HUMAN VISUAL-VESTIBULAR INTERACTIONS DURING POSTURAL RESPONSES TO BRIEF FALLS

by

ROGER WILLIAM WICKE

S.B. in Electrical Engineering,
Massachusetts Institute of Technology (1975)

S.M. in Electrical Engineering,
Massachusetts Institute of Technology (1976)

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Signature of Authc ________________________
Department of Electrical Engineering
9 June 1980

Certified by ________________________
Thesis Supervisor

Accepted by ________________________
Chairman, Committee on Biomedical Engineering

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ABSTRACT

Human subjects were suspended in a safety harness 28 cm above the floor by a steel cable connected to a computer controlled force generator (electromagnetic brake). After the subjects were unexpectedly released, various controlled patterns of downward acceleration (less than one g) could be produced. During the falls, EMG activity was recorded simultaneously from the gastrocnemius, soleus, tibialis anterior, rectus femoris, and biceps femoris, along with knee and ankle joint angle in one leg. Subjects were tested eyes closed and also eyes open, both in darkness and in light using a wide field visual display. The display scene could be moved downwards at exactly the same velocity as the moving subject, left fixed with respect to the laboratory ("normal visual field"), or moved upwards at a speed equal to the subject's falling speed ("upward moving visual field"). Ten vestibularly normal subjects each underwent a total of 45 drops, experiencing three replications of each vision/motion combination used.

Under normal visual field conditions, both short and long latency postural responses were seen, which were dependent on the magnitude of the acceleration stimulus. Certain of the visual conditions significantly altered both the short and long latency responses in most of the muscles tested. Effects were particularly prominent in the gastrocnemius and soleus, and were also more pronounced during slow (0.5G) falls. The upward moving visual field condition increased the short latency EMG reaction in gastrocnemius and soleus for 0.5G falls. A preliminary model for visual-vestibular interaction in short latency EMG responses is presented. Long latency responses are more variable and are not conducive to a simple interpretation.

Thesis Supervisor: Charles M. Oman
Title: Helmholtz Associate Professor of Aeronautics
and Astronautics; Principal Research Scientist

MEMBERS OF DOCTORAL ADVISORY COMMITTEE

Charles M. Oman, Ph.D
Helmholtz Associate Professor; Principal Research Scientist
Department of Aeronautics and Astronautics
Massachusetts Institute of Technology

Laurence R. Young, Sc.D.
Professor
Department of Aeronautics and Astronautics
Massachusetts Institute of Technology

Sheldon R. Simon, M.D.
Associate in Orthopedic Surgery,
Director of Gait Laboratory, Children's Hospital,
Boston, Massachusetts;
Lecturer, Department of Mechanical Engineering
Massachusetts Institute of Technology

Douglas G. D. Watt, M.D., Ph.D.
Assistant Professor
Department of Physiology
McGill University

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CHAPTER 1

INTRODUCTION:
UNEXPECTED FALLS AS A TOOL FOR STUDYING VESTIBULOSPINAL MECHANISMS

The labyrinth organs of the inner ear, which include the semicircular canals and otoliths, provide acceleration and gravitational orientation information which is extremely useful for maintaining postural stability. People who develop labyrinthine disorders initially suffer from difficulty in maintaining balance, which may reach severe proportions. However, in cases of permanent vestibular disorders, patients are often capable of compensating for the loss of vestibular function by increasing the role of vision and proprioception in postural maintenance.

This phenomenon raises the question of what role vision might have in contributing to postural reactions in normal people. Recent reports have indicated that in man, conflicting visual cues may induce destabilizing postural reactions with very short latencies (Lestienne et al., 1977; Nashner and Berthoz, 1978; Vidal et al., 1979, in the baboon). Therefore, one problem is to determine the manner in which visual cues are combined with vestibular information under various circumstances.

Because the motor system is designed to accomplish a far greater variety of tasks than merely the maintenance of stable posture, motor commands arising from the vestibular system must be coordinated to the current state of activity. A wide variety of motor activities seem to be organized in terms of synergistic muscle activation patterns; exertion of vestibular influence upon these muscle groups might be expected to be similarly organized. The results of single unit recording and of electrical stimulation of descending motor tracts reveal highly coordinated vestibulospinal activity with respect to extension and flexion of the limb, as in locomotion (Grillner et al., 1970, 1971; Hongo et al., 1975; Kots, 1976; Shik and Orlovsky, 1976). The initial posture of the subject may also influence which muscles are affected by vestibulospinal commands. For example, if one leg is flexed, the distribution of commands is asymmetric. For a more extensive review of vestibulospinal mechanisms, see Appendix B, pages 227-252.

1.1 Rationale for choosing unexpected falls

One goal of this study is to investigate visual-vestibular interactions during rapid postural adjustments. Sensory interaction and vestibulospinal motor synthesis are two aspects of the problem which are treated simultaneously in this study.

With this goal, the first major task consisted of choosing an appropriate paradigm for studying rapid postural reactions. Investigations of human postural reactions to external disturbances of body position during stance have been performed by Nashner (1970, 1971, 1973, 1976, 1977). Visual field motions were later added to the basic paradigm (Nashner and Berthoz, 1978), which consisted of asking a person to maintain upright stance on a platform which could be servo-controlled to eliminate ankle angle feedback and could also be suddenly moved in an anteroposterior direction. While this type of experiment is conducive to linear system analysis of a response to an external disturbance, the fact that proprioceptive sensors at the ankle and hip, semicircular canals, otoliths, and vision all contribute significant information makes fundamental physiological interpretation difficult. In addition, the nature of this test makes it difficult to extract any kind of information about sensory to motor processing and transmission latencies.

Unexpected, short falls were finally chosen as the external disturbance in this study because of a number of advantageous features. The onset of the stimulus is clearly defined, allowing various sensory-motor latencies to be clearly determined. The primary effect of postural reactions during the fall is to minimize jolts and loss of balance after landing. Unlike the case of disturbance during stance in which the reaction itself immediately affects the stimulus to the vestibular organs in a closed-loop feedback mode, the postural reactions during a fall are not part of a corrective feedback scheme. Instead, a predictive strategy must be employed. Feedback of a different nature must not be overlooked, though; neck muscle contractions following release may alter the head position, and, thus, alter the effective stimulus to the labyrinths. Activation of neck gamma motoneurones may result in even faster changes in neck afferent feedback reaching vestibulospinal tract neurons. In addition, since the mass of the legs is a significant fraction of body mass, knee and hip flexion will also result in motion of the upper body and head which would be different from that of a passive body.

By surrounding the subject with a movable visual field, the visual cues can be altered independently of the acceleration stimuli.

By confining the study to vertical accelerations and vertical visual field motions, any significant effects can probably be explained in terms of gravireceptor involvement, without the confounding effects of semicircular canal influence. (If the head is facing forward during initiation of the fall, antero-posterior head motion due to passive effects was observed to be minimal.) Experimental separation of the linear and angular modes is important, since spinal influences from the canals and otoliths may be channeled through different pathways, and intermediate processing of angular and linear accelerations may be totally different in character (Precht, 1974).

The remainder of this chapter consists of a discussion of the rationale underlying the development of the basic procedure, with references to the literature. The action of the major leg muscle groups is reviewed in the context of an appropriate reaction to a short fall, followed by a summary of observed EMG reactions during falls as reported by other authors. After the essential features of the reactions to falls are outlined, individual articles from the literature are examined in more detail. Throughout the review, the findings are discussed with emphasis on their significance in motivating certain aspects of the present study.

1.2 Brief description of procedure

Each subject was suspended in a safety harness connected by a cable to an electric brake and surrounded by a patterned visual field which could be moved vertically. The subject was dropped unexpectedly at accelerations of 0.85 g (somewhat slower than free fall) or less, and the visual field could be moved either up, down, or remain stationary with respect to the laboratory during the fall. In addition, by varying the acceleration in mid-fall, it may be possible to determine if the sensorimotor system is capable of adjusting the motor response timing to account for the alteration.

1.3 Action of major leg muscles

In this study, EMG measurements from five muscles of the leg were recorded using surface EMG electrodes. These muscles were the gastrocnemius, soleus, tibialis anterior, rectus femoris and biceps femoris. In order to aid interpretation of the EMG recordings, the primary action of each of these muscles will be reviewed, as well as other important muscles of the hip and leg which are not accessible with surface recording techniques.

Figure 1.1 on page 21 shows a schematized version of the major muscle groups of the leg. The ideal strategy of muscle activation to prepare for landing involves both proper positioning of the joints and adjustment of the effective stiffness about each joint during landing. In order to minimize transmission of impact forces of the landing to the upper part of the body and spinal column, the hip and knee should be flexed, as shown in figure 1.2 on page 21. In such a position, the weight and momentum of the body during impact will tend to cause further passive flexion.

EMG recordings do not allow quantitative conclusions about the associated muscle forces; only qualitative features are indicated in comparisons of the recordings of different muscles. With this in mind, some of the constraints involved

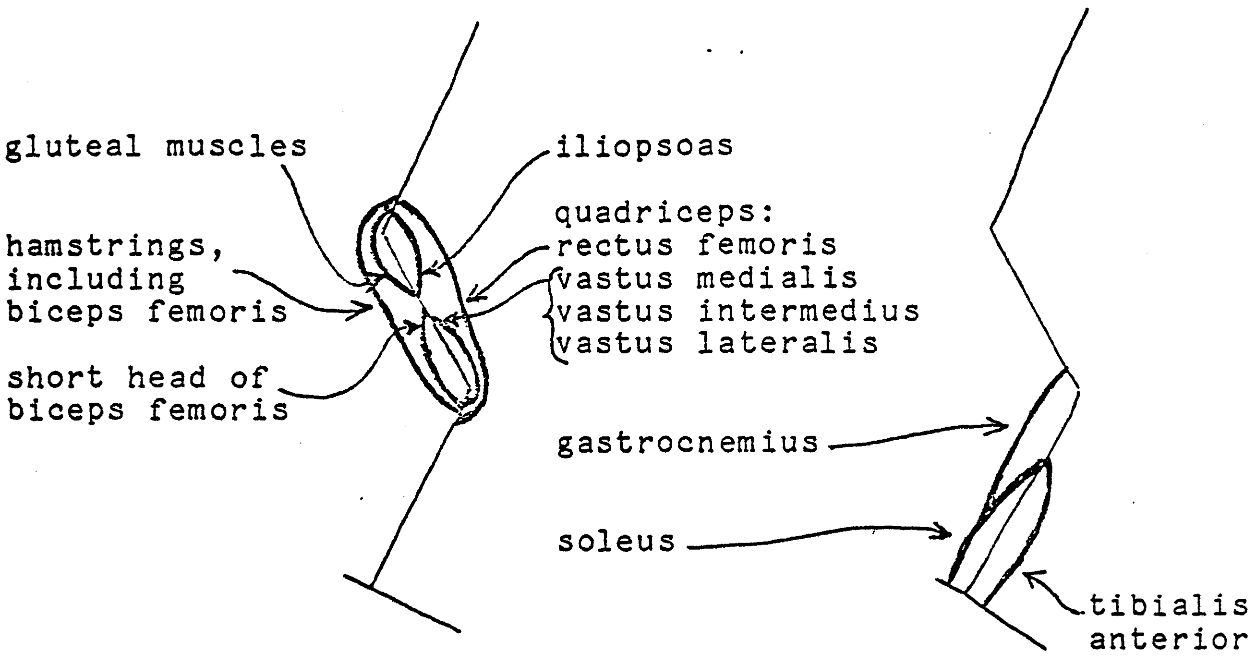

Figure 1.1. Major muscles of the hip, thigh and leg.

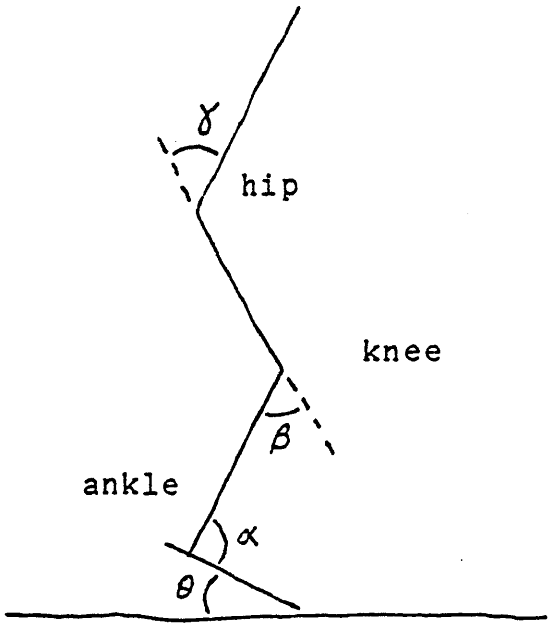

Figure 1.2. Idealized limb positioning at the instant of contact with the ground following a short fall.

in possible landing strategies should be considered.

It is obvious that if the hip is extended (γ=0) and the knee is fully extended (β=0), then the impact of landing on the upper body can only be reduced by plantar flexing the feet such that θ>0 at contact. Contraction of the soleus muscle at contact will slow the passive dorsiflexion of the ankle in order to reduce the velocity of the heel when it contacts the floor a fraction of a second later. During the fall, if the tibialis anterior is contracted simultaneously with the soleus, the ankle position may not change significantly, but the effective stiffness will increase. If the knee and hip are extended, the forces of contact at the heel will be transmitted directly upward through the leg bones and spinal column, analogous to a rigid pillar hitting the ground.

For even short falls, the previous hypothetical strategy would be painful if not dangerous. By flexing the knee prior to contact, much of the impact can be absorbed by further passive flexion. In addition, all of the muscles acting at the knee joint can then exert fine control of the landing with varying degrees of contraction. Since the gastrocnemius muscle acts at both the knee and ankle joints, contraction will achieve the same effect as the soleus as in the prior strategy, but will also act to flex the knee. The hamstring muscles, including the biceps femoris also aid in knee flexion.

Hip flexion prior to contact will further reduce the peak forces acting on the spinal column. The iliopsoas muscle is the most effective flexor of the hip, but the rectus femoris also contributes to hip flexion. Because the iliopsoas is a deep muscle attached to the intra-abdominal face of the iliac pelvis and spine, it is inaccessible with surface EMG techniques. The rectus femoris lies just beneath the fascia lata of the anterior thigh and is easily recorded with surface electrodes. However, the rectus femoris also contributes to knee extension since it is part of the quadriceps group.

Since the biceps femoris, in addition to flexing the knee, also extends the hip, recordings from rectus femoris and biceps femoris do not allow accurate conclusions concerning hip flexion. Many other muscles affect hip flexion and extension, so that any results obtained from biceps femoris and rectus femoris must be interpreted from a more phenomenological perspective. The gastrocnemius, soleus, and tibialis anterior are the prime movers of the ankle joint, so that more definite indications concerning mechanical strategies should be evident from EMG recordings.

The previous discussion has been concerned primarily with proper limb positioning in order to allow passive flexion of the hip, knee, and ankle joints during contact.

