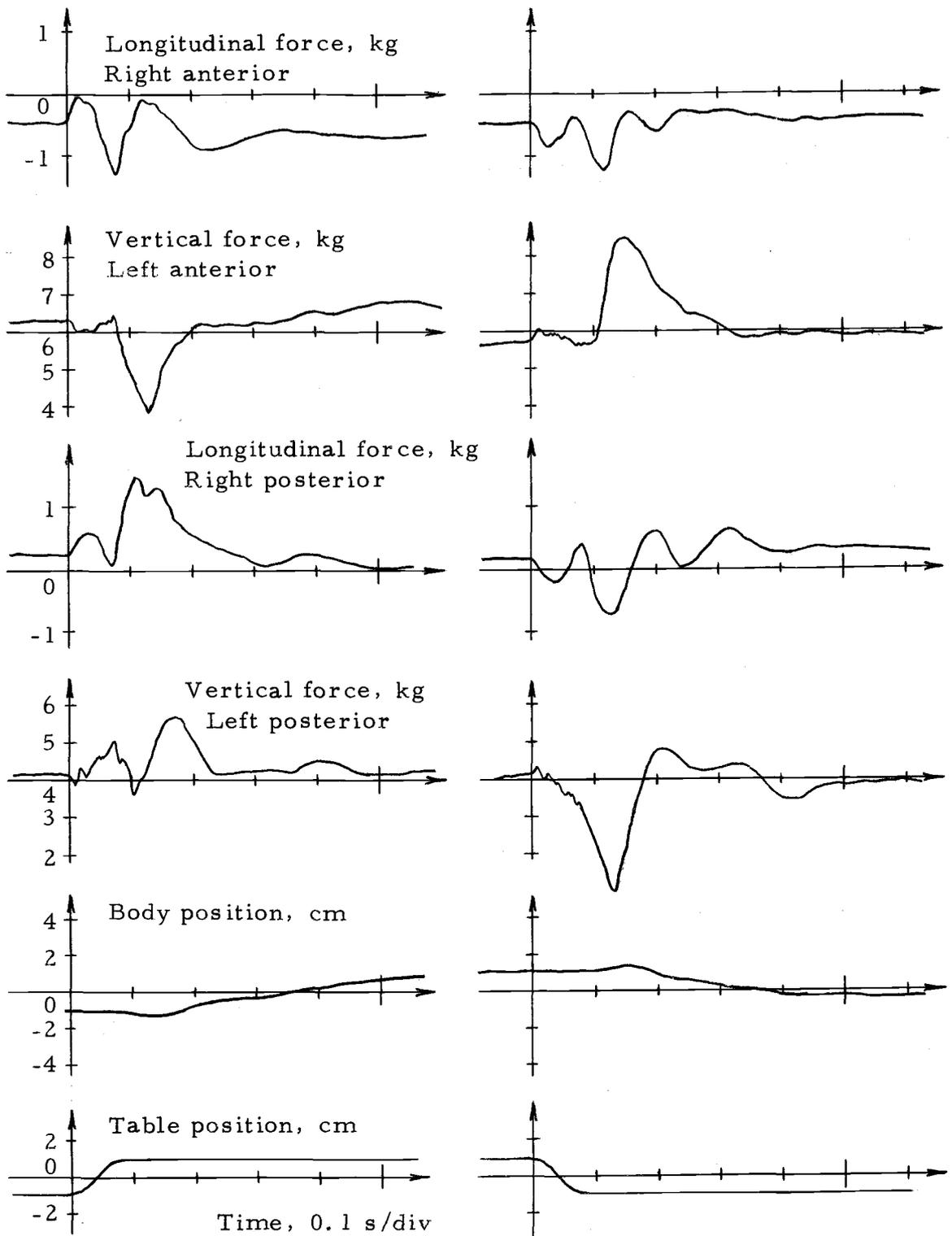Figure 23. Vertical and horizontal force responses to 2 cm ramps for Dog 8531.
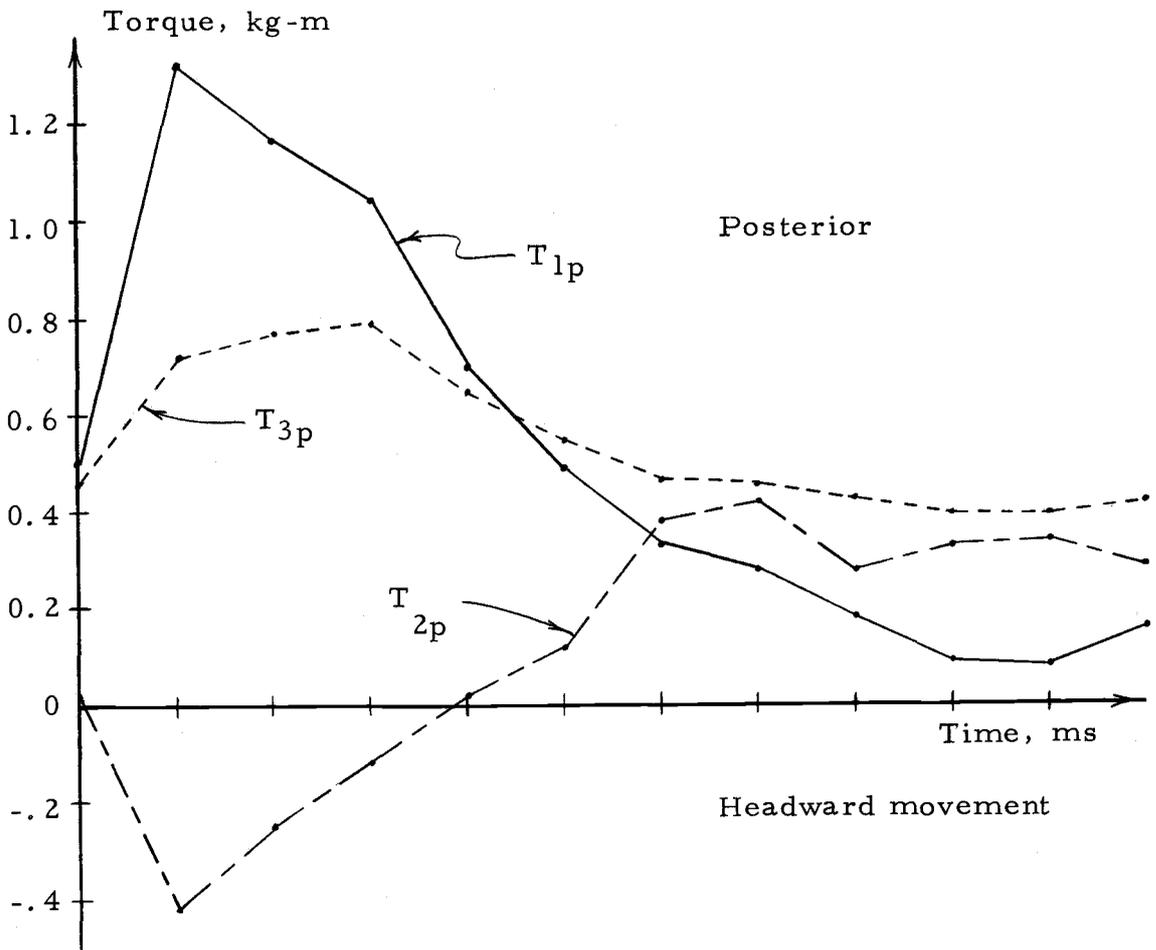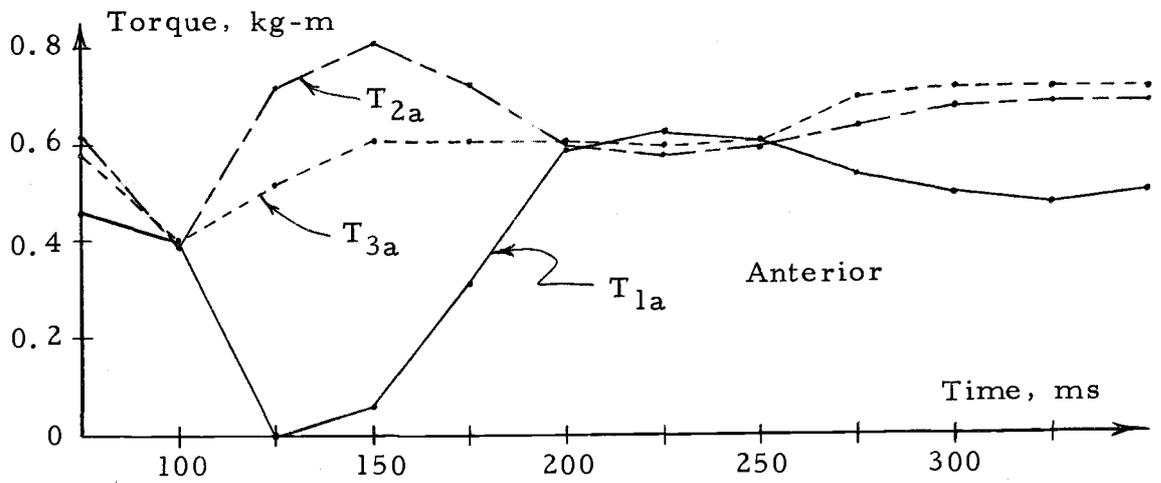
Figure 24. Joint torque response to a headward table movement for Dog 8531. The torque values were calculated for the 2 cm headward ramp response shown in Figure 23.
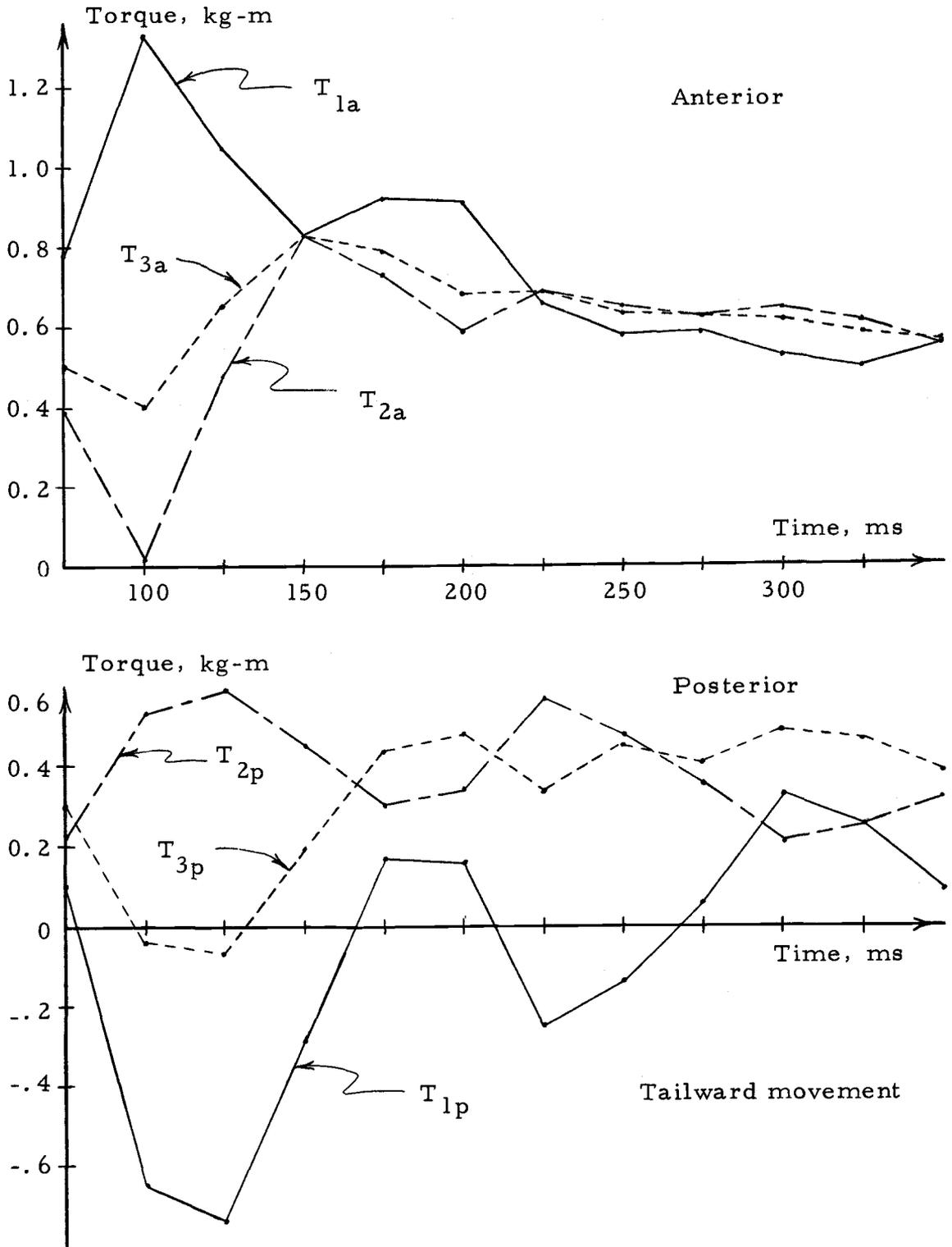
Figure 25. Joint torque response to a tailward table movement for
Dog 8531. The torque values were calculated for the 2 cm
tailward ramp response shown in Figure 23.

the posterior limb would follow from opposite changes in each of the torques.

Another intuitively sound conclusion from these figures is that for headward movements, torque changes in the posterior limbs are greater than for tailward movements. In the anterior limbs, torque perturbations are greater for tailward movements. In this way, the legs are used more to push the body than to pull it.

It should be noted that a forward directed force perturbation in the anterior limbs is actually a reduction of the normally present rearward acting bias force. (The direction of the force will not change until major efforts of movement occur.) This force reduction may be accomplished by reducing excitation of muscles normally active in quiet standing as well as by increasing excitation of their antagonists. It is quite possible that a rearward acting pulse is produced by increasing excitation of the normally active muscles and that a forward acting pulse follows from decreasing excitation of the same muscles. (The opposite condition will exist in the posterior limbs.) This factor may also make it more practical to push the body than to pull it.

There is one remaining observation which can be best presented by returning to Figures 16 and 17. In these figures, each succession of directed line segments represents the time history of torque changes (from Figures 24 and 25) during the response to a table movement.

P_0 is a representative quiescent level and points P_1 and P_2 give

the maximum deviation from the quiescent torque levels. By recalling

the explanation given earlier, we see that in the transition from P_0

to either P_1 or P_2, there is a decrease in vertical force. The

succession of points returning from the points of maximum torque

change shows that the body was lifted as the torques settled back to

quiescent levels. In this way, the effort of lifting the body was

delayed until after the maximum horizontal force perturbations had

occurred.

IV. IMPLICATIONS RELATING TO FUNCTION

Introduction

The purpose of this chapter is to examine the functional signifi-
cance of certain properties of the biomechanical and neuromuscular
structures of the dog which were not revealed by the mechanical
analysis given earlier in Chapter II. Because muscles and bones
reduce conveniently to mechanical levers and elastic tension genera-
tors, the functional significance of an anatomical structure can be
discerned reasonably well. The CNS, however, is electrochemical
rather than mechanical in its nature and very few of its integrative
functions can be directly related to neuro-anatomy. For this reason,
observations concerning biomechanical properties can be presented
with some confidence whereas statements regarding the CNS can be
advanced only as speculations.

Sensory Functions

The analysis of skeletal mechanics given earlier provided
several arguments for expecting that a dog would stand with a slight
forward inclination of both anterior and posterior legs and that he
would generate a significant (1/2 kg per foot) horizontal shear force
(the bias force) at each foot by attempting to spread his legs longi-
tudinally. These combined actions tended to produce a favorable

distribution of effort among the various joints without a really sig-

nificant increase in the total effort of standing. Beyond this, the

bias force may also improve sensory functions in the feet.

To be more specific, we recall that the major peak in a typical

force response has been identified as class 2a (or class 2d). Because

the sensory stimulus associated with table acceleration is a perturba-

tion of shear force on each foot, we can conclude that shear force

detection is an important sensory function. We now speculate that the

presence of a bias force will improve detection of force perturbations

by the subcutaneous sensors in each foot pad. Two reasons for this

speculation follow below.

First, the shear force would produce tension in the tissues of a

foot pad and thereby elevate the steady-state output level of the sub-

cutaneous sensors. This "biasing" of the sensory receptors could

make them more sensitive to change and perhaps reduce the tendency

toward adaptation. (In neurology, adaptation refers to the process of

gradually losing sensory acuteness during prolonged periods of

unchanging tactile stimulation.)