It should be pointed out that during suspension in a safety harness, the knee and hip are usually slightly flexed when relaxed; any additional flexion may be achieved by relatively low level contractions of the correct muscles because the limbs are unloaded. By contrast, the forces needed to prevent collapse following contact are much greater due to the sudden loading of the legs by the weight and momentum of the body.

1.4 Salient features of the electromyographic response

Electromyographic (EMG) reactions in the lower leg muscles, and numerous other muscles including those of the neck and around the eye, demonstrate stereotyped patterns during unexpected falls. These EMG patterns include manifestations of an involuntary response of vestibular origin, and as such, they provide an excellent medium for the study of otolith function and motor responses to phasic stimuli. The involuntary reaction in the soleus muscle begins about 75 msec after release and continues for about 100 msec. Greenwood and Hopkins (1976a) found that this reaction was absent in the two labrynthine defective patients which they tested. Lacour et al. (1978) showed that in baboons, this response could be separated into two subcomponents, the first of which disappears after bilateral labyrinthectomy and the second of which is only reduced in magnitude. These results indicate that the labyrinths, and presumably the otoliths specifically, are primarily responsible for triggering the early response following release, though other sensory systems may contribute.

If the duration of the fall is long enough, the first response is followed by a period of diminished EMG, and then, a subsequent increase which reaches a maximum 40 to 140 msec prior to contact. This latter reaction is presumed to be of voluntary origin and is dependent upon both the subject's judgement of his height above the landing platform and his downward rate of acceleration. If the subject releases himself, no initial involuntary or "startle" reaction is seen (Greenwood and Hopkins, 1976a). The EMG reactions seem to be preprogrammed responses similar to the second EMG burst during unexpected falls.

1.5 Effects of habituation and expectation

The initial EMG responses habituate very rapidly (Greenwood and Hopkins, 1976a). Amplitudes decrease significantly over the first several drops, but persist at a relatively steady level thereafter, for drops of the same height and acceleration.

In this study the ordering of different test conditions was randomized. Therefore, in addition to overall habituation to the drops, the testing order may be significant. For example, the results of a given test may depend on the parameters of the previous test. These problems were not insuperable, but it was necessary to be aware of such potential interactions for the purpose of overall experimental design. (See Chapter 3.)

1.6 Preprogrammed aspects versus continually updated parameters of the reaction

Many aspects of a voluntary jump appear to be preprogrammed. It is of central concern to determine what features of the motor sequence can be modified during the fall. For example, according to Greenwood and Hopkins (1976b), it seems that for falls of sufficient duration, the timing of the second, functional EMG response prior to landing depends upon the subject's perception of his height above the ground and his rate of acceleration. It was hypothesized that the magnitude of the initial transient in acceleration during release is the cue that determines the timing of the EMG prior to landing. One way to test this would be to change the pattern of acceleration during the fall. Instead of an initial step in acceleration, either a gradual increase or a series of smaller steps in acceleration could be achieved with an appropriate sequence of restraining forces on the harness suspension during the fall. By this method, falls of equal duration, but radically different acceleration sequences could be compared.

If acceleration changes after release can be shown to affect the response, then it is clear that there must exist a time after which acceleration information from the otoliths can no longer modify the timing of the pre-contact EMG. This latency might be comparable to the latency of the initial involuntary response, but not necessarily, since the two latencies reflect processing and neural transmission times for different phenomena.

The fact that the earliest response following an unexpected release occurs at a latency of 75 msec should not be used to infer that this represents the minimum time for vestibulospinal commands to be transmitted to the soleus muscle, for example. Soleus H-reflex tests in humans by Kots (1976) indicate that galvanic stimulation of the vestibular apparatus causes potentiation of the H-reflex as soon as 30 msec following the onset of the stimulus. Studies by Matthews and Whiteside (1960) in the human and by Watt in the cat (1980, personal communication) revealed effects on the H-reflex with a similarly short latency, but the effect was initially inhibitory, followed by a period of facilitation. It was hypothesized that the earliest EMG reaction is a manifestation of this facilitatory period, since the timing of the two events coincides. These latter results cannot be reconciled with those of Kots, but it is clear that the early EMG reaction does not reflect the earliest activity occuring at the segmental level.

1.7 Previous studies of unexpected falls

Melvill Jones and Watt (1971a) tested unexpected falls by electromagnetically releasing an overhead handle onto which a subject held. They demonstrated that the reaction during landing could not be explained as a functional stretch reflex, since such a reflex would have occurred too late to be of assistance in preventing collapse. (See Appendix B, section B.16, for a review of the functional stretch reflex.) By dropping subjects from different heights, they showed that the gastrocnemius reaction timing was determined prior to contact; for falls of less than 160 msec duration, landings were characterized by an uncomfortable jolt because of insufficient time for a functional response to occur. If a functional stretch reflex were responsible, then the quality of the landing should be independent of height. The short latency response, occuring with a latency of 74 msec independently of drop height, was also first documented by Melvill Jones and Watt.

Recent experiments of Watt (1980, personal communication) have been performed in the horizontal position and in zero-g conditions in parabolic aircraft flight. The experimental protocol was similar to that in the previous experiment, except that elastic bungee cords connecting the subject to the landing platform replaced the gravitational force; with the bungee cords under tension, the subject would be propelled toward the landing platform upon release of the overhead handle. The results from these tests indicated that the early response magnitude is greatly reduced. For the horizontal position, over a period of several hours the response gradually increases toward the magnitude seen in the vertical, one-g situation. This suggests that the one-g biasing of the saccules has a potentiating effect on the early response which is temporarily diminished when the saccules are unbiased.

In addition to substantiating the results of Melvill Jones and Watt, and demonstrating the absence of the early response in labrynthine defective patients, Greenwood and Hopkins (1976a,b) showed that the soleus early response magnitude is an increasing function of the acceleration. Their subjects were suspended in a harness connected by a cable to an electromagnetic release and a system of counterweights. By varying the counterweighting, step acceleration profiles of less than one-g could be tested.

Several other variations of the procedure revealed interesting features of the response. If the subjects were allowed to release themselves, no early response occurred; only the functional pre-contact response remained. In another variation, unexpected falls were tested in which the subject's eyes were closed and the fall height was chosen at random from one of two heights; the late reaction occurred with a latency which was between those for falls from the two heights when the subject knew the height beforehand. These tests usually elicited sensations of surprise from the subjects, indicating that the actual fall duration was either greater or less than expected. This further verified that the late EMG reaction is under voluntary control and shows none of the features of a functional stretch reflex, since the timing can vary relative to the contact time in ambiguous situations.

1.8 Possible visual-vestibular interactions

The initial involuntary reaction may prove to be a useful tool for studying vestibulospinal interactions with other motor systems, provided that it can be clearly shown to be generated primarily by the vestibular system. Its absence in totally labyrinthine-defective people strongly implicates the vestibular system as its origin. The fact that this initial reaction is still present in cats with plugged semicircular canals, but disappears after labyrinthectomy, indicates that the otoliths are probably responsible (Watt, 1976). Several other possibilities must be considered, though. For example, while peripheral degeneration of the vestibular organs may cause degeneration of primary vestibular neurons, this degeneration may also cause interruption of visual and oculomotor pathways through the vestibular nuclei, which may affect motor function. The vestibular nuclei may act as gates, requiring vestibular input to trigger descending activity, but channeling both visual and vestibular information into the synthesis of vestibulospinal motor commands. This possibility seems especially likely, considering recent physiological evidence of visual-vestibular interaction in the vestibular nuclei

(Keller and Precht, 1978, 1979a,b; Waespe and Henn, 1977; Daunton et al., 1979; Henn et al., 1974; Dichgans et al., 1973; Allum et al., 1976) and behavioral experiments (Nashner and Berthoz, 1978; Lestienne et al., 1977; Vidal et al., 1979).

The Keller and Precht studies revealed ubiquitous visual influence on the firing rates of neurones in the vestibular nuclei. Cells receiving input from the horizontal semicircular canals also showed substantial modulation of firing rate with horizontal rotation of the visual surround, such that rotation of the visual field had a similar effect to rotation of the animal in the opposite direction. The response dynamics of these cells were linear for combinations of horizontal visual and vestibular stimulation; the rolloff frequency for the response to visual field velocity was about 0.25 Hz.

Contrary to previous theories, the cerebellum was shown to be unnecessary for mediating these visual influences on vestibular nuclei units. However, cerebellectomized cats do not show adaptation of the vestibulo-ocular reflex when reversing prisms are worn, indicating that the cerebellum is necessary for mediating such adaptation. Saturation of the response of the vestibular neurons occurred for visual field velocities above 3 to 10 degrees/sec, whereas floccular units typically saturate at visual velocities greater than

1 degree/sec. Though this latter figure for the floccular units may be of questionable accuracy since the results were obtained with anesthetized animals (Simpson and Alley, 1974), a significant difference between the saturation velocity for floccular and vestibular units further suggests that non-cerebellar sources are responsible for the visual input to the vestibular nuclei.

One method for testing this is to drop subjects unexpectedly in a visually patterned chamber which can be dropped with the subject or moved opposite to the direction of fall. In addition, the test should be performed with eyes closed and in the dark with eyes open, since nulling of visual field motion is not necessarily equivalent to no visual input (Huang and Young, 1980; Waespe et al., 1980). Any differences might be observed as changes in the magnitude of the integrated soleus EMG "startle" reaction, since different accelerations have been shown to result in different response magnitudes (Greenwood and Hopkins, 1976b). Since visual cues in these experiments may be misleading, an ideal strategy might be to minimize the influence of visual information throughout the entire testing sequence after realizing that the cues are misleading. This implies that these experiments may demonstrate the minimum influence that the visual input can have on the motor response system.

A completely analogous argument applies to tactile cues; unfortunately, tactile and other proprioceptive cues cannot be totally separated from the vestibular cues. In order to account for all possibilities, the paradigm can be considered as a test of utilization of generalized proprioception, which includes sensory input from tactile, muscle, joint, internal visceral and vestibular receptors. In the case of the early response, specifically, the reaction can be considered as a test of generalized proprioception which requires intact labyrinths to provide the predominant component.

Vidal et al. (1979) recently completed a set of animal experiments somewhat similar to those reported here. Baboons were seated in a chair which was unexpectedly dropped. Contact was slowed with an elastic system. Both this feature and the fact that the baboons were in a seated position obviated the late pre-contact response in the leg muscles, which rapidly disappeared with repetition. However, the short-latency early response did not disappear, and it is this EMG reaction which was measured in the soleus muscle. This early response was shown to be reduced in situations of stabilized vision and darkness relative to falls in a normal visual environment. A lighted box was placed over the baboon's head to provide stabilized vision, whereas the normal visual field consisted of the laboratory environment. The reported results might be explained simply by the possibility that the baboon could preset the reflex gain before the fall depending upon the visual conditions beforehand. These issues will be discussed further in Chapter 5.

Vidal subdivided the early response into two subcomponents which could be readily distinguished in records of the raw EMG. In the baboon, the first subcomponent occurs from 60 to 100 msec after initiation of the drop. Different visual field conditions were reported to affect predominantly the second subcomponent, although the first subcomponent was affected in certain cases, also. Lacour et al. (1978) reported that labyrinthectomy eliminates the first subcomponent, but only reduces the second, implying that other sensory modalities contribute to the second subcomponent. However, Vidal has reported that visual field conditions also sometimes modify the amplitude of the first subcomponent.

Nashner and Berthoz (1978) tested visual-vestibular interaction during rapid postural reactions to induced antero-posterior sway during standing. A cart mounted on rails could be suddenly displaced backwards, causing the subject who was standing on it to sway forward. A box surrounding the subject provided a visual field which could be moved relative to the subject during the induced sway. Three conditions were investigated. In the first case (N, normal) the box and cart were rigidly connected, resulting in relative visual field displacement in the opposite direction to the direction of sway. In the second condition (S, stabilized) the box was stabilized with respect to the head so that no relative visual field motion occurred. In the third case (E, enhanced) relative visual field motion was enhanced by reversing the box motion relative to the head; in this situation the relative visual field velocity was twice that of the normal (N) condition.

Gastrocnemius EMG recordings from the above experiments revealed visual influences on the response as early as 100 msec. During the 100 to 150 msec interval following onset of the stimulus, EMG in the S condition was suppressed relative to the N condition. Perhaps more surprising was the result that the E condition also suppressed the response in this time interval, but not as much. These findings were interpreted as suggesting that any visual discongruence with other senses caused the short latency response to be reduced, allowing more time for the discongruence to be resolved prior to longer latency reactions. However, the longer latency responses of the gastrocnemius clearly resulted in an increased magnitude of sway in the S condition, and the E condition reduced the magnitude relative to the N condition. This suggests that the longer latency reactions are compensatory in nature, whereas the short latency responses are not.

Sequential repetition of the S conditions revealed that the short latency (100 to 150 msec) response was susceptible to adaptation; the reaction to the discongruent conditions became increasingly similar to that during the normal (N) condition after several repetitions.

Thus, Nashner and Berthoz have convincingly demonstrated visual motion influence on rapid motor reactions during a postural disturbance. Assuming a transmission time of 30 to 50 msec from brain to gastrocnemius muscle, visual information must be processed within the first 50 to 70 msec following onset of the stimulus.

Pathways involving the superior colliculus have been suggested as possible routes for these fast visual influences. Maeda et al. (1977) have shown in the frog that stimulation of both tectum and vestibular nerve produce a complex pattern of IPSP's and EPSP's in spinal motoneurones, which is consistent with the fact that these pathways to the motoneurones are at least disynaptic. Interaction studies revealed that the vestibular and optic pathways to the neck and forelimb motoneurones are independent and do not significantly interact until the influences of these pathways are integrated at the motoneurone level. However, this should obviously not be interpreted to mean that no visual-vestibular interactions are transmitted via these pathways, since both the tectum and vestibular nuclei receive both vestibular and visual inputs. It is possible that visual-vestibular interactions of a different nature can be conveyed to the spinal level via both the vestibulospinal and the tectospinal pathways. Studies were performed in the cat (Anderson et al., 1971) to determine the influence of superior colliculus on neck motoneurones; it was determined that both tectospinal and tectoreticulospinal pathways may be responsible for mediating the effects of collicular stimulation on neck motoneurones.

For a general overview of postural tests of vestibular function, see Appendix A beginning on page 190. Anatomy and physiology of brainstem structures relevant to the vestibular system and posture control are reviewed in Appendix B beginning on page 200.

CHAPTER 2

DESCRIPTION OF APPARATUS

Because much of the equipment used in this study was custom built to accommodate the necessary stimulus conditions, it is appropriate to describe the equipment before detailing the experimental procedure itself. This chapter includes a description of the apparatus sufficient to illustrate how the proper stimulus conditions were created and controlled and how data was processed and recorded.

The basic procedure required suspending a human subject in a safety harness in an upright position and unexpectedly releasing him upon deactivation of an electric brake. A checkered pattern covering most of the subject's visual field could be moved vertically during the fall. Electromyographic (EMG) activity in various leg muscles was recorded in order to observe the relationships between vertical gravireceptive and visual cues and the preparation for landing.

The major components of the apparatus included an electric brake and controller; harness and suspension system, plus various safety devices; moving visual field; EMG processor; accelerometer and goniometers (for joint angle measurements); and PDP-11 computer, which output the stimulus waveform to the brake controller and converted EMG, acceleration, and joint angle data to digital form for storage.

2.1 Electric brake and controller

The harness was connected to a 1/8 inch diameter steel cable, which passed over a pair of pulley wheels near the ceiling and wound around a 4-inch diameter take-up drum. See figure 2.1 on page 42. The take-up drum was mounted on a shaft together with a Warner PB-500 electric brake. See figure 2.2 on page 43. Full activation of the brake armature to -90 VDC provided a static braking torque of 40 ft.-lbs. This is the equivalent of 240 lbs. of restraining force at a drum radius of 2 inches, which was adequate for all of the subjects tested.

Maximum acceleration during a drop could be achieved by reducing the armature voltage to zero. Primarily because of the armature and take-up drum inertia, the maximum acceleration achievable was 0.9 g. Any acceleration less than 0.9 g could be obtained by reducing the magnitude of the armature voltage from 90 VDC to some value between 0 and 90 VDC. The torque-velocity characteristics for a given activation level of the brake complicated the problem of providing a constant restraining force during the drop. This was partially overcome by predetermining the appropriate armature voltage as a function of time following release.

The brake armature was powered by a modified Warner

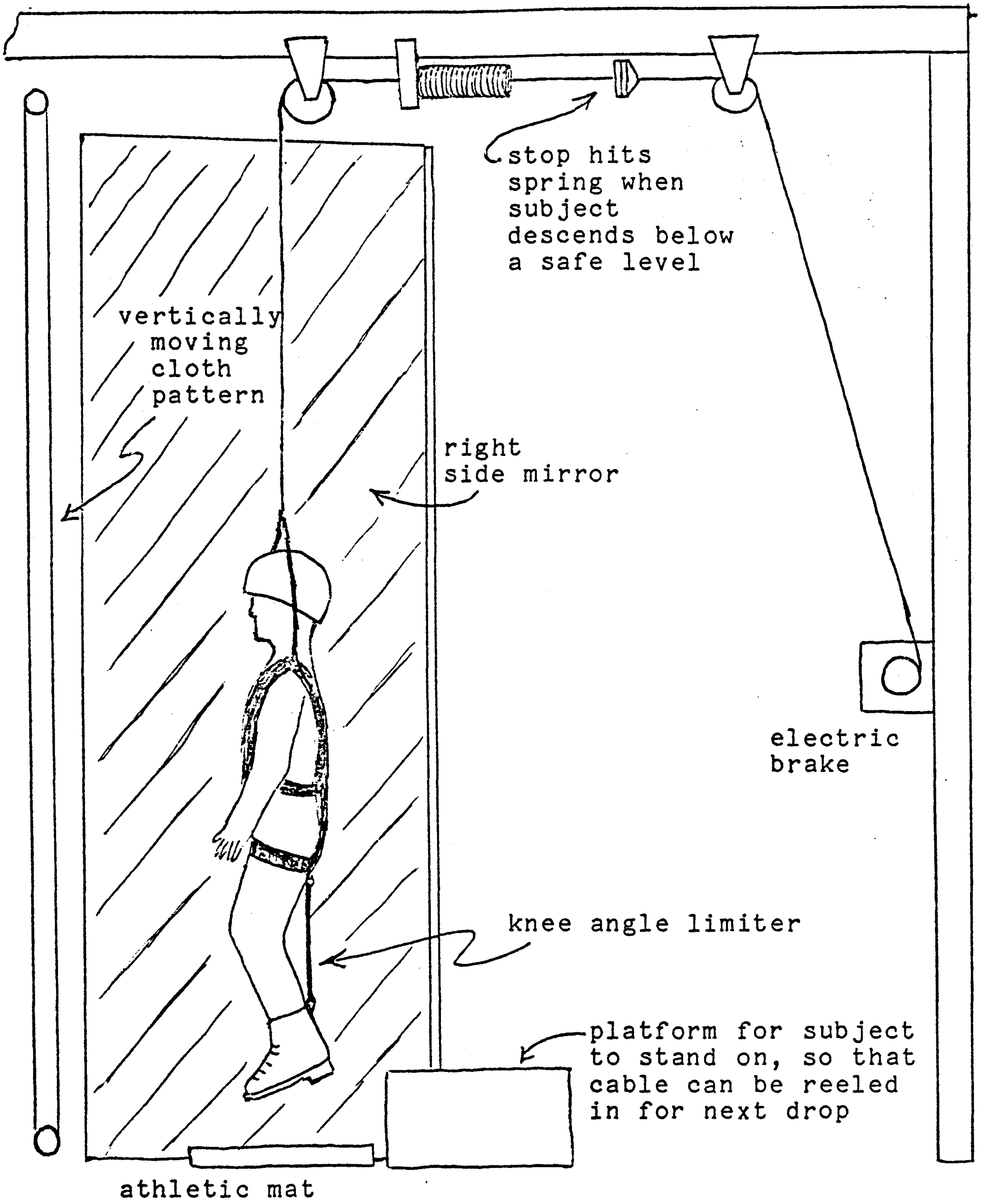

Figure 2.1. Subject suspension system and safety devices.

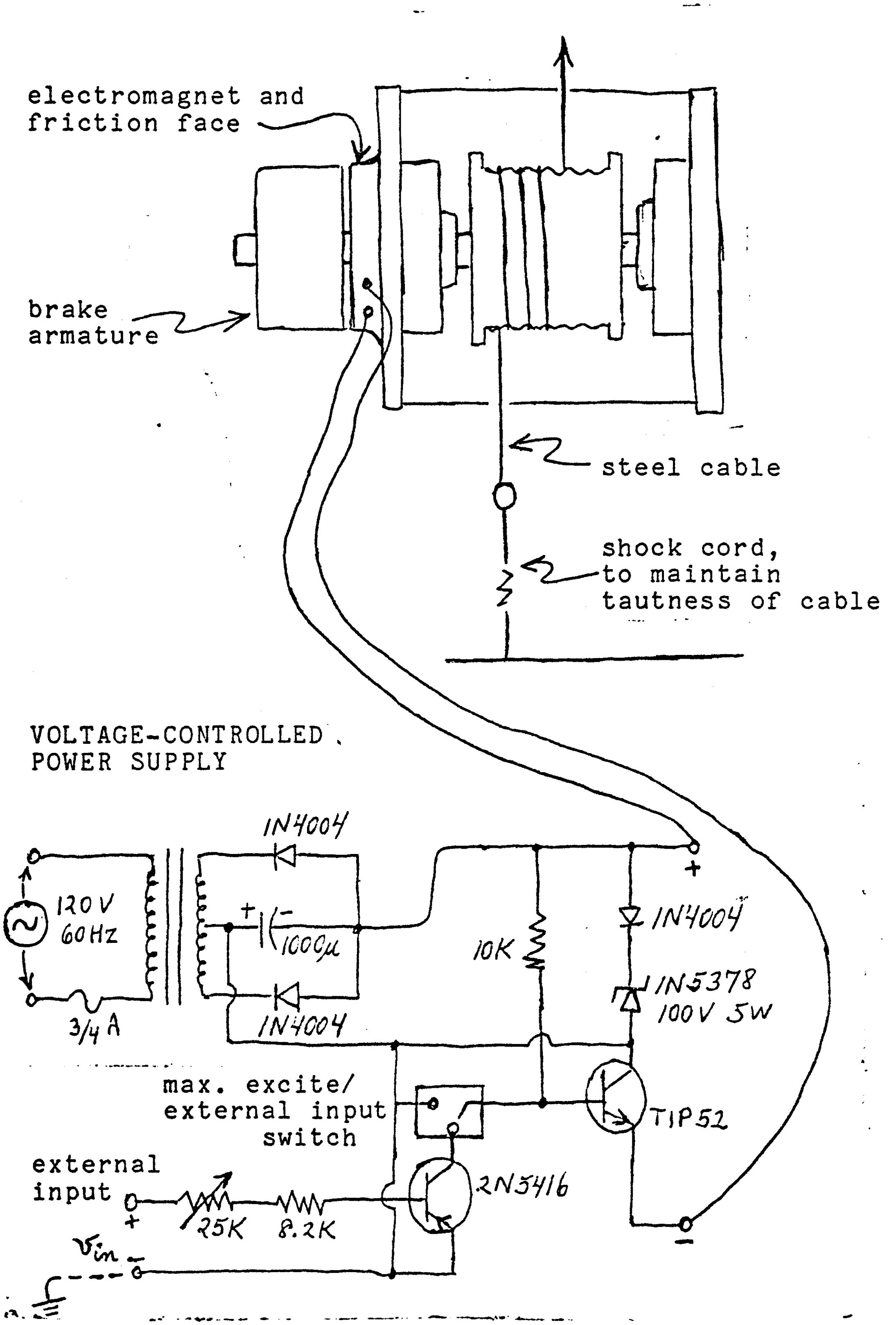

Figure 2.2. Braking system.

MCS-153-3. The original device was only capable of manually controlled on-off switching and potentiometer-adjustable excitation voltage. This had to be modified to allow an externally provided voltage from a computer D/A channel to control the armature voltage. The gain was adjusted such that a 5-volt input resulted in the maximum -90 VDC output. The gain could be increased in order to accommodate subjects weighing more than 160 lbs. All except one subject weighed slightly less than 160 lbs., and in these cases, weights were added above the harness assembly in order to bring the total weight to 160 lbs. This precluded having to change the input waveforms for a desired acceleration profile.

In order to check the accuracy and repeatability of the desired acceleration profiles, the brake system was tested with 160 lbs. of iron weights attached to the harness. The repeatability was such that time of contact with the landing surface varied less than 5%. The electromechanical time constant for armature deactivation was about 40 msec.

2.2 Harness and suspension system

The safety harness (Mori Safety Products, Toronto, part number 444) was connected to the steel cable as shown in figure 2.1 on page 42 and figure 2.3 on page 45. Aluminum tubing guideways prevented the subject from swinging excessively and eliminated rotation about the vertical axis. The left and right steel cables to the harness passed through

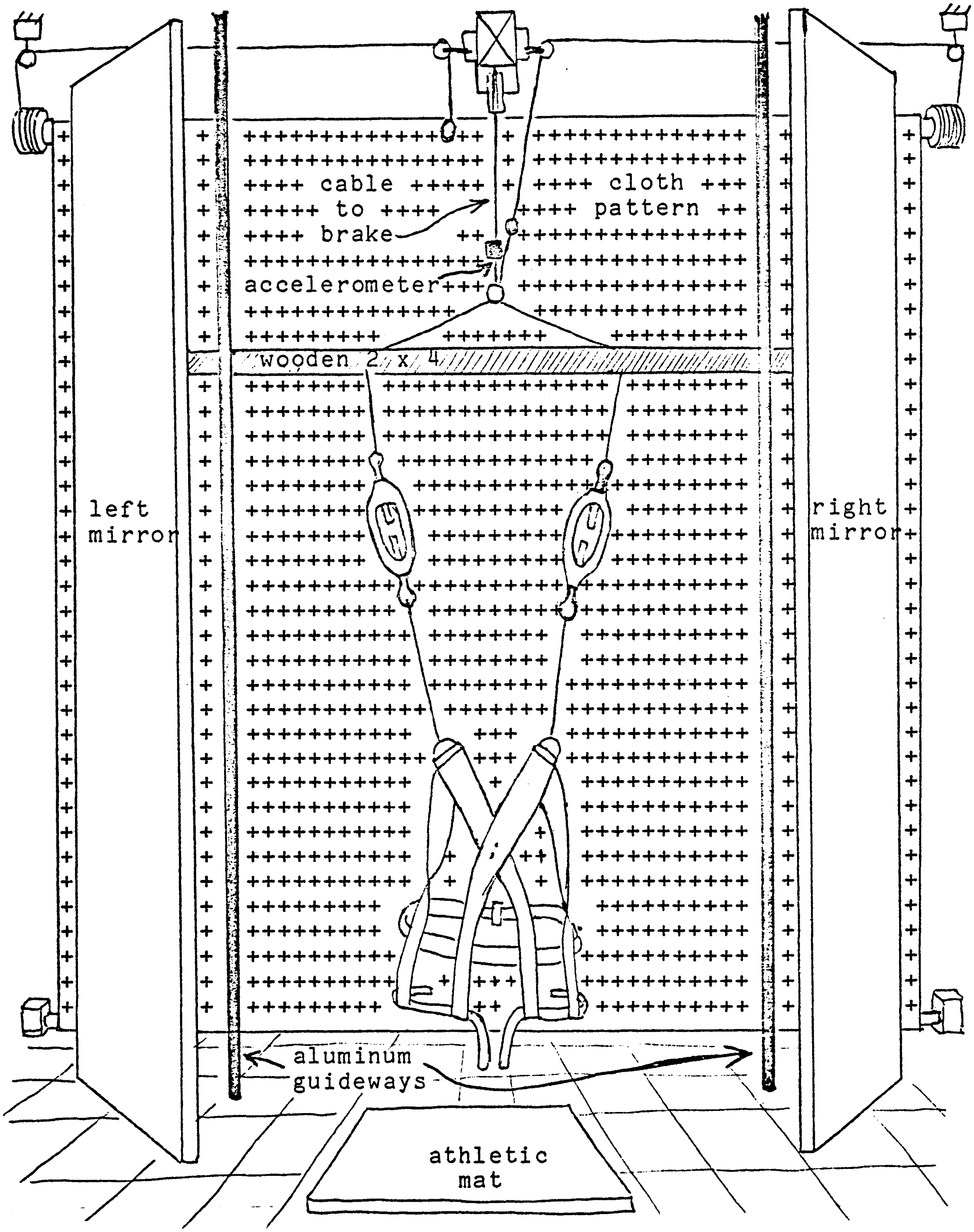

Figure 2.3. Visual field motion system.

the wooden 2x4, which slid freely on the guideways. Since the holes in the 2x4 were oversized compared to the guideway diameter, and the guideway itself was somewhat flexible, friction was insignificant and jamming never occured. The large turnbuckles above the harness allowed the assembly to be adjusted for subjects of varying heights.

As a preventive measure in the case of a completely inappropriate landing, the subject was prevented from collapsing to the floor by means of a large spring mounted between the two pulleys wheels above the harness assembly. The metal stopper mounted on the cable would hit the spring and begin to compress it whenever the subject fell below a certain level. This level was chosen to be 4 inches below the subject's fully erect height. In a well controlled landing, the maximum knee flexion was such that most subjects did not fall below this level.

2.3 Additional safety measures

Subjects were required to wear hiking boots to provide ankle support and to minimize the possibility of sprain or injury due to accidental inversion of the foot. A nylon strap was connected from the rear of the boot to the rear of the harness, acting as a knee angle limiter. This insured that when the subject was suspended, his knees would be slightly flexed. The degree of flexion was not much greater than would normally occur for a passive leg in the suspended position, but did insure that active extension did not occur before contact with the landing surface. Such active extension and possible locking of the knees would have resulted in a jolting and unsafe landing. When the subject was standing on a surface, the harness became unloaded, allowing the nylon straps to slacken. Full knee extension was then possible, preventing unnecessary fatigue. In addition, all subjects wore elastic knee braces (Bauer and Black no. 202495, medium; no. 202657, large).