Second, because the foot tissues would be stretched lightly there

would be less chance for rocking and sliding of the feet on the pads.

This would produce better mechanical stability by "taking up the slack"

in the foot contacts and thereby reduce the level of "noise" in the

sensory data. In this regard, it is interesting to note that a dog has considerable difficulty standing or walking on a slick surface such as ice or a smooth floor where the advantages of a bias force are absent.

To introduce another topic we note that, in the process of quiet standing, one function of the CNS must be to evaluate the body posture and compare it with what has been learned as the "correct" posture. The regulation of quiet standing in normal animals has been examined by Brookhart et al. (1965) who hypothesized that quiescent postural control was accomplished by the continuous correction of small errors in body position. The dog was not able to maintain exact control, but drifted irregularly over a distance of ±1 cm from a mean reference point. The suggested causes of this "noise" observed in the body position were various neural instabilities and/or fatigue of muscle tissue. So far, it has not been possible to determine what sensory processes are employed to determine body posture, although certain sensory inputs appear to subserve roles of minor importance (Nakao and Brookhart, 1967; Mori, Reynolds and Brookhart, 1970).

The current observations have suggested that sensory data regarding shear force at each foot is of primary importance for rapid body movement, but there is no new suggestion regarding the control of quiet standing. We can, however, reinforce the idea that muscle fatigue and general comfort do indeed contribute to the continuous drifting of the dog during quiet standing.

The data given in Chapter II show the quantitative variations of joint torques with respect to body position and as a function of the horizontal bias force. A movement of 1 cm combined with adjustments of the bias force would serve to relieve muscles which had been fatigued. It is reasonable that this factor alone could account for most of the wandering movement which is seen. Unfortunately, there is no apparent method available to test this supposition.

Two-Joint Muscles

A brief inspection of muscle anatomy (see Figure 5) reveals the presence of several large muscles of the posterior limb which connect directly from the pelvis to the tibia, thus spanning both the hip and knee joints. The utility of these muscles will become apparent in the discussion below.

During quiet standing the torques at the hip and knee are normally positive, that is, the femur is pulled backward at the hip and the knee is held open. Biceps anterior, a division of the large muscle biceps femoris, connects to the pelvis behind the hip pivot and then passes over the front of the knee to connect to the tibia. Tension in this muscle will extend both the hip and the knee, thus acting to support the body. It is among the few muscles which acts to extend two adjacent joints.

Two other muscles, semitendinosis and the caudal belly of

semimembranosis, are connected to the pelvis behind the hip pivot and then attach to the tibia behind the knee. These muscles will close the knee joint while pulling the thigh backward at the hip, i.e., increase T_{1p} but decrease T_{2p}. This action will thrust the body forward without a disproportionate upward action (see Figure 17). As the body responds by moving forward, the femur will rotate backward while the knee opens. The opposite actions at the hip and knee will allow considerable body movement without much change in the length of the muscle. If separate muscles at the hip and knee were used to move the body, the hip muscle would have to lengthen as the knee muscle shortened. On the front of the thigh, the muscles rectus femoris and sartorius perform symmetric functions.

There are several other properties of the two-joint thigh muscles which make them particularly convenient for horizontal thrusting. First, because these muscles increase T_{1p} and reduce T_{2p}, the condition of equilibrium given in Equation (16) will be nearly satisfied without large changes in T_{3p}. In fact, if the lever arms at the hip and knee were in the ratio of $0.021/0.018$, respectively, the tension changes in the two-joint muscle would not disrupt the equilibrium condition at all. The second advantage of these muscles follows because the line given by $T_{1p} = (0.021/0.018)T_{2p}$ is nearly perpendicular to Grad F_{vp} as shown in Figure 17. Thus, if the torque changes at the hip and knee preserve the equilibrium condition, they

will also cause horizontal thrust but no large vertical thrust. The particular muscles which exist probably do not exactly satisfy these conditions, but they are certainly well designed to exploit the mechanical properties of the leg.

If we consider the problem of controlling the leg, there are further advantages of the two-joint thigh muscles. The most obvious is that a horizontal thrust can be developed with only one muscle group rather than two. If separate muscle groups were used at the hip and knee, it would be necessary to control each of them separately and to "match" their tension outputs to maintain the equilibrium condition of Equation (16). Because each muscle will have distinct dynamic properties, the close matching of tension output during major rapid efforts could be difficult to achieve. The significant time delays for tension response after application of a nerve stimulus as well as propogation delays in the nerves themselves could lead to a system with tendencies toward unstable behavior.

Despite the utility of the large two-joint muscles of the thigh for rapid horizontal thrusting, they do not assist in the task of supporting the body except in the case of biceps anterior (the section of biceps femoris mentioned above). A tension in this muscle will increase the value of T_{1p} and T_{2p}, tending to lift the body, but also violating the equilibrium condition of Equation (16). To restore equilibrium, we can increase T_{3p} and/or decrease T_{2p} using

other muscles. The gastrocnemius is a two-joint muscle of the lower

leg which will accomplish at least part of the required adjustments

and is the major muscle acting at the ankle. The remaining effort for

body support is probably provided by the large one-joint muscles such

as adductor magnus and semimembranosis (cranial belly) at the hip

and vastus lateralis, medialis and intermedius at the knee. Regard-

less of which muscles are used, supporting the body weight requires

action of at least two muscle groups. There is probably less need for

rapid pulsing in the vertical direction, hence, the timing requirements

for the muscle control system are somewhat relaxed.

During the discussion regarding stability of the posterior limb

given in Chapter II, it was shown that of the three joint torques, only

two could be independent. The two-joint muscles are nature's answer

to the problem since they create dependent torque changes at their

proximal joints. Even more elegant than this is the three-joint action

of semitendinosis and biceps femoris. At the point where semiten-

dinosis attaches to the tibia just below the knee, there is a tendon

which joins with the Achilies tendon at the heel. Thus, semitendino-

sis will tend to increase T_{1p} and T_{3p} while decreasing T_{2p}.

When in the proper proportion, this action will again satisfy the

equilibrium condition. It is clearly possible to produce dependent

torque changes at all three joints by using only one muscle. This

again makes the leg more readily controllable and quite effective for

the combined task of lifting and thrusting forward.

In the anterior limb where the primary task is to support the body weight, the triceps brachii long head is the only powerful two-joint muscle. Tension in this muscle will increase T_{2a} and decrease T_{1a}. A check with the gradients shown in Figure 16 shows that this action will produce a forward thrust without much vertical thrust. In this leg, the equilibrium problem does not occur, so that control of the muscles is less critical than before. The burden of supporting the body weight again falls on powerful one-joint muscles.

V. SUGGESTIONS FOR A MODEL

Introduction

The analysis of a complex system such as we have described is severely limited because of the indefinite structure of the CNS and because many internal variables can not be measured without altering the behavior of the system. In modern science, many complex life systems are gradually being described by models which can be examined via computer simulation. This method is very useful because every aspect of the system model can be observed or altered as desired. The final contribution of this study will be to describe certain attributes which a model of the postural system must possess. These attributes are presented in a general form and, unfortunately, do not provide enough detail to justify implementation of the model.