All landings were on one-inch-thick athletic matting (Resilite). The type of surface, as well as boots and knee supports, may significantly affect the parameters of the postural responses, but since all of the tests were performed using these mats, this factor was not an uncontrolled variable.

2.4 Visual field motion

Because of the importance of peripheral vision in detecting motion, the visual field motion system was designed to allow as much field coverage as possible. A 7-foot wide loop of cloth was stretched taut between two horizontal aluminum tubes, one near the floor and the other near the ceiling, 12 feet high. See figure 2.3 on page 45. The top tube could be connected to the wooden 2x4 of the harness assembly via a 1/16-inch diameter steel cable on either the left or right side of the tube. Each end of the top tube was fitted with an adapter with spiral grooves such that the left and right cables were wound in opposite directions. By choosing to connect either the left or the right cable to the harness assembly, the visual field could be driven up or down at exactly the same speed as the subject. In addition, by attaching an extension cable to either the left or right cable, the visual field could be moved manually while the subject remained suspended.

Acceleration of the subject during the fall was slowed less than 3% because of the additional inertial and frictional loads of the visual field motion system.

The cloth pattern was blue checkered gingham with one-inch alternating blue and white stripes, running vertically and horizontally. See figure 2.4 on page 49 for an example of the type of pattern used. The distance from the subject to the plane of the cloth pattern was 76 cm. Assuming that the subject fixates on a point level with his eyes, the spatial frequency varies from about 0.2 cycles per degree at the fovea to 0.8 cycles per degree at 60 degrees from the fovea. The pattern was quite uniform so that relative positional cues were unlikely. Patterns with spatial frequencies in this range are quite effective in generating linear vection sensation (Lestienne et al., 1977); this particular pattern was chosen in order to provide a powerful visual velocity cue.

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Figure 2.4. Example of type of visual field pattern used (scale, 1:1).

A pair of 12-foot-high, metal-backed acrylic mirrors were placed at 60-degree angles to the cloth pattern in order to extend reflections of the pattern into the lateral-most regions of the visual field. The acrylic mirrors had noticeable imperfections in flatness when viewed directly, but these defects were not objectionable when viewed in the periphery; peripheral vision is very sensitive to velocity cues, but is notably insensitive to pattern variations.

Ski goggles with clear (non-tinted) lenses were worn by subjects in order to eliminate areas of the floor and ceiling from view. Stationary regions of the peripheral visual field tend to cancel the vection effects of moving regions, so it was considered important to attempt to eliminate the effect. No stationary regions were visible using the apparatus and procedure outlined in this study. See figure 2.5 on page 51 for a plot of the approximate region of the visual field remaining with the goggles on, compared to the unrestricted field. The actual area may have varied somewhat, but in all cases none of the subjects could see the floor when facing straight ahead. Perhaps the greatest variability in effective field area arose for myopic subjects who needed to wear corrective lenses. The goggles fit over the lenses without difficulty, but it is possible that myopic people who wear glasses may interpret visual influences outside the corrected field differently.

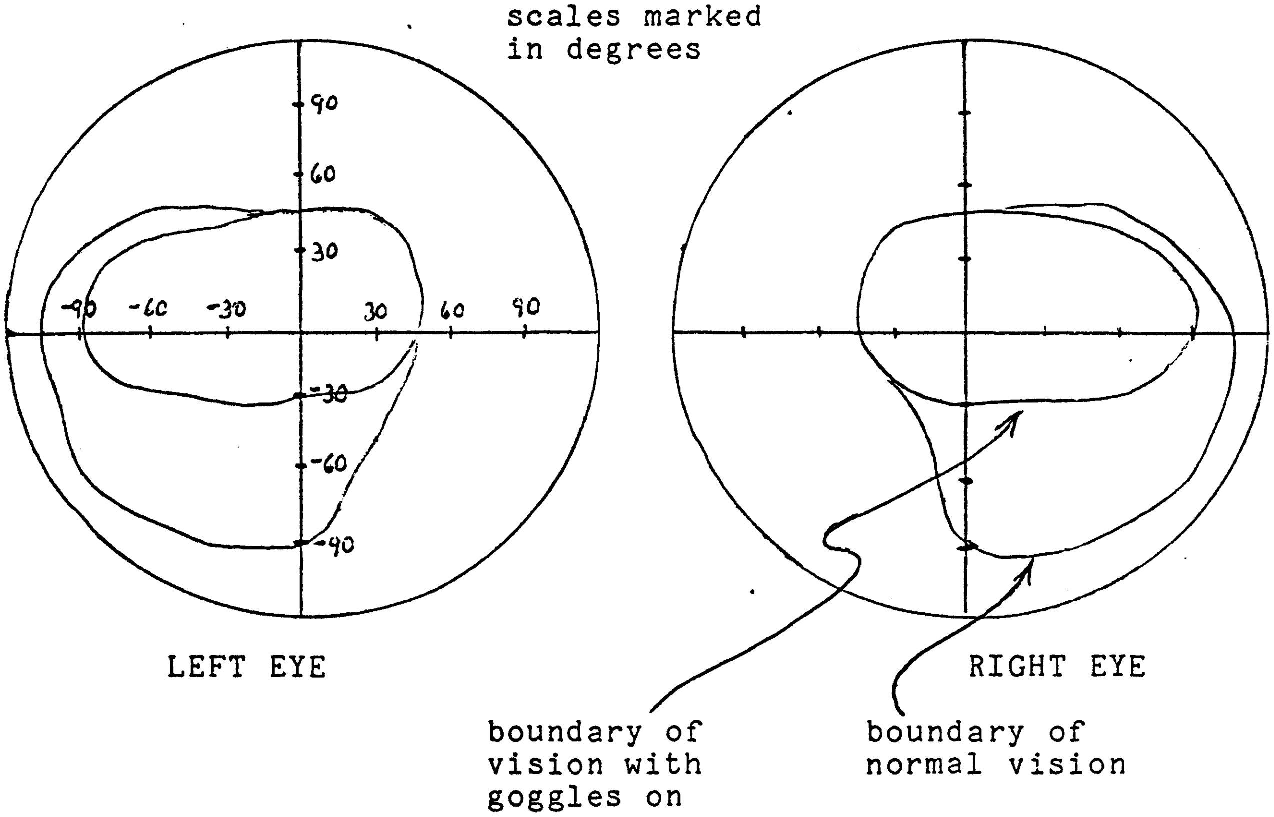


Figure 2.5. Map of restricted visual field using goggles.

The visual field was illuminated with indirect incandescent light, in order to eliminate shadows and to prevent possible stroboscopic effects with fluorescent lighting. The spatial frequency of the pattern was high enough for the latter problem to be of concern, and shadows would provide undesirable stationary cues. Eight 150-watt incandescent lamps were aimed at the walls to the left and right, with front and rear shields to eliminate direct light and to minimize light reflecting from the rear wall. Shadows on the cloth pattern were almost imperceptible and very diffuse.

2.5 EMG electrodes and preamplification

Differential EMG signals were obtained from each muscle of interest using a pair of Hewlett-Packard pre-gelled, disposable, Ag/AgCl surface electrodes (part number 14245B, with snap-on type electrode leads, part number 14279A). These electrodes have a wide adhesive collar which was very effective in preventing accidental detachment during testing.

The electrode pairs provided the input to small differential preamplifiers which were strapped to the leg. The primary component of each preamplifier was an Analog Devices AD521K instrumentation amplifier with a CMRR greater than 90 dB and used with a circuit gain of 100. A matched pair of 100 kilohm resistors was placed in series with the input in order to decrease the possibility of accidental electric shock. See figure 2.6 on page 54 for a schematic. The electrodes were initially checked for artifacts by tapping and pushing on them. No motion artifacts were visible when using the application procedure described in the next chapter.

Differential preamplification near the source virtually eliminated electrostatic and electromagnetic interference normally caused by long leads from high impedance sources. However, another source of distortion is introduced which is due to the nature of the differential configuration, and involves the effect of the travelling wave delay of muscle fibre depolarization between the two electrodes (Hogan, 1976).

2.6 EMG processing

Each channel of the EMG processor consisted of a gain stage, band-pass stage, full wave rectifier, and averager. Gain could be varied from 0 to 10, and the raw EMG could be recorded directly from the output of this initial gain stage. Band-passing was adjusted to include frequencies from 20 to 1000 Hz. This range of frequencies has been demonstrated to be highly correlated to muscle force (Hogan, 1976). Above 1 KHz, the correlation decreases. Full wave rectification is one of the better methods for obtaining a signal which is highly correlated with muscle force (Kreifeldt and Yao, 1974). The rectified signal was then passed through a third

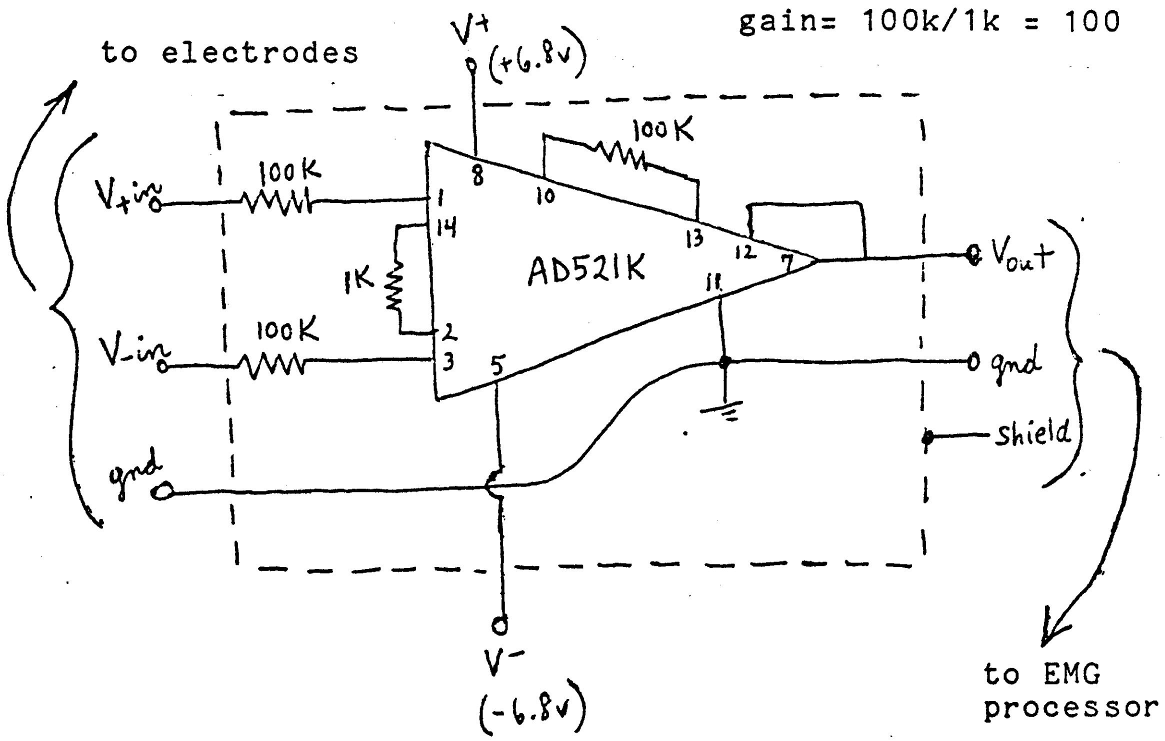


Figure 2.6. Electrode preamplifier schematic.

order averaging filter (Garland et al., 1972), which increases the signal to ripple ratio by 50% compared to a single pole RC filter with a comparable step rise time. The averaging time during all experiments was set to 10 msec. The averaging time is defined to be the time required for the step response to reach 95% of steady state value. Thus, this time would contribute only several msec compared to the brake time constant for the purpose of determining EMG latencies. See Appendix C for a circuit schematic and transfer functions of each stage.

2.7 Acceleration measurements

A single axis, strain-gauge bridge accelerometer (Statham Laboratories F-10-350, -10 to +10g range) was mounted to the cable above the harness assembly to verify the actual acceleration profile during each drop. See figure 2.7 for a schematic of the accelerometer and preamplifier. During tests in which the subject was stationary and the visual field pattern was moved manually, an identical accelerometer was attached to the extension cable used to pull the visual field pattern.

2.8 Goniometers

Knee and ankle flexion measurements were made with a prototype goniometer system developed by the Canadian Arthritic and Rheumatism Society and the University of

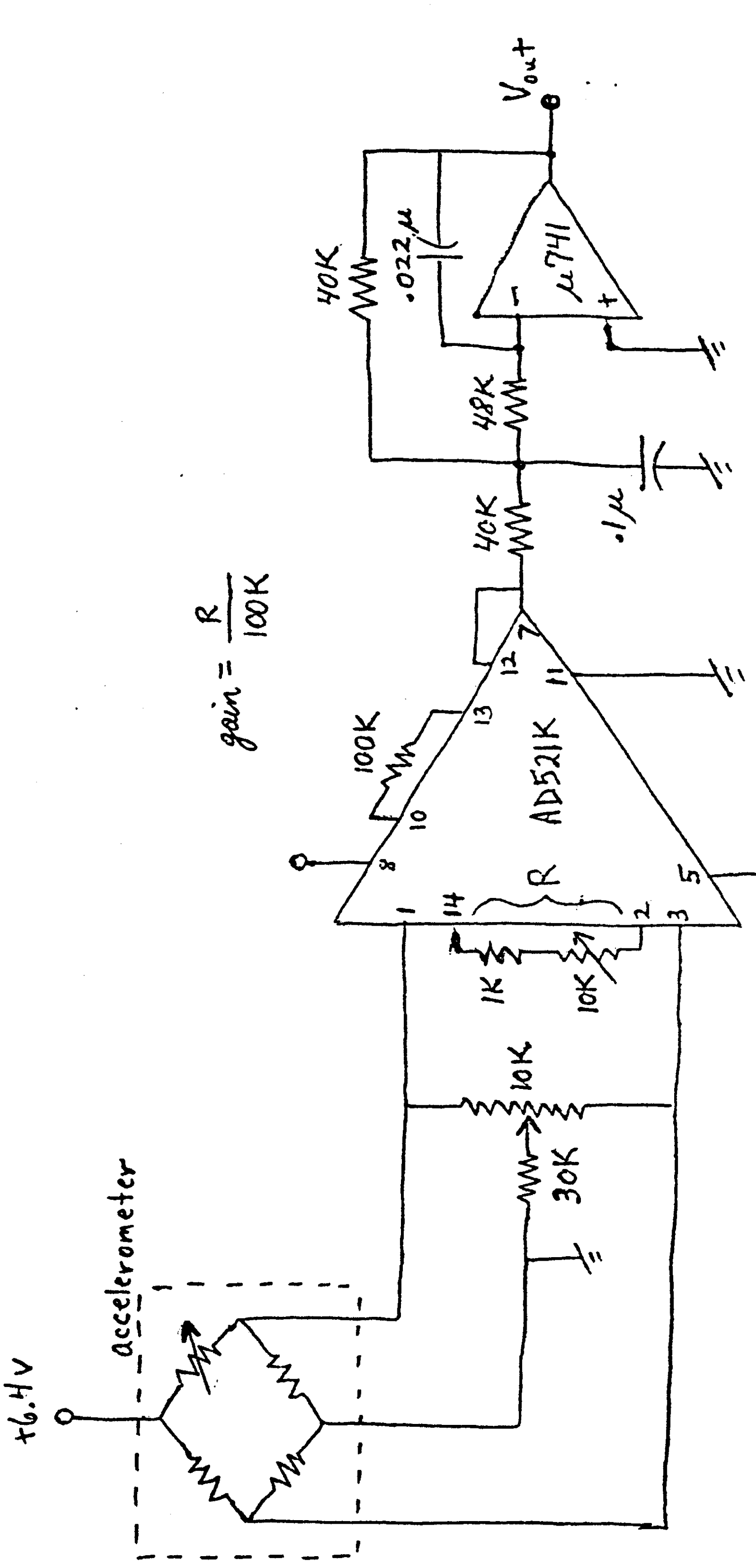


Figure 2.7. Accelerometer and amplifier schematic.