The Skeleton and Muscles

The most certain part of the model is the mechanical structure representing the skeleton and major muscles. The suggested model given in Figure 26 represents a simplification of the dog's body which is justified by the high degree of lateral symmetry usually present during postural experiments. Each joint has been reduced to one degree of freedom and the leg segments (including the feet) have been replaced with rigid levers. This simple model should adequately
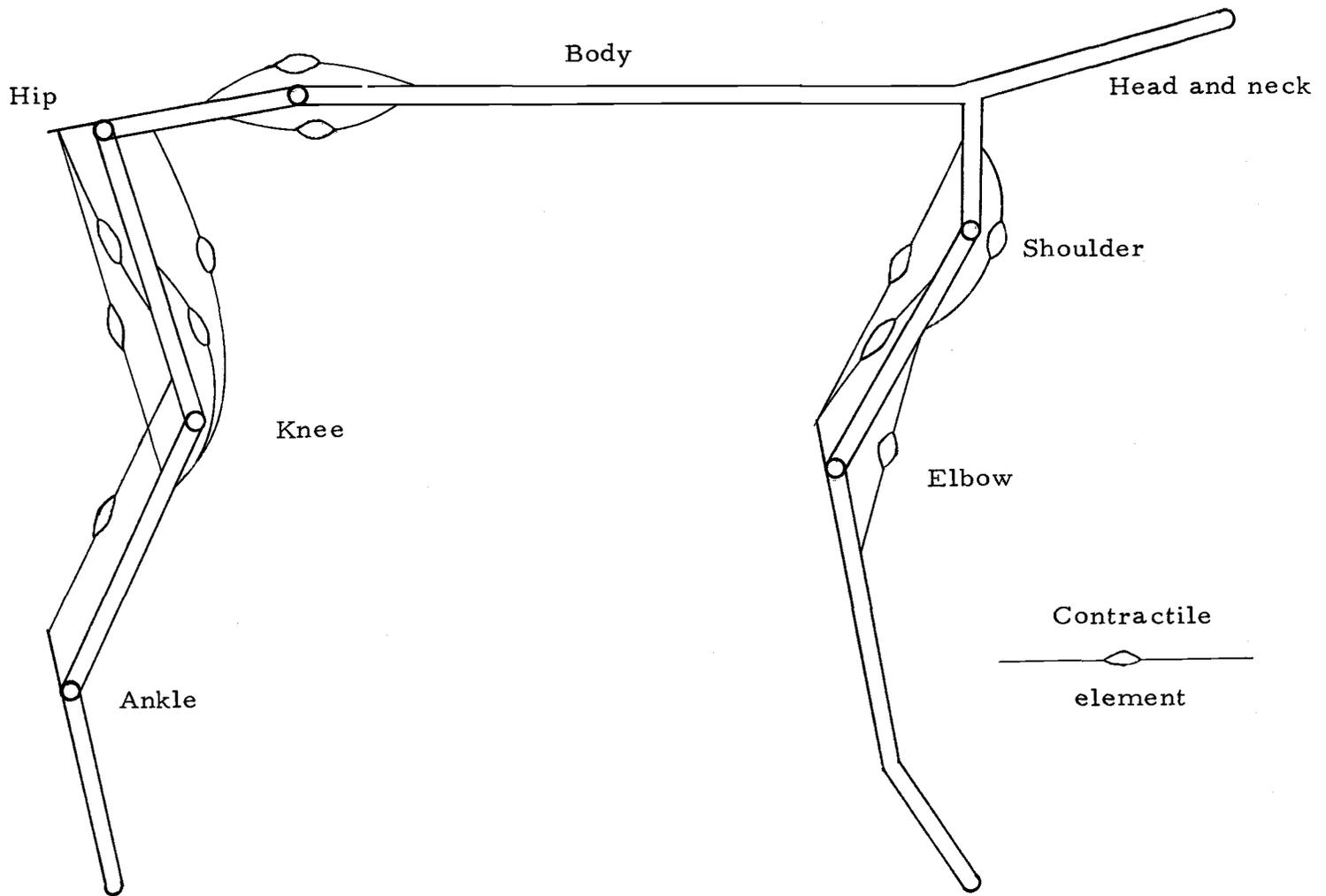
Figure 26. A proposed model for the skeleton and musculature. All joints have one degree of freedom. The model is suggested only for longitudinal movements which are accomplished without moving the feet.

represent the essential mechanical features of the dog required for fixed-foot longitudinal movements. The mass of the body, head and neck should be distributed to give proper moments of inertia and centers of gravity. The mass of the leg segments can be neglected when considering only gross body movements.

In Chapter II, we spoke of choosing the joint moments in a leg so that the desired end-reaction forces would occur at each foot. The posterior leg model contains five major muscles. This means that the tension in each muscle must be chosen to preserve equilibrium while also generating the desired end-reaction forces. Since any muscle can be replaced with an ideal torque generator at the joints which it covers, each joint torque will become a linear combination of one or more of the muscle tensions. The equilibrium condition for the joint torques can be rewritten as a condition on the muscle tensions. The control problem is to find a way to vary the muscle tensions for effective thrusting without violating the equilibrium conditions.

Before a controller for the posterior leg model can be developed, it will be necessary to determine what constitutes "effective thrusting" as it is employed by the dog. This question can be partially answered by observing the quantitative relationship between vertical and horizontal forces during a large number of typical responses to table movement. From these data, the common patterns of torque changes (as in Figures 24 and 25) and associated muscle tension changes could

be calculated and classified according to the body movements which they produced. The leg controller would then be designed to produce similar patterns of tension changes. This kind of study has been delayed by the need for simultaneous measurement of vertical and horizontal forces at each foot.

A second difficulty in designing a controller will arise in trying to determine how each muscle participates and particularly whether antagonistic muscles are simultaneously active. The best method for examining these questions may lie in rather elaborate EMG monitoring during periods of thrusting. Previous EMG studies on the dog by Mori and Brookhart (1968) and Brookhart, Mori and Reynolds (1970) have been quite successful but were not accompanied by two-component force measurements at the feet. However, the EMG timing patterns reported by these authors show a qualitative agreement with force patterns as presented in this work. A careful selection of measurement sites should provide EMG records which would correlate well with calculated patterns of muscle tensions.

Another aid in determining relative levels of muscle activity is found in a "minimum effort" principle. Except where rapid movements are intended, the muscle tensions are undoubtedly adjusted to levels requiring a near minimum of biological effort. This principle will be developed somewhat further in the discussion below.

Characteristics of a Controller

In a normal dog, the task of controlling each muscle is probably
handled at two levels which we might call the primary and secondary
control levels. The primary level of control is provided by the higher
centers of the CNS normally considered to be part of the brain. The
primary control would likely produce adjustments of posture to con-
form with the "learned" stance while relieving a fatigued muscle, or
it could assess the penalty associated with movement, etc. The
inputs to this level would be all sensory data and the outputs would be
nerve commands specifying desired tension and length as inputs to the
secondary or local level for each muscle. The secondary control is
accomplished within spinal reflex arcs which form a closed-loop feed-
back system to correct errors between the commands from the
primary controller and the outputs of the particular muscle. Models
for the dynamic behavior of this neuromuscular system are available
and reasonably well supported by observed behavior (McRuer et al.,
1967; Soechting et al., 1971; Mains and Soechting, 1971; Vickers,
1968; Mountcastle, 1968). Our concern now is the generation of the
secondary control inputs by the primary controller residing within the
higher centers of the CNS. In the kind of postural experiment which
has been described, there is dramatic difference between the force
magnitudes required for rapid movements following a disturbance and

the small perturbations normally experienced during quiet standing.
The function of the primary controller appears to be of much greater
importance than is true for the secondary controller.

The observations which we have discussed point rather clearly
to a primary controller which regulates quiescent behavior through
continuous fine adjustments while producing gross movements with a
series of force pulses. In the posterior limb, the pulses are pro-
duced partly by muscles which are not active during quiet standing.
In both anterior and posterior limbs, there is also some augmentation
of the excitation to muscles used for body support. The task of the
primary controller is to determine what level of force is required,
perhaps by a learned impulse-momentum criterion, and then to dis-
tribute the burden of effort among the muscles of each leg. The
pattern of this distribution is also determined by a learning process.
The learned patterns should produce changes in joint torques which
conform with the analysis of thrusting given in Chapter II.

After body motion has been initiated by one or more pulses of
thrust, the system must return to a quiescent state smoothly. If the
primary controller sets all control levels at typical values for correct
posture, then the return to this position would be governed by the
secondary controller. The most important sensors providing feedback
in the secondary system are the muscle spindles which are sensitive
both to muscle length and the rate of stretching. If the tension is

increased in every muscle which is stretching and decreased other-
wise, the movement of the body would be slowed after the initial
rapid movement. At low velocities, the position control could take
over to establish the final posture.

The long term regulation of quiet standing is expected to be a
process which produces the best overall comfort at any given time.
The secondary control system has provision to compensate for muscle
fatigue without allowing a loss in tension output. However, this
functions at the expense of comfort in that muscle. It is the primary
controller which must redistribute the effort of standing to relieve a
fatigued muscle.

Discomfort in a muscle is probably determined by the amount of
tension output required as compared with the maximum possible out-
put, the amount of elongation and the recent past history of muscle
output. The current level of knowledge in physiology should allow
development of a "fatigue function" f_i such that the product of mus-
cle tension t_i and muscle fatigue f_i would give an inverse
assessment of comfort for the i-th muscle. The strategy of the
quiescent control could be to minimize the sum of all comfort indices
over the muscles which were active without allowing a serious dis-
tortion of posture.

To summarize, we have suggested that a model for muscle
control should have two levels. The primary level of control would

determine the accuracy of posture currently required and then regulate muscle activity to minimize effort while relieving fatigued muscles. The secondary level provides local control of the muscle to reduce undesired stretching and to maintain muscle output at the levels required by the command signals from the primary controller.

BIBLIOGRAPHY

Agarwal, Gyan C. and Gerald L. Gottlieb. 1969. Analysis of step tracking in normal human subjects. IEEE Transactions on Man-Machine Systems MMS-10:132-137.

Agarwal, Gyan C., Bradley M. Berman and Lawrence Stark. 1970. Studies in postural control systems part I: torque disturbance input. IEEE Transactions on Systems Science and Cybernetics SSC-6:116-121.

Agarwal, Gyan C. et al. 1970. Studies in postural control systems part II: tendon jerk input. IEEE Transactions on Systems Science and Cybernetics SSC-6:122-126.

Bigland, Brenda and O.C.J. Lippold. 1954. The relation between force, velocity and integrated electrical activity in human muscles. Journal of Physiology, London 123:214-224.

Ballance, Jeffrey D. 1973. MINITRAN: an on-line function translator with capabilities for solving ordinary differential equations. Master's thesis. Corvallis, Oregon State University. 79 numb. leaves.

Brookhart, J.M., P.L. Parmeggiani, W.A. Petersen and S.A. Stone. 1965. Postural stability in the dog. American Journal of Physiology 208:1047-1057.

Brookhart, John M., Shigemi Mori and Patrick J. Reynolds. 1970. Postural reactions in two directions of displacement in dogs. American Journal of Physiology 218:719-725.

Chaffin, Don B. 1969. A computerized biomechanical model-- development of and use in studying body actions. Journal of Biomechanics 2:429-441.

Coggshall, J.C. and G.A. Bekey. 1970. EMG-force dynamics in human skeletal muscle. Medical and Biological Engineering 8:265-270.

Dewhurst, David J. 1967. Neuromuscular control system. IEEE Transactions on Bio-medical Engineering BME-14:167-171.

During, J. and T.C.M. Van Miltenburg. 1967. An EMG-operated control system for a prosthesis. Medical and Biological Engineering 5:597-601.

Frank, Andrew A. 1970. An approach to the dynamic analysis and synthesis of biped locomotion machines. Medical and Biological Engineering 8:465-476.

Gottlieb, Gerald L., Gyan C. Agarwal and L. Stark. 1970. Interactions between voluntary and postural mechanisms of the human motor system. Journal of Neurophysiology 33:365-381.

Gottlieb, Gerald L., Gyan C. Agarwal and Lawrence Stark. 1970. Studies in postural control systems part III: A muscle spindle model. IEEE Transactions on Systems Science and Cybernetics SSC-6:127-132.

Gottlieb, Gerald L. and Gyan C. Agarwal. 1971. Control and regulation of the human motor system. IEEE Transactions on Systems, Man and Cybernetics SMC-1:379-383.

Gottlieb, Gerald L. and Gyan C. Agarwal. 1971. Dynamic relationship between isometric muscle tension and the electromyogram in man. Journal of Applied Physiology 30:345-351.

Gray, J. 1944. Studies in the mechanics of the tetrapod skeleton. Journal of Experimental Biology 20:88-116.

Gray, James. 1956. Muscular activity during locomotion. British Medical Bulletin 12:203-209.

Houk, James C., Joshua J. Singer and Mark R. Goldman. 1970. An evaluation of length and force feedback to soleus muscles of decerebrate cats. Journal of Neurophysiology 33:784-811.

Isaacson, Eugene and Herbert Bishop Keller. 1966. Analysis of numerical methods. New York, Wiley. 541 p.

Kostyuk, P.G. and D.A. Vasilenko. 1968. Transformation of cortical motor signals in spinal cord. Proceedings of the IEEE 56:1049-1058.

McDonnell, J.D. 1966. A preliminary study of human operator behavior following a step change in the controlled element. IEEE Transactions on Human Factors in Electronics HFE-7:125-128.

McRuer, D. T. et al. 1968. New approaches to human-pilot/vehicle dynamics analysis. Ohio. 188 p. (Wright-Patterson Air Force Base. Air Force Flight Dynamics Laboratory. Technical report AFFDL-TR-67-150).

Mains, R. E. and J. F. Soechting. 1971. A model for the neuro-muscular response to sudden disturbances. Providence, Brown University, Center for Biophysical Sciences and Biomedical Engineering. 20 p.

Manter, John T. 1938. The dynamics of quadrupedal walking. Journal of Experimental Biology 15:522-539.

Melvill Jones, G. and D. G. D. Watt. 1971. Observations on the control of stepping and hopping movements in man. Journal of Physiology, London 219:709-727.

Miller, Malcolm E., George C. Christensen and Howard E. Evans. 1964. Anatomy of the Dog. Philadelphia, W. B. Saunders Company. 941 p.

Moffatt, Charles A., Edward H. Harris and Edward T. Haslam. 1969. An experimental and analytic study of the dynamic properties of the human leg. Journal of Biomechanics 2:373-387.

Mori, Shigemi and John M. Brookhart. 1968. Characteristics of the postural reaction of the dog to a controlled disturbance. American Journal of Physiology 215:339-348.

Mori, Shigemi, Patrick J. Reynolds and John M. Brookhart. 1970. Contribution of pedal afferents to postural control in the dog. American Journal of Physiology 218:726-734.

Mountcastle, Vernon B. (ed.). 1968. Medical physiology. Vol. 2 Neural Control of Movement and Posture. Saint Louis, C. V. Mosby Company. 1858 p.

Nakao, C. and J. M. Brookhart. 1967. Effect of labyrinthine and visual deprivation on postural stability. (Abstract) Physiologist 10:259.

Nashner, L. M. 1971. A model describing vestibular detection of body sway motion. Acta Oto-laryngologica 72:429-436.

Nashner, Lewis M. 1972. Vestibular postural control model. Kybernetik 10:106-110.

Navas, Fernando and Lawrence Stark. 1968. Sampling or intermittency in hand control system dynamics. Biophysical Journal 8:252-302.

Petersen, W.A., J.M. Brookhart and Solon A. Stone. 1965. A strain-gage platform for force measurements. Journal of Applied Physiology 20:1095-1097.

Phatak, Anil V. and George A. Bekey. 1969. Decision processes in the adaptive behavior of human controllers. IEEE Transactions on Systems Science and Cybernetics SSC-5:339-351.

Phatak, Anil V. and George A. Bekey. 1969. Model of the adaptive behavior of the human operator in response to a sudden change in the control situation. IEEE Transactions on Man-Machine Systems MMS-10:72-80.

Reynolds, P.J., R.E. Talbott and J.M. Brookhart. 1972. Control of postural reactions in the dog: the role of the dorsal column feedback pathway. Brain Research 40:159-164.

Robinson, David A. 1968. The oculomotor control system: a review. Proceedings of the IEEE 56:1032-1049.

Smith, Otto J.M. 1962. Nonlinear computations in the human controller. IRE Transactions on Bio-medical Electronics BME-9:125-128.

Soechting, J.F. et al. 1971. Evaluation of neuro-muscular parameters describing human reflex motion. Providence, Brown University, Center for Biophysical Sciences and Biomedical Engineering. 19 p.

Vickers, William H. 1968. A physiologically based model of neuro-muscular system dynamics. IEEE Transactions on Man-Machine Systems MMS-9:21-23.

APPENDICES

APPENDIX A

Data Acquisition Equipment

The experimental facilities used in this work were located at the University of Oregon Medical School Department of Physiology (UOMS) in Portland. The basic equipment consisted of a hydraulically controlled table with one degree of freedom, position transducers for reading the table and dog movements, an eight-channel strip chart recorder for monitoring experiments, force measurement transducers for each foot of the dog, a signal generator for manually producing simple table movements and a seven-track FM-analog recorder. Table control signals were generally produced remotely using an EAI 690 Hybrid Computation System and prerecorded. At the experiment site, the table was controlled from the recorder playback while the data was simultaneously recorded in the unused tracks. The analog signals were then digitized remotely again using the EAI 690 Hybrid Computing System.