British Columbia (McKechnie and Cousins, 1976). The knee and ankle goniometers were connected by a sliding link, and the flexion axes of the rotation potentiometers were self-aligning. The entire assembly did not noticeably impede movement, and the accuracy in this particular application was estimated to be better than 3%, based on observed amounts of slippage during testing and manufacturer's claims of 1% accuracy. See figure 2.8 on page 58 for a diagram of the goniometer assembly.

The goniometer system was applied to the left leg only, the right leg being completely occupied by EMG electrodes. A hip goniometer section was available, but the safety harness holding the subject made secure placement of the hip goniometer impracticable. While it was possible that timing differences occurred between the two legs, Watt (personal communication) has indicated that the reactions in both legs are well coordinated and that the two feet make contact within a few milliseconds of each other.

2.9 Computer control of stimuli and data conversion

Initiation of the fall and data conversion were under the control of a PDP-11/34 computer. The waveforms for controlling the brake activation during the fall were stored on disk and transferred to memory prior to output via the D/A channels. The only other real time output was the activation of an LED in the experiment room to indicate that data

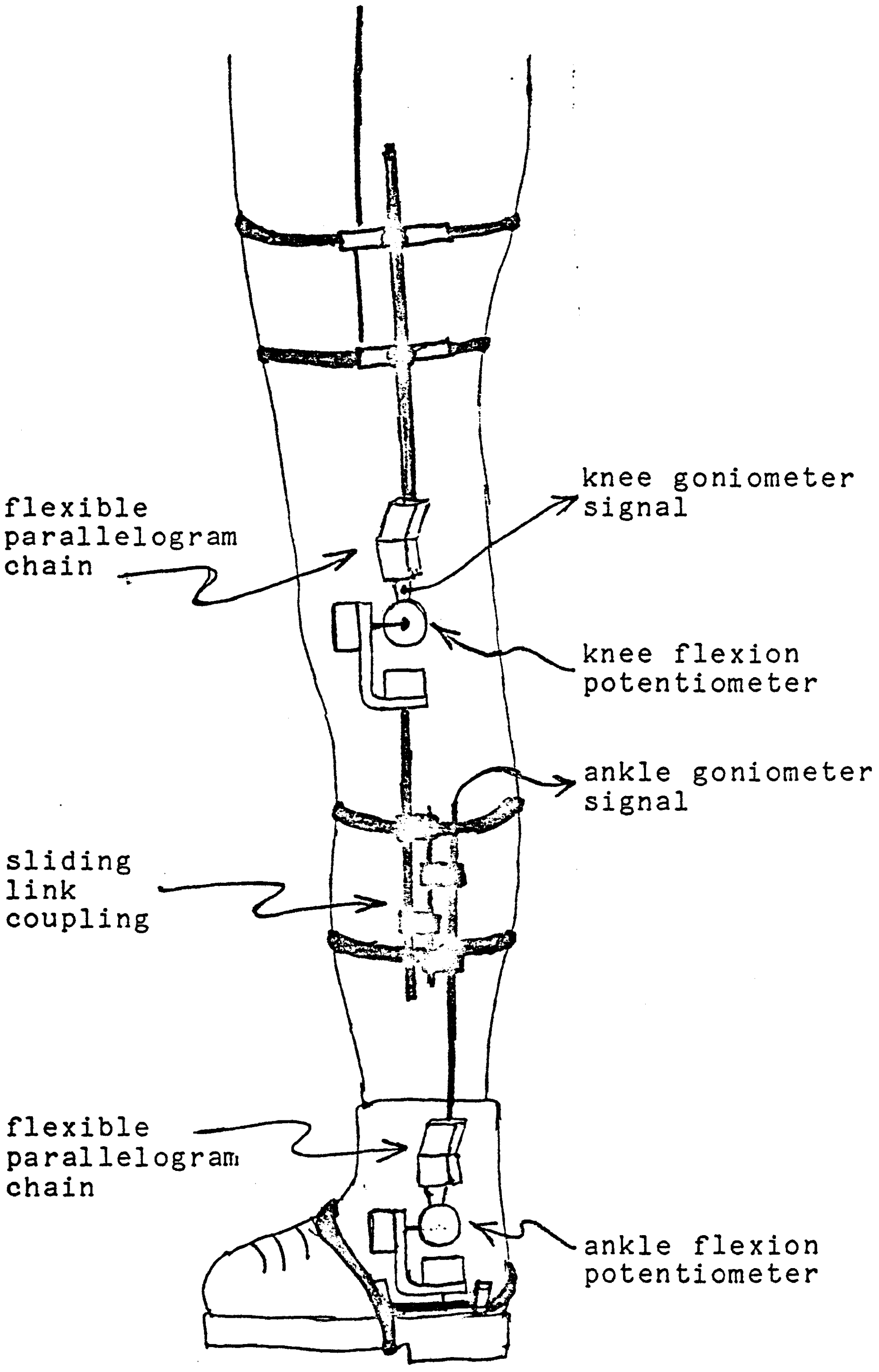


Figure 2.8. Leg goniometer assembly.

conversion had begun; this was used as a cue by the experimenter to begin moving the visual field in cases where the subject remained suspended during visual field motion.

Eight A/D channels were available; five were used to convert filtered EMG output from the EMG processor, two were used for the knee and ankle flexion signals, and one was used to convert the amplified acceleration signal. This last channel was connected to either the amplified signal from the accelerometer above the harness, or the signal from the accelerometer connected to the extension cable for manual visual field operation. (See section 2.3 describing the visual field system.) The sampling rate was 500 Hz for all channels. One second of data was taken from each channel and stored on disk.

2.10 Miscellaneous equipment

Each subject wore a crash helmet to provide protection against potential falling objects, and to provide a convenient anchor on which to place earphones for noise masking. The masking noise consisted of Gaussian noise at a sufficient level to distract from most, but not all, equipment noises. It was switched on at a random time just prior to each drop and switched off immediately after to prevent habituation (and possible irritability). The only loud, impulsive noise occurred after the subject landed, due to the metal stop hitting the spring above the harness assembly. (See figure 2.1 on page 42.)

CHAPTER 3

EXPERIMENTAL PROCEDURE AND STATISTICAL DESIGN

This chapter outlines the actual procedure followed to prepare the subject and install him in the apparatus, and perform a sequence of drop tests. This is followed by a discussion of the overall experimental design from a statistical perspective. For a more detailed description of the rationale behind the use of a particular device, refer to the previous chapter.

3.1 Preparation of the subject

All subjects were examined for neurological and orthopedic problems by a surgeon specialized in posture and gait disorders. Prior history of broken bones, sprained ankles or knee joints, stretched ligaments, backache, or poor reflexes was sufficient to disqualify a potential subject. A vestibular system diagnostic procedure was also performed, which included checks for abnormal eye movements during horizontal rotation, positional nystagmus, and abnormal response to an air caloric vestibular test. While these are all tests of semicircular canal function rather than the otoliths, in most cases of otolith disorders the canals are also affected. Currently, there are no selective clinical tests of otolith function.

Each subject witnessed a demonstration drop test before participating. A brief questionaire was given to the subject which included subjective estimation of his own level of anxiety and alertness, both on a scale from 1 to 7, and a report of past sports activities. All of these factors might be expected to have an effect on the patterns observed in the EMG responses.

Prior to electrode application, each site was shaved, wiped with alcohol, and scratched with a hypodermic needle in order to break through the stratum corneum. This method has been demonstrated to consistently provide low resistence paths from electrode to muscle and reduce muscle artifacts (Tam and Webster, 1977; Webster, 1977). A large component of motion artifact is due to variations in skin potential with pressure on the skin; reducing the skin resistance by scratching diminishes the degree to which the skin potential is reflected in the measured voltage. Raw EMG (preamplified but unfiltered) was recorded with an FM tape recorder during experiments on the first three subjects to check for possible motion artifacts. The only artifacts which were ever observed occurred when an electrode had accidentally broken from contact with the skin, creating very large voltage swings which were also quite obvious in the filtered EMG. Because of this, it was judged unnecessary to record raw EMG.

During the testing, EMG signals were recorded simultaneously from the quadriceps (rectus femoris), hamstrings (biceps femoris), tibialis anterior, right gastrocnemius and soleus muscles of the right leg. Electrode pairs were placed over the approximate middle of each muscle body, and a single common ground electrode was placed over the anterior tibial ridge. Each pair was oriented in the lengthwise direction of the muscle, and the centers of the electrodes were spaced 5.7 cm apart. See figure 3.1 on page 65 for exact electrode locations on the right leg.

After electrode placement, the subject then put on the elastic knee braces, hiking boots, and the knee and ankle goniometers. In the experiment room the input leads to the EMG preamlifiers were attached to the electrodes on the subject's right leg and the goniometer signal cables were connected. The EMG and goniometer channels were checked while asking the subject to hop up and down. Then, the subject put on the crash helmet and goggles and was placed in the harness. Knee angle limiters were attached from the rear of each boot to the harness and were adjusted.

3.2 Basic procedure for each drop

At this point the subject was ready to begin the procedure for the first drop. First, a platform was placed under the subject so that the cable to the harness could be reeled in manually to a predetermined calibration mark. The turnbuckles above the harness were adjusted so that the

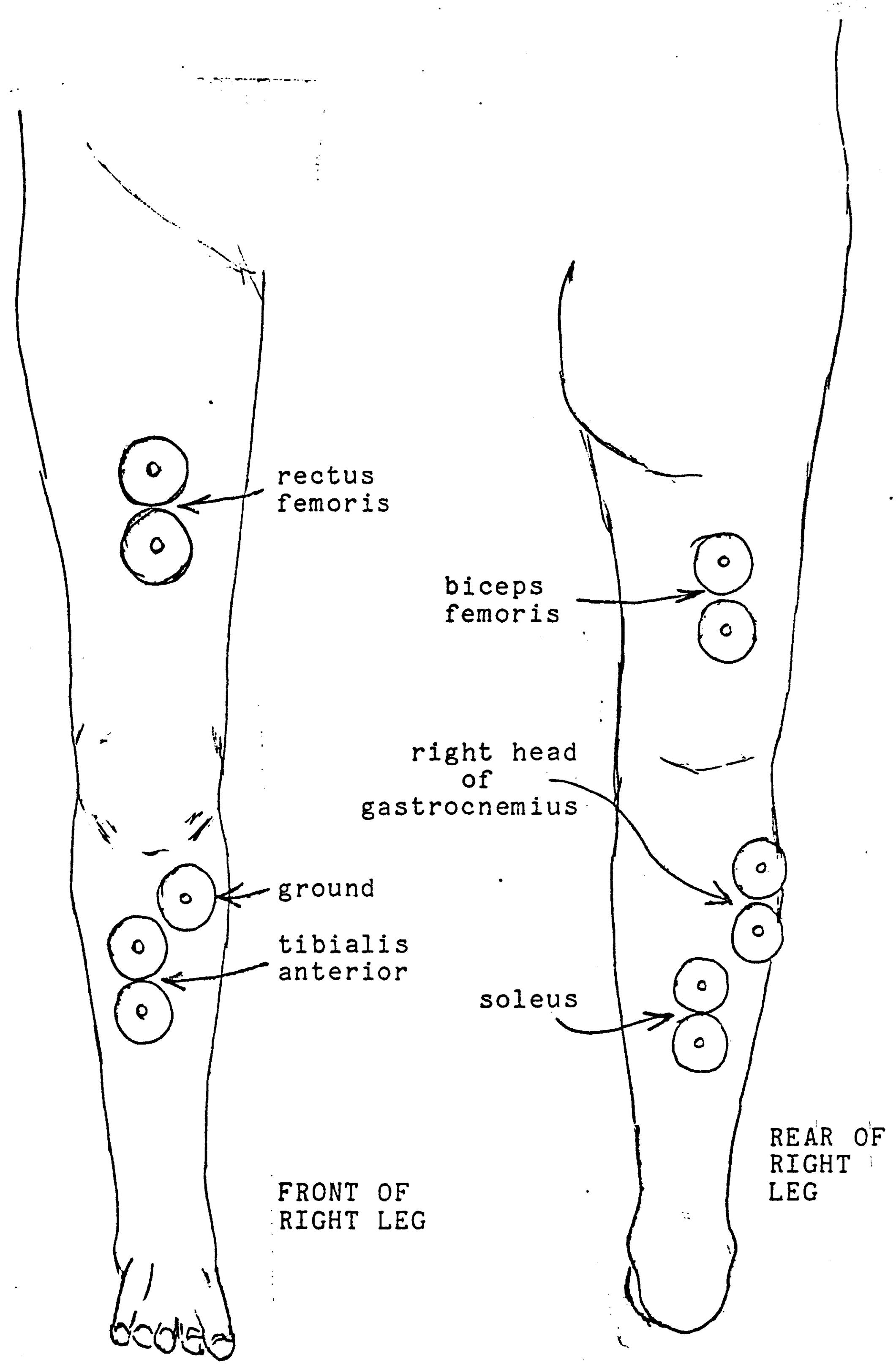


Figure 3.1. Leg electrode positions.

subject's heels were barely resting on the platform. This adjustment was necessary only before the first drop, and insured that the height for all drops was the same. Until the fall began, the harness position was held by switching the brake controller to "maximum excitation". The platform height could be chosen to be either 28 or 43 cm for a given test.

With the subject still standing on the platform, he was told to close his eyes. The masking noise was then switched on and desired mechanical connections to the visual field motion system were made. This procedure was followed even when no visual field motion was desired, in order to prevent the subject from deducing the nature of the subsequent test. After this procedure, the subject was instructed to either close or open his eyes, depending upon the parameters of the test.