Both table and dog position were obtained from infinite resolution potentiometers followed by suitable amplifiers. Vertical forces at each foot could be obtained from existing transducers which used strain gage sensors and the Tektronix 3C66 Carrier Amplifier (Petersen, Brookhart and Stone, 1965). There was, however, no equipment for measurement of horizontal forces exerted by the feet.

The remainder of this appendix is devoted to the description of a transducer for measuring horizontal longitudinal forces at each foot.

The general objective was to build a device for supporting the dog's paw which would withstand mechanical overload, measure horizontal forces in one direction independent of the vertical load and have a low physical profile. The support surface was to be about 4 in square. A measurement resolution of 0.05 kg in the recorded data was desired with a maximum of 5-10 kg at full scale. Since most observations would involve short time periods, drift requirements were not stringent.

The final device as shown in Figure A1 consisted of a base milled from 1 in aluminum plate and a support platform milled from 1/2 in plate. The platform was suspended between two steel bands made from bandsaw blade. These bands were clamped to opposite sides of the platform with the four ends fixed to pedestals which were part of the base structure. This left the platform rigid in the axial direction of the supporting bands but relatively free for elastic displacement perpendicular to the bands. The four flexure supports could also carry a substantial vertical load without significant deformation. The platform was restrained from movement perpendicular to the bands by a single strut from the center of the platform horizontally to another pedestal on the base. This strut carried four strain-gage sensors to measure the elastic strain which was
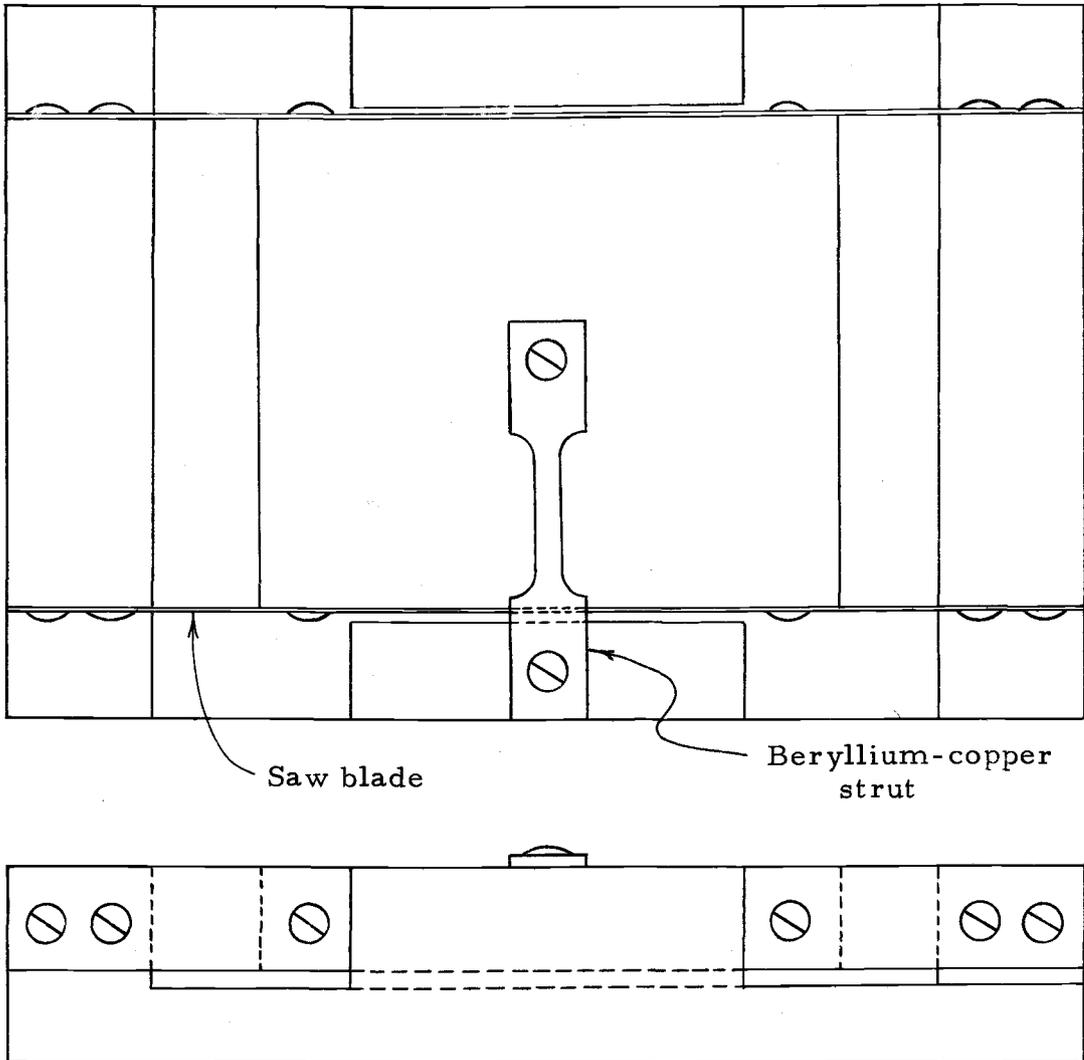
Saw blade

Beryllium-copper
strut

Figure Al.   A horizontal force transducer with the protective
cover removed.   The drawing is shown in actual
size.

proportional to horizontal force applied to the platform. A light-weight cover with a soft pad protected the strut and enlarged the support surface for the dog's paw.

An essential requirement for the transducer was that it should not produce a significant output in response to horizontal accelerations associated with table movement. Table accelerations could reach an estimated 30 m/s^2. Although the mass of the support platform was only 0.08 kg, the force of acceleration at 30 m/s^2 was 0.08 x 30 = 2.4 N or about 0.24 kg, which is clearly a significant force relative to desired measurement levels. To correct for this "accelerometer" effect, a fifth transducer was placed on the table as a dummy and its output signal was electronically substracted from the other four devices. This reduced the unwanted output from table accelerations to less than 10 percent of the uncompensated level on all four devices with the dog off. The success of this method was very much dependent on having physically equivalent devices with resonant frequencies well above the highest measurement frequency. The measured resonance for each device (about 1.5 kHz) was more than one decade higher than the maximum frequency of 40 Hz which was expected in the data. The output of each force measurement channel was applied to a two-pole low-pass filter whose circuit diagram appears in Figure A2 along with the bridge amplifier circuit. The approximate filter transfer function is given as Equation A1. There
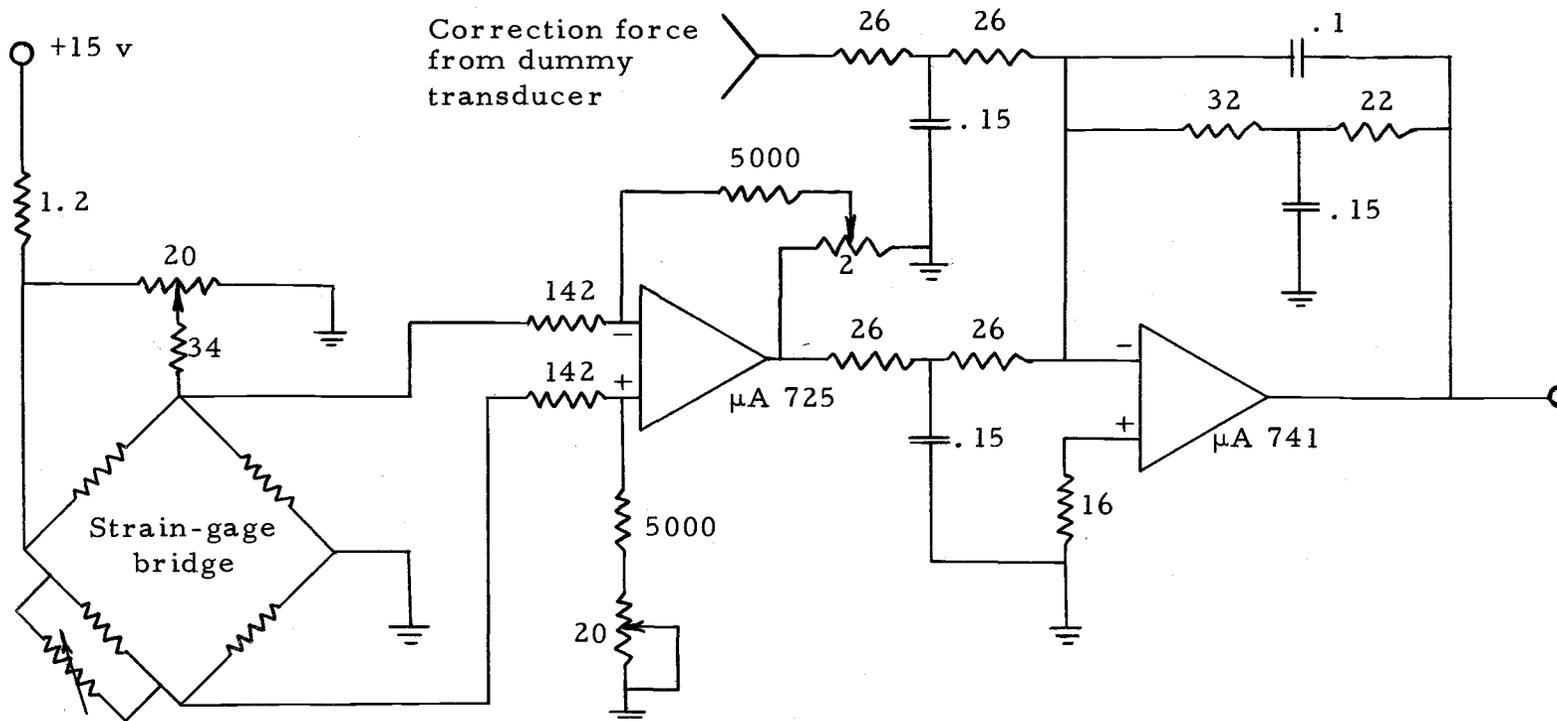
Strain gages - Whittaker
Micro-sensor P01-05-500
Nominal resistance - 0.5
Gage factor - 145