To standardize the initial head position, the subject was also instructed to maintain the head erect and fixate on a point on the screen level with the eyes. In cases in which the eyes were closed or the room was darkened, the subject was asked to position his head and eyes in the same manner, as if he were looking at the screen. The platform was pulled out from beneath, and the drop then occurred unexpectedly, but within the next 10 seconds. Although flexion and extension of the head was not measured, no head motion was visible during the falls. Since the head was constrained from further extension by the helmet and the suspension cables to either side, the subject's head was in a position of maximal extension allowed by the apparatus, both before and during the fall. This constraint was such as to allow the head to be maintained in a erect position. After the fall, the subject was told to switch the masking noise off.

To summarize the possible test conditions: the height of the drop could be 28 or 43 cm; the acceleration profile could be selected from a pre-synthesized set of profiles, including the case when no drop occurs; and, the visual field could move down with the subject, it could move exactly opposite to the subject's motion, it could remain stationary, or it could be moved manually. The drop could also occur in the dark (eyes open) or with eyes closed. Thus, the only variables of which the subject was aware beforehand was the initial height, and whether the room was darkened or his eyes were closed.

This entire procedure was followed for all experiments, except for minor variations in certain cases. In the report of the results, any such exceptions to this procedure will be mentioned.

3.3 Statistical design of experiments

The investigation of the primary effects of acceleration profile, initial height, and visual field conditions is complicated by possible adaptation which may occur as the experiment proceeds and by the possible interaction of previous tests with the reaction in subsequent tests. For example, since a moving visual field provides a misleading cue, the subject might be expected to reduce the influence of vision on his reaction during the test immediately following. Therefore, statistical considerations were of prime importance in determining the experimental design and the order of testing.

A three way split plot design was chosen as a method which would allow separation of the effects of adaptation and interaction of adjacent tests as well as the main effects of acceleration and visual field motion (McNemar, 1969; Cochran and Cox, 1950). In a three way split plot design, there are B(blocks) x R(rows) x C(columns) cells, where each column represents a particular set of conditions for a drop, each row represents a different subject, and a block represents a particular order of testing. A different set of subjects was used in each block. Each repetition of a set of drop conditions must be categorized in a new column, since the temporal position in the testing sequence must also be considered as a variation of the drop conditions.

See Appendix D for the procedure for determining statistical significance for main block and column effects and block by column interactions.

Actual combinations of acceleration, height, visual field parameters, and the order of testing will be specified for each set of experiments discussed in the following chapters.

CHAPTER 4

EXPERIMENTS AND RESULTS

The experimental procedures described in the previous chapter were completed on a total of thirteen subjects between the ages of 20 and 30 years, two of whom were females. One subject had a case of asymptomatic lumbar scoliosis, which did not pose a safety risk, but was of concern because scoliosis may affect reflex characteristics. However, no unusual variations were observed in the data relative to the other subjects. See table 4.1 on page 72 for a brief description of the ten subjects who were included in the final, perfected paradigm.

Vestibular system function was tested for normality by a series of standard clinical procedures which are mentioned in the previous chapter. No abnormalities were indicated in any of the subjects.

4.1 Stimulus combinations

A total of five different acceleration profiles were tested, which are shown in figure 4.1 on page 73. The corresponding velocity profiles for each acceleration are also shown. These included a 0.5g step, a 0.85g step, two profiles with a double acceleration step, and an acceleration ramp. An additional condition was included in which the subject was not dropped while the visual field was moved

Table 4.1. Description of subjects.

subject's initials	sex	height (ft,in.)	weight (lbs.)	sports activities, misc.
Block 1:				
EMA	M	5'10"	145	moderate activity in skiing
PNE	M	6' 0"	160	none
PRI	F	5' 8"	150	moderate activity in skiing myopic, wore glasses during testing
DDL	M	6' 1"	155	weight lifting, bowling
TED	M	5' 9"	137	tennis, basketball, soccer
Block 2:				
TWA	M	5' 7"	140	some swimming; past skydiving, but not currently active
RWA	M	6' 0"	175	running,skiing, Zen meditation
PPE	M	5' 7"	145	some swimming and weight lifting myopic, wore glasses during testing
LLA	F	5' 5"	111	considerable activity in gymnastics
APA	M	5' 9"	115	fencing, Tae-kwon-do myopic, wore contact lenses during testing

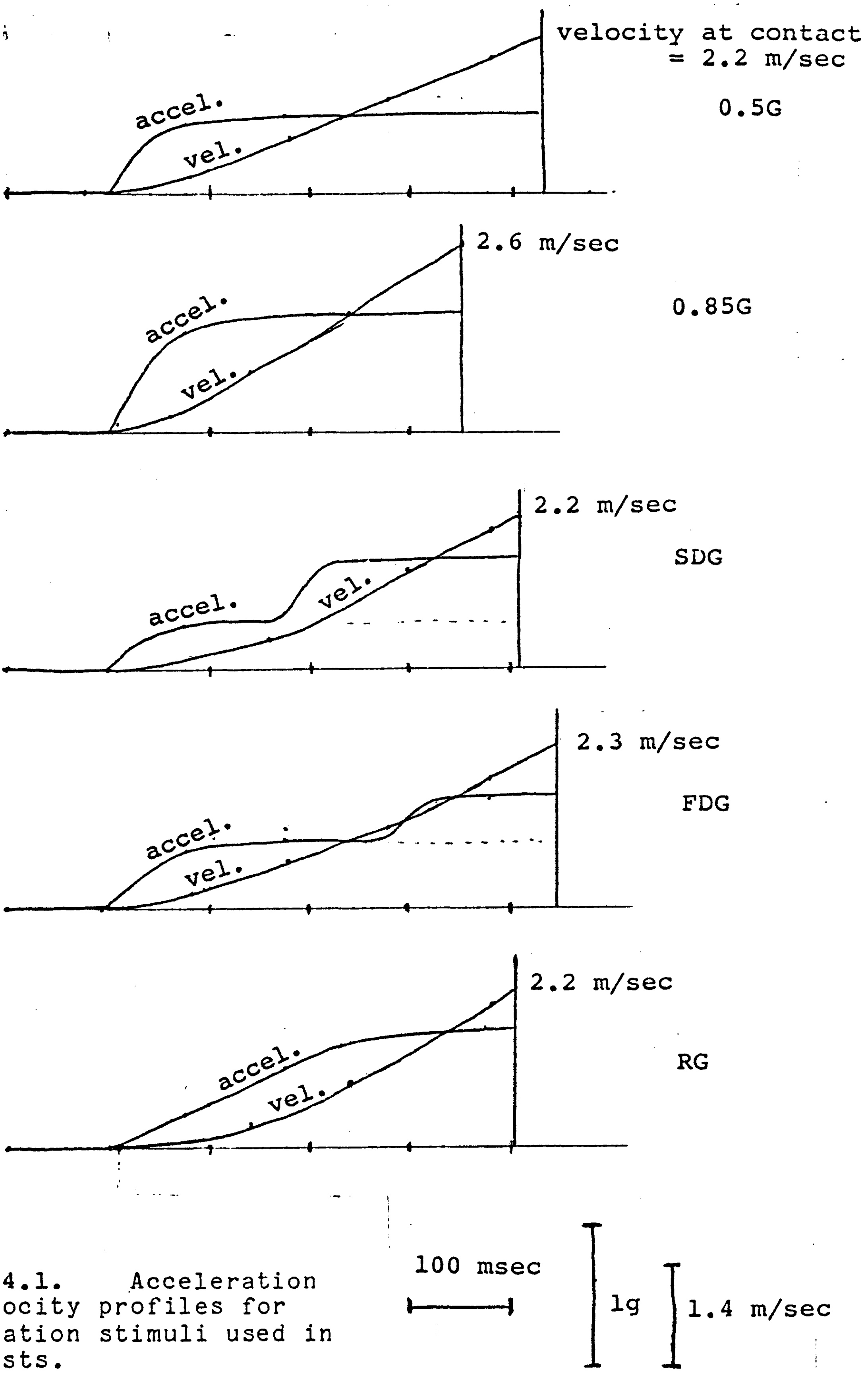


Figure 4.1. Acceleration and velocity profiles for acceleration stimuli used in drop tests.

unexpectedly. In order to facilitate discussion, these conditions will be referred to as 0.5G, 0.85G, SDG (slow double step), FDG (fast double step), RG (ramp), and 0G (no drop).

Visual field conditions were as follows: no unusual effects, visual field moved down during the drop, visual field moved up while the subject was dropped, eyes were closed during the fall, and, eyes were open but room was darkened during the fall. These conditions will be referred to as N (normal), D (down), U (up), EC (eyes closed), and DK (dark), respectively. Subjects reported that they could see nothing in the darkened condition. Only 10 seconds were available for any dark adaptation, which was insignificant.

Since the distance, d, between the subject's eyes and the screen was 76 cm, the relative angular visual velocity at the central part of the visual field can be obtained by the following relationship:

$$\omega_{vis} = n \cdot \left(\frac{-v}{d}\right) \qquad n = \begin{Bmatrix} 0 \text{ for /D condition} \\ 1 \text{ for /N} \\ 2 \text{ for /U} \end{Bmatrix}$$

where ω_{vis} is the relative visual field velocity and v is the actual downward velocity of the subject. For example, to obtain the relative angular velocity in degrees/sec for the /N condition, multiply the subject's actual linear velocity in m/sec (as shown in figure 4.1) by the factor,

-75 degrees/m (-1/0.76m x 57.3deg/radian).

A total of fifteen different combinations of acceleration and visual field conditions were tested and are listed in table 4.2 on page 76. The acceleration double steps and ramp cases were tested only under the normal visual field condition, since the primary objective of these tests was to determine the ability of the subject to respond to acceleration changes after the initial release.

4.2 Preliminary tests

Several modifications of the experimental procedure were made after testing the first three subjects. A number of problems were encountered during these initial tests concerning issues which are relevant to the interpretation of the data.

For the first three subjects, the design of the brake drum was such that the cable would sometimes wind around the drum in a plane which was not exactly perpendicular to the drum axis. This resulted in variations of acceleration profile during unwinding. By adding grooves to the drum, this problem was eliminated and the acceleration profile achieved a much greater degree of standardization.

Acceleration measurements on the first three subjects were made by fixing one accelerometer to the safety helmet and another to the subject's boots. Due to variations in

Table 4.2. Combinations of acceleration profile and visual field conditions which were tested.

acceleration profile	visual field condition
0.5G	N (normal)
	D (field moved down during fall)
	U (field moved up during fall)
	EC (eyes closed)
	DK (darkened room)
0.85G	N
	D
	U
	EC
	DK
SDG (slow double step)	N
FDG (fast double step)	N
RG (ramp)	N
OG (no fall)	D
	U

head position, this was unacceptable as a method for monitoring the accuracy of the acceleration profile. An accelerometer was placed on the boot in the hope of obtaining a simple indicator of moment of contact, but the signal did not allow a precise determination of contact; plantar flexion of the foot usually cushioned the landing sufficiently to eliminate sudden deceleration.

The acceleration measurement repeatability was improved by attaching an accelerometer on the cable above the harness assembly above the 2x4 but beneath the pulley. (See figure 2.3 on page 45.) This allowed accurate placement of the accelerometer with respect to the vertical. The major disadvantage of this placement was that vibration artifacts arising from the natural frequency of the support structure were superimposed on the acceleration signal as measured at the harness; the harness effectively dampened most of the vibration, though. Acceleration measurements recorded during calibration tests at the harness with a 160-lb. load are shown in figure 4.2 on page 78. Compare these to the acceleration measurements at the cable which were taken during each drop test; see figures 4.3.1-14 on pages 85-98, the sixth channel of each figure. Since the cable continued to unreel for a short distance after the subject contacted the floor, the acceleration information after contact is irrelevant. The main utility of acceleration measurement during a drop was as an indicator of release time and as a

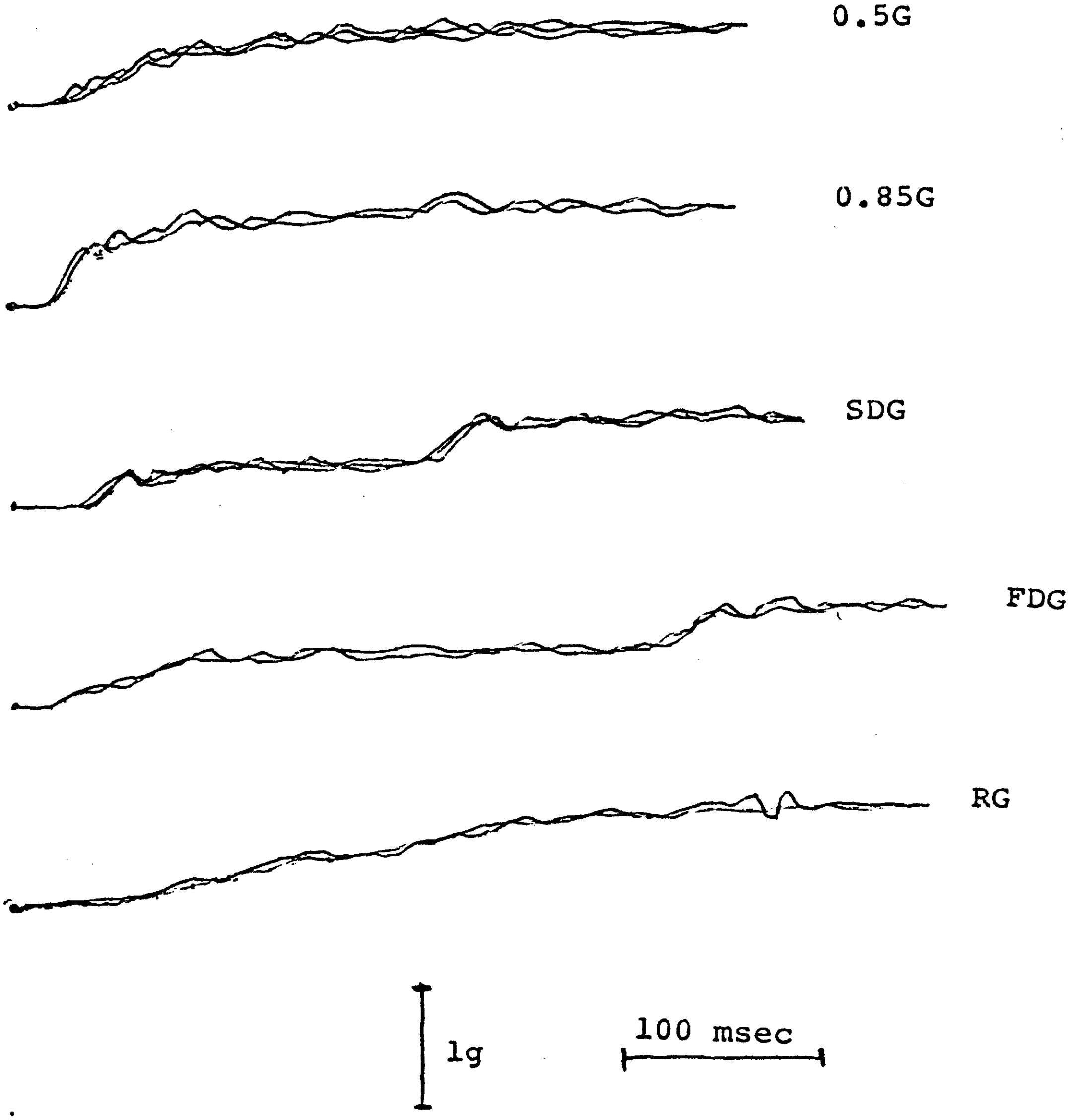


Figure 4.2. Acceleration measurements taken at the harness with 160 lbs. of added weight for calibration.

gross check of repeatability.