Resistance and capacitance units are kΩ and μF, respectively.
Power, offset null and compensation connections not shown on operational amplifiers.

Figure A2. A schematic diagram for the strain gage amplifier and filter. The amplifier gain was adjusted for an output level of 2.0 v per kg horizontal force. The filter cut-off frequency is about 49 Hz.

was good agreement between the calculated and measured frequency

$$H(s) = \frac{98619(s+511)}{(s^2+511s+94697)(s+513)}$$ (A1)

response curves, both of which indicated a corner frequency of 49 Hz. Any output caused by platform oscillation at the inherent resonance would be highly attenuated by the filter.

After completing all experiments, the combined errors resulting from gain drift and non-linearity was found to be less than 3 percent in the worst case. The most significant errors during experiments resulted from a drifting of the zero-force reference when the weight of the dog was applied as a vertical load. This drift was less than 0.2 kg and was not a serious problem since the primary interest was to examine relative force changes over short time periods.

APPENDIX B

Data Processing

The principal objective of data processing was to reduce the bulk prior to digital plotting and to calculate derivatives (velocities) of the dog's relative and absolute position. The data reduction process is explained in Chapter I and needs no further comment. The numerical smoothing and differentiation used to overcome noise will be described below.

Since all digitized data were corrupted by noise from FM-analog recording and playback as well as transducer noise, the numerical differentiation method had to be chosen with care. The final algorithms selected were developed using an on-line computer graphics system which was released experimentally by the Oregon State University Computer Center during the course of data acquisition.[1] This system allowed the rapid comparison of results computed from typical data using test programs. First and even second derivative estimates compared favorably with predicted values and were certainly suitable for the plotting which followed.

The digital smoothing was accomplished by taking a symmetrical weighted average for each point in the smoothed data series. If we let T be the sample interval and define $x_k \equiv x(kT)$ and $y_k \equiv y(kT)$, then

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[1] Ballance, J. D. , Research Assistant, OSU Computer Center. Private communication, 1972.

$$y_k = x_k + \sum_{j=1}^{n-1} w_{j+1}(x_{k+j} + x_{k-j}) , \qquad (B1)$$

where y_k is a point in the smooth series and the total number of

points in the weighted average is $2n-1$. The weights were calculated

from the formula for the well-known Parzen taper given as Equations

B2.

$$w_j = \frac{1}{S}(1 - 6(\frac{j-1}{n})^2 + 6(\frac{j-1}{n})^3) \qquad 0 \leq \frac{j-1}{n} < \frac{1}{2}$$

$$= \frac{1}{S}(2(1 - (\frac{j-1}{n}))^3) \qquad \frac{1}{2} \leq \frac{j-1}{n} < 1 \qquad (B2)$$

$$S = w_1 + \sum_{j=2}^{n} 2w_j$$

The formula for the derivative estimate is given by Equations

(B3). This formula is derived from a knowledge of the errors in

$$y1 = (y_{k+1} - y_{k-1})/2T$$

$$y2 = (y_{k+2} - y_{k-2})/4T \qquad (B3)$$

$$y'_k = y1 + (y1 + y2)/3$$

the difference formula approximation for the derivative and the

Richardson extrapolation method (Isaacson and Keller, 1966, p. 374;

Ballance, 1973, p. 58). The equations to approximate the derivative

contain error terms as follows:

$$y1 = y'_k + E(T^2) + E(T^3) + \ldots$$

$$y2 = y'_k + E((2T)^2) + E((2T)^3) + \ldots \qquad (B4)$$

$$= y'_k + 4E(T^2) + 8E(T^3) + \ldots ,$$

where $E(z)$ denotes error terms which are a function of the argument. These two equations may be combined to eliminate the $E(T^2)$ term, resulting in the above formula which contains errors of the third-order and higher.

Several properties of digital smoothing are worth noting. First, the effect is very literally to smooth or "smear" the features of the data series. In this sense, the averaging process removes the higher frequency components, most of which are unwanted noise. The attenuation of a particular frequency depends on the number of points included in the weighted average. The attenuation versus frequency curve for a Parzen taper with nine $(n = 5)$ weights is given in Figure B1. The one-half and one-fourth power bandwidths are about 9.2 and 12.7 Hz, respectively. This taper was chosen because it adequately removed noise but did not attenuate any significant components in the position responses of the dog. Power spectral calculations showed significant energy in the force responses up to 15 Hz, but the body itself could not respond at those frequencies. Most energy of the

Figure B1. Attenuation curve for the Parzen taper. The digitized data for body position and relative position were smoothed before numerical differentiation was applied. An advantage of the Parzen taper is that there are no negative side lobes in the attenuation curve.

Attenuation curve for the Parzen taper,

n = 5

Half-power bandwidth--9 Hz
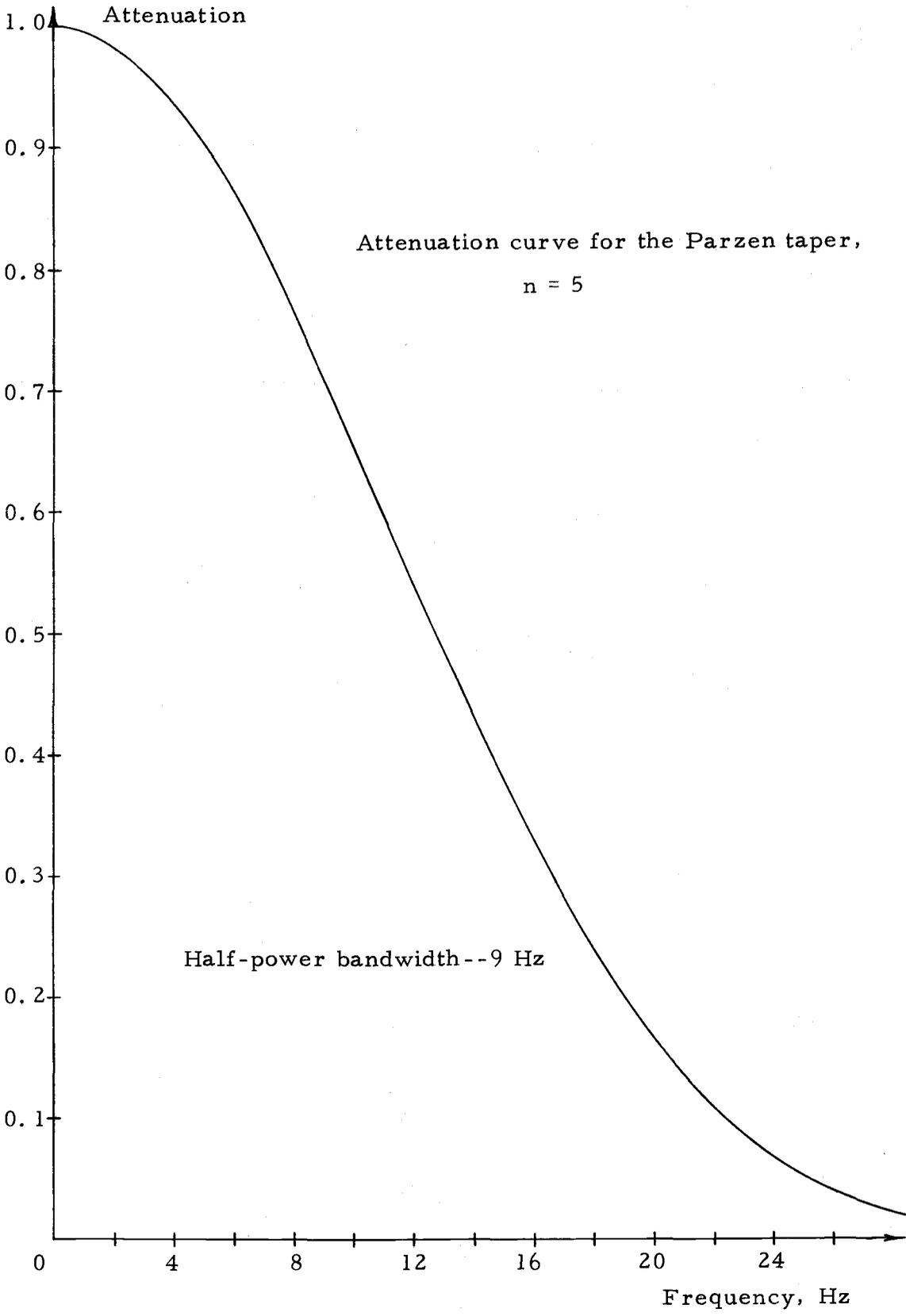
position responses was below 6 Hz.