In general, the accuracy of the acceleration profiles was not as great as desired. However, because of the statistical treatment of the data, any acceleration variability would be incorporated into experimental error and correctly reflected in the significance values obtained. Since test conditions were compared within the data for each subject, any consistent bias in acceleration for a given subject would be factored out. The main source of such a bias would possibly be failure to accurately compensate for weight differences among subjects.

The goniometers which were available for use with the last ten subjects greatly improved the determination of contact time; ankle angle is forced to undergo a sudden dorsiflexion as the ball of the foot hits the ground. Some of the goniometer records manifested artifacts due to intermittent connections with the power supply caused by jolts during landing. However, the initial onset of ankle dorsiflexion always preceded any such artifacts, and provided a reliable indicator of contact.

In addition to the stimulus measurement problems, the procedure used in testing the first three subjects revealed more fundamental difficulties in obtaining repeatable responses. Since the procedure had just been developed, frequent adjustments of the apparatus necessitated interruptions of the experimental sequence. By the time the fourth subject was tested, the intertrial interval was never more than several minutes, which probably reduced fatigue and boredom significantly.

For the first three subjects, each test condition listed in table 4.2 was repeated at heights of 28 and 43 cm, three times at each height. This required a total of 90 trials, randomized with respect to test conditions. These 90 trials had to be broken down into several sessions in order to complete the session within two hours. Longer times would have been excessively fatiguing. Since testing order was one of the important conditions of the experiment, breaking the sequence into several sessions made interpretations of the sequencing effects impossible except for tests within a single session. In addition, failure to replace surface electrodes on exactly the same location from session to session, as well as changes in the subject's physical condition, would make comparison even more difficult.

Since the subject could observe his initial height and could successfully account for this variable, the drops from 28 cm were eliminated from the sequence for the last ten subjects. One of the primary objectives of this study was to investigate ability to respond to cues during the fall, so it was considered desirable to standardize conditions prior to release as much as possible.

Thus, with the improved standardization of the acceleration profiles, the addition of goniometers, and the shortening of the procedure to 45 trials during a single session, the procedure was considered adequate for testing without further changes. The procedure as described in the previous chapter applies to the last ten subjects. Any statistics which are given in the text use only the data from these last ten subjects.

4.3 Testing order and coding of trials

Since the split plot experimental design is highly sensitive to main block effects and block by treatment interactions when the number of treatments is large, two blocks were considered adequate. Because of the limited number of subjects, this is superior to dividing the available subject pool into a larger number of blocks; data from a large number of blocks with few subjects in each block would be of lesser value, since the likelihood that block differences were due to real interblock subject differences would increase.

In this experiment each of the two blocks represents a different order of testing. Each testing sequence is the exact reverse of the other. This allows each test to be preceded by a different test in each block while permitting simple comparisons of overall adaptation or habituation effects because of the symmetry. Testing sequence for both blocks is shown in table 4.3 on page 83. Table 4.4 on page 84 groups the tests by stimulus condition and lists the sequence position for each test.

In order to facilitate references to particular drop tests, a code will be used in the discussion which is of the form acceleration/ visual field condition/ block number/ repetition number. For example, the code 0.5G/EC/B2/3 refers to the third repetition in block 2 of the test for which the acceleration was 0.5g and the subject's eyes were closed during the fall; the code 0.5G//B1/ refers to all 0.5G drops in block 1.

4.4 General description of the EMG response

Several examples of actual EMG recordings are shown in figures 4.3.1-14 on pages 85-98. These examples illustrate many of the characteristics which are discussed in this section. Each page shows superimposed waveforms for all three repetitions for a given subject and test condition. The waveforms were reconstructed from the sampled versions of the original raw data; thus, the top five waveforms represent the sampled, rectified, filtered EMG data.

In the discussion which follows, the five pairs of electrode leads will be referred to as GN (gastrocnemius), SL (soleus), TA (tibialis anterior), RF (rectus femoris), and BF (biceps femoris). These muscle abbreviations refer

(cont. on p. 99)

Table 4.3. Drop test sequence for block 1 and block 2 (reverse of block 1).

test code	sequence number: block 1	block 2
0.85G/U	1	45
0G/D	2	44
0.5G/EC	3	43
0.85G/EC	4	42
0.85G/DK	5	41
0.5G/D	6	40
0.85G/DK	7	39
0.5G/EC	8	38
0.5G/N	9	37
SDG/N	10	36
0.85G/D	11	35
0G/U	12	34
0.5G/EC	13	33
0.85G/N	14	32
0.5G/D	15	31
0.85G/N	16	30
SDG/N	17	29
0.5G/N	18	28
0.5G/U	19	27
FDG/N	20	26
0.85G/U	21	25
RG/N	22	24
0.85G/EC	23	23
0G/D	24	22
0.5G/N	25	21
0.85G/U	26	20
0.5G/D	27	19
0.85G/DK	28	18
0.5G/DK	29	17
0.85G/D	30	16
0.85G/EC	31	15
0.5G/DK	32	14
FDG/N	33	13
RG/N	34	12
0G/U	35	11
0.5G/U	36	10
0G/D	37	9
0G/U	38	8
0.5G/U	39	7
FDG/N	40	6
0.85G/N	41	5
0.85G/D	42	4
SDG/N	43	3
0.5G/DK	44	2
RG/N	45	1

Table 4.4. Drop tests grouped by test type, giving sequence positions in blocks 1 and 2.

test code	BLOCK 1 sequence position	mean sequence position	BLOCK 2 sequence position	mean sequence position
0.5G/N//1	9	17	21	29
2	18		28	
3	25		37	
/D//1	6	16	19	30
2	15		31	
3	27		40	
/U//1	19	31	7	15
2	36		10	
3	39		27	
/EC//1	3	8	33	38
2	8		38	
3	13		43	
/DK//1	29	35	2	11
2	32		14	
3	44		17	
0.85G/N//1	14	24	5	22
2	16		30	
3	41		32	
/D//1	11	28	4	18
2	30		16	
3	42		35	
/U//1	1	16	20	30
2	21		25	
3	26		45	
/EC//1	4	19	15	27
2	23		23	
3	31		42	
/DK//1	5	13	18	33
2	7		39	
3	28		41	
SDG/N//1	10	23	3	23
2	17		29	
3	43		36	
FDG/N//1	20	31	6	15
2	33		13	
3	40		26	
RG/N//1	22	34	1	12
2	34		12	
3	45		24	
OG/D//1	2	21	9	25
2	24		22	
3	37		44	
/U//1	12	28	8	18
2	35		11	
3	38		34	

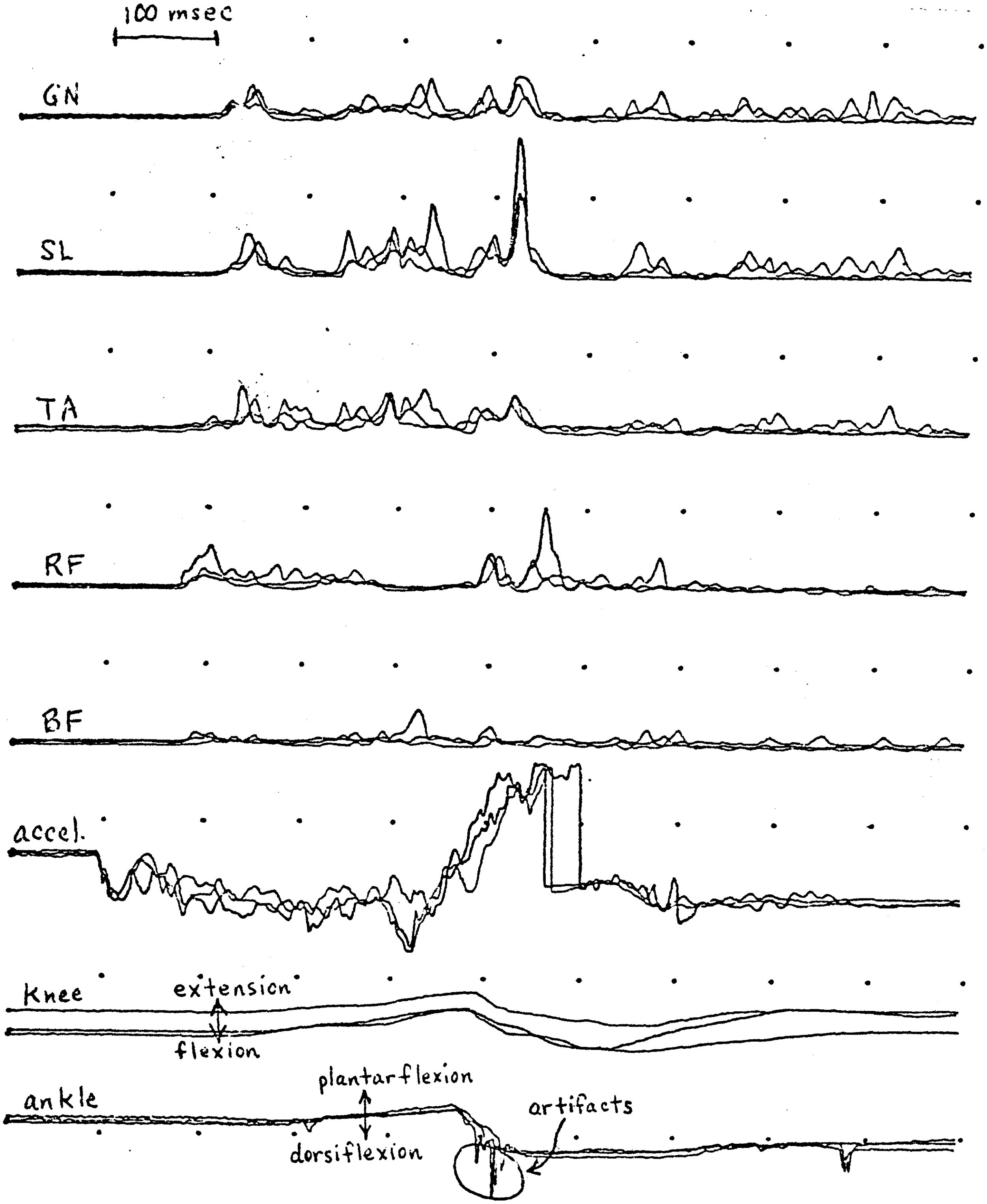


Figure 4.3.1. Subject EMA, tests 0.5G/N/B1/1-3.

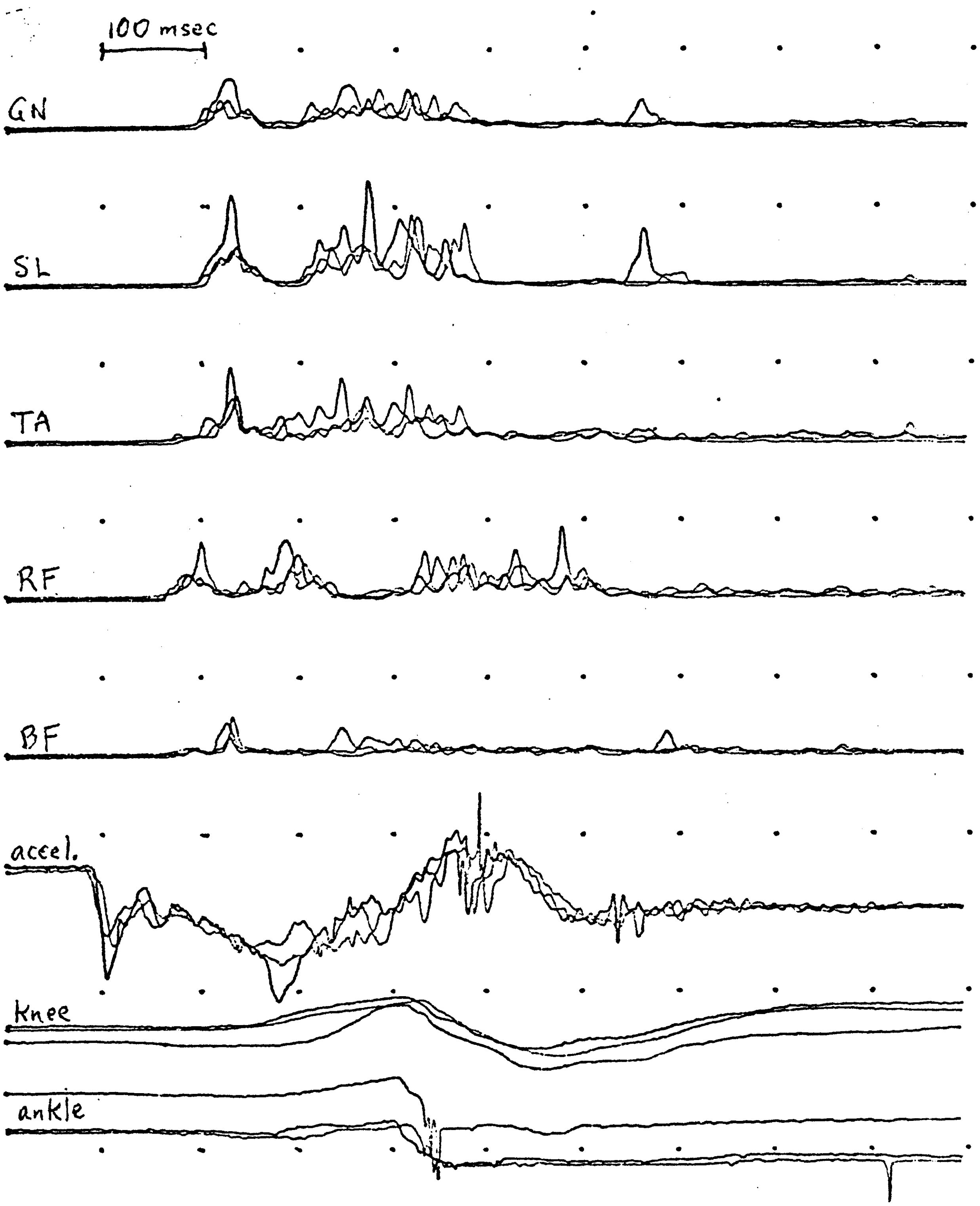


Figure 4.3.2. Subject EMA, tests 0.85G/N/B1/1-3.