The second point regarding the smoothing process can be illustrated by supposing that the data series was a unit step at point m. In the smoothed data series, the level transition will be spread out over nine points centered at point m. Thus, abrupt jumps in data levels are actually "felt" in the smoothed data in advance of their occurrence. When a data series for the dog or table position is differentiated, it will appear that movement occurred before it actually did. Since the differentiation formula also spreads over five points, the first effects of a jump in the data series will be observed in the differentiated series at six points in advance of its true point of occurrence. Of these six, four are contributed by the smoothing and two by the differentiation.

APPENDIX C

Examination of Inertia Forces

The purpose of this appendix is to estimate the moment of inertia of a dog's leg about its body proximal joint. We will then provide data to show that, for a period of about 80 ms after the onset of a rapid table displacement, the legs swing under the body with little muscle resistance or frictional loss.

To calculate the moment of inertia for a typical leg--actually, a composite of all four legs--the mass distribution for the limbs of several dogs used in earlier terminal experiments was obtained from records kept upon dissection of the animals. A 16-18 kg dog carried about 3.8 kg in the legs with most of the mass near the body. A typical paw was only 0.17 kg, but accounted for at least half of the moment of inertia because it was most distant from the pivot point of the leg. The mass of each segment of the leg was assumed to be uniformly distributed over the segment. This assumption is not good for the upper leg but has little effect since the contribution from this portion was small. The calculation yielded a value of 0.2 kg-m^2. For the two heaviest dogs, about 28 kg, a value of 0.3 kg-m^2 could be justified. This also assumes that the leg rotates as a mechanical unit without much bending at the joints.

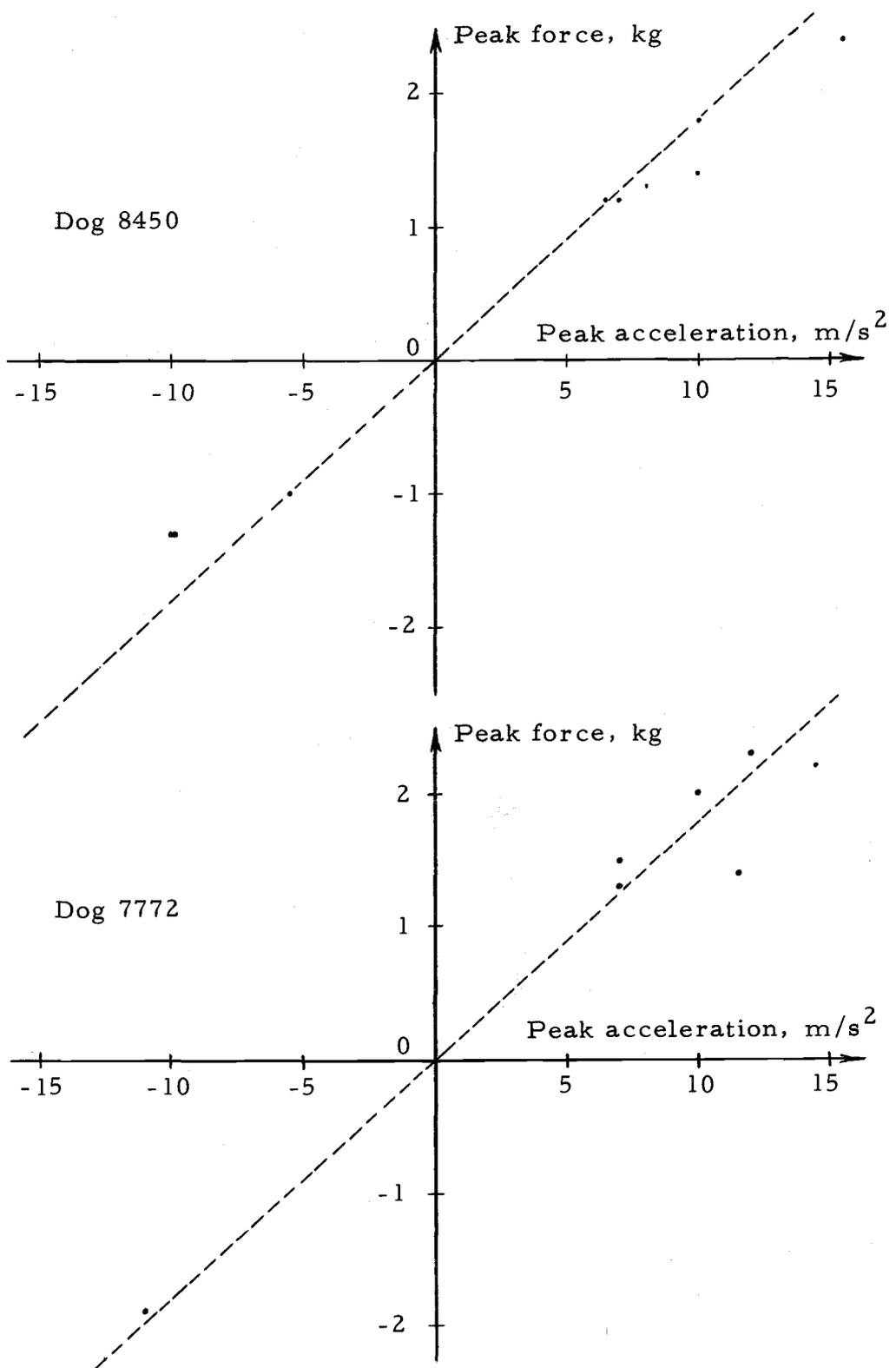Figure Cl is a plot of peak horizontal force (total of all four

Figure C1. Peak inertia force vs. peak table acceleration. The peak
table accelerations were estimated from the strip chart
records and the known control signal.

feet) versus peak table acceleration for a number of samples from the two largest dogs. The dotted line gives the expected values of force assuming the moment of inertia is 0.3 kg-m^2. The slope of this line would obviously decrease for smaller values.

The force peaks measured occurred about 40 ms after the onset of table movement and were associated with accelerating the legs to follow the table. The force required to stop the legs was exerted at the end of table movement simultaneously with forces of physiological origin resulting from muscle action. Because the early force peaks occurred before any significant muscle response was expected to develop, their timing and magnitude should depend only on mechanical properties of the leg, the foot contact with the table and the table accelerations. The two plots given show reasonable agreement with these conditions. A certain degree of variability will obviously result because the leg can bend at its joints while pivoting about the body proximal joint. This type of bending will be irregular because the position and loading of the leg at the onset of table movement will affect the foot coupling properties and the transmission of direct thrusts from bone to bone across the several leg joints.