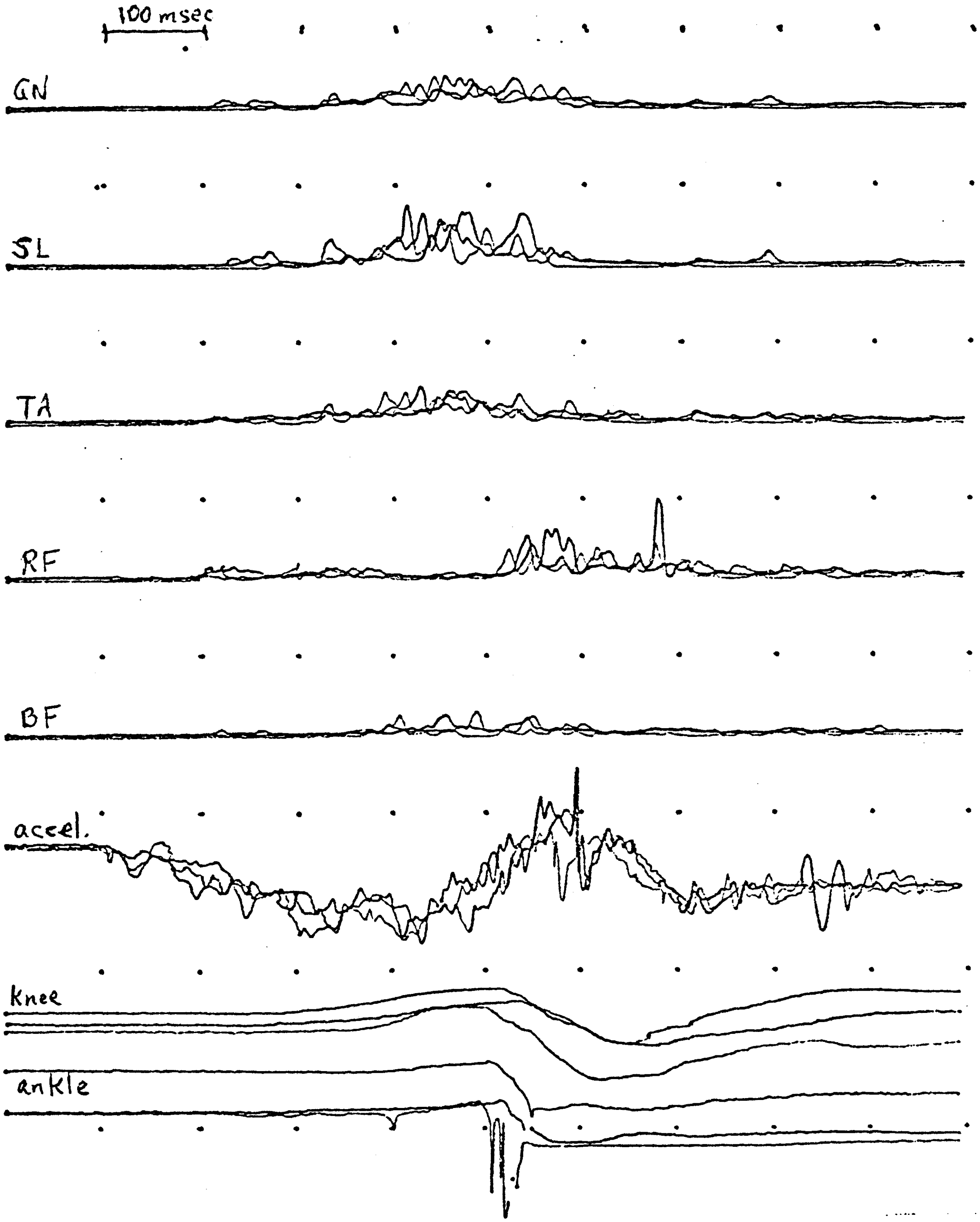
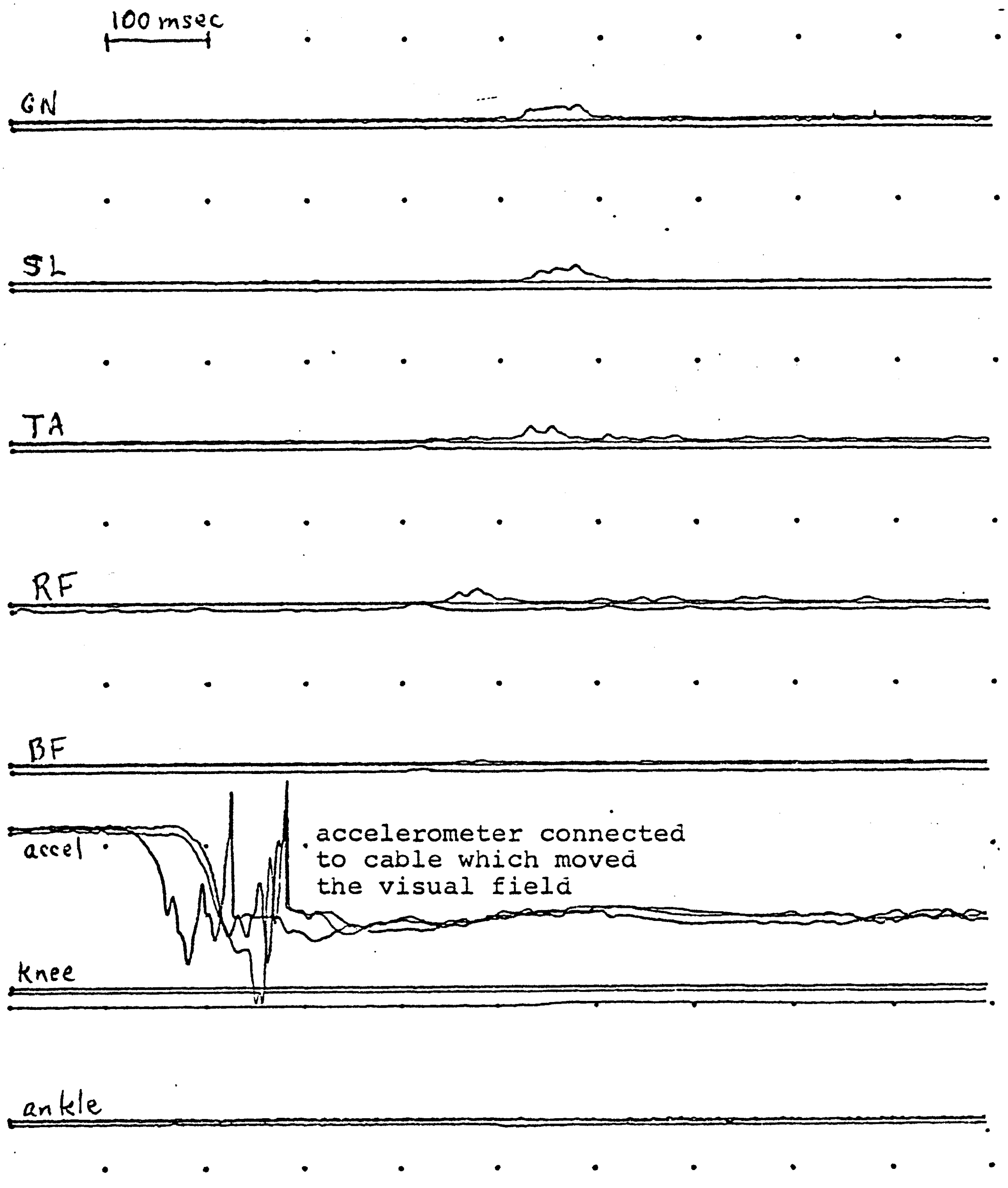


Figure 4.3.3. Subject EMA, tests RG/N/B1/1-3.



accelerometer connected to cable which moved the visual field

Figure 4.3.4. Subject EMA, tests OG/D/B1/1-3.

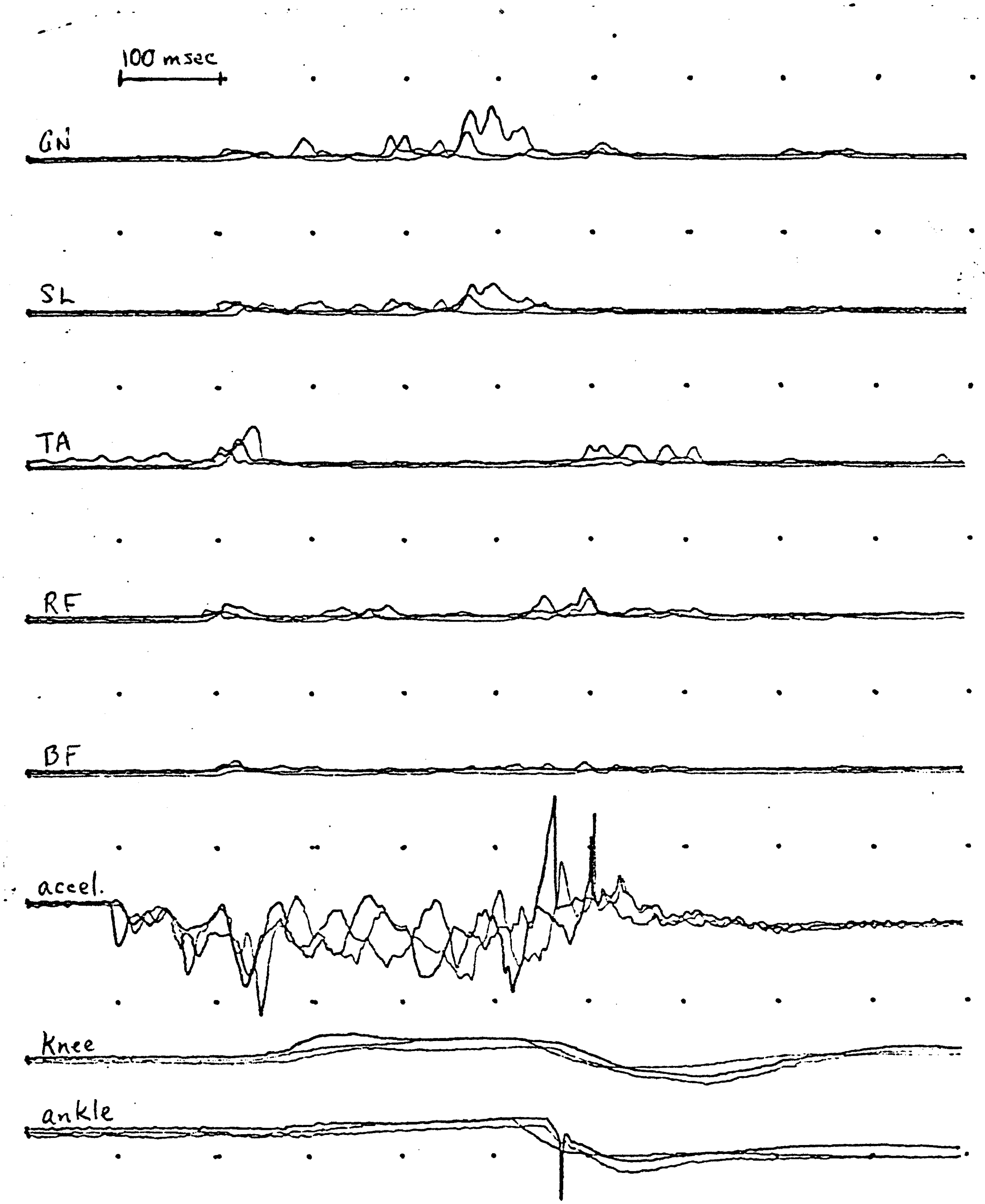


Figure 4.3.5. Subject DDL, tests 0.5G/N/B1/1-3.

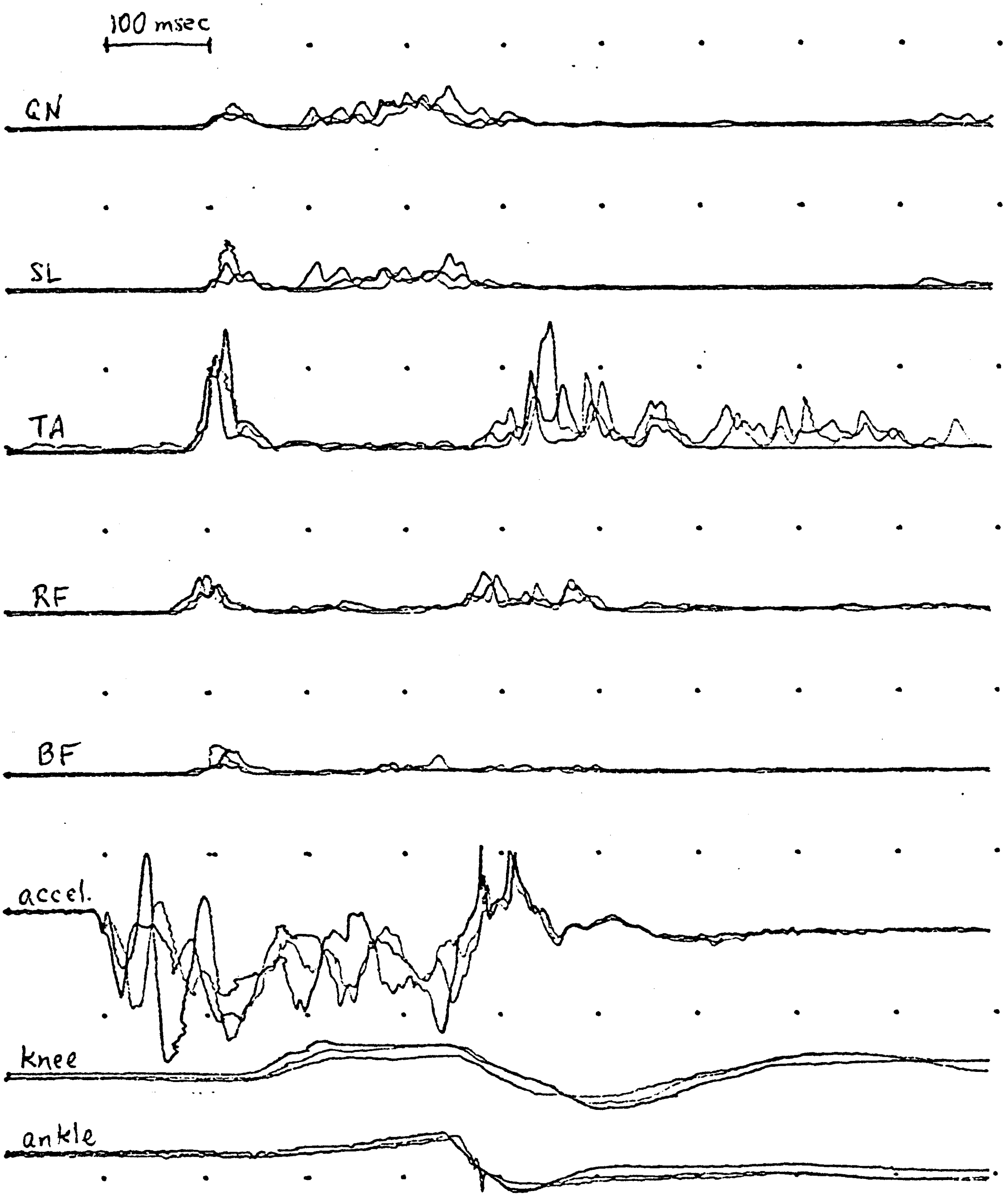


Figure 4.3.6. Subject DDL, tests 0.85G/N/B1/1-3.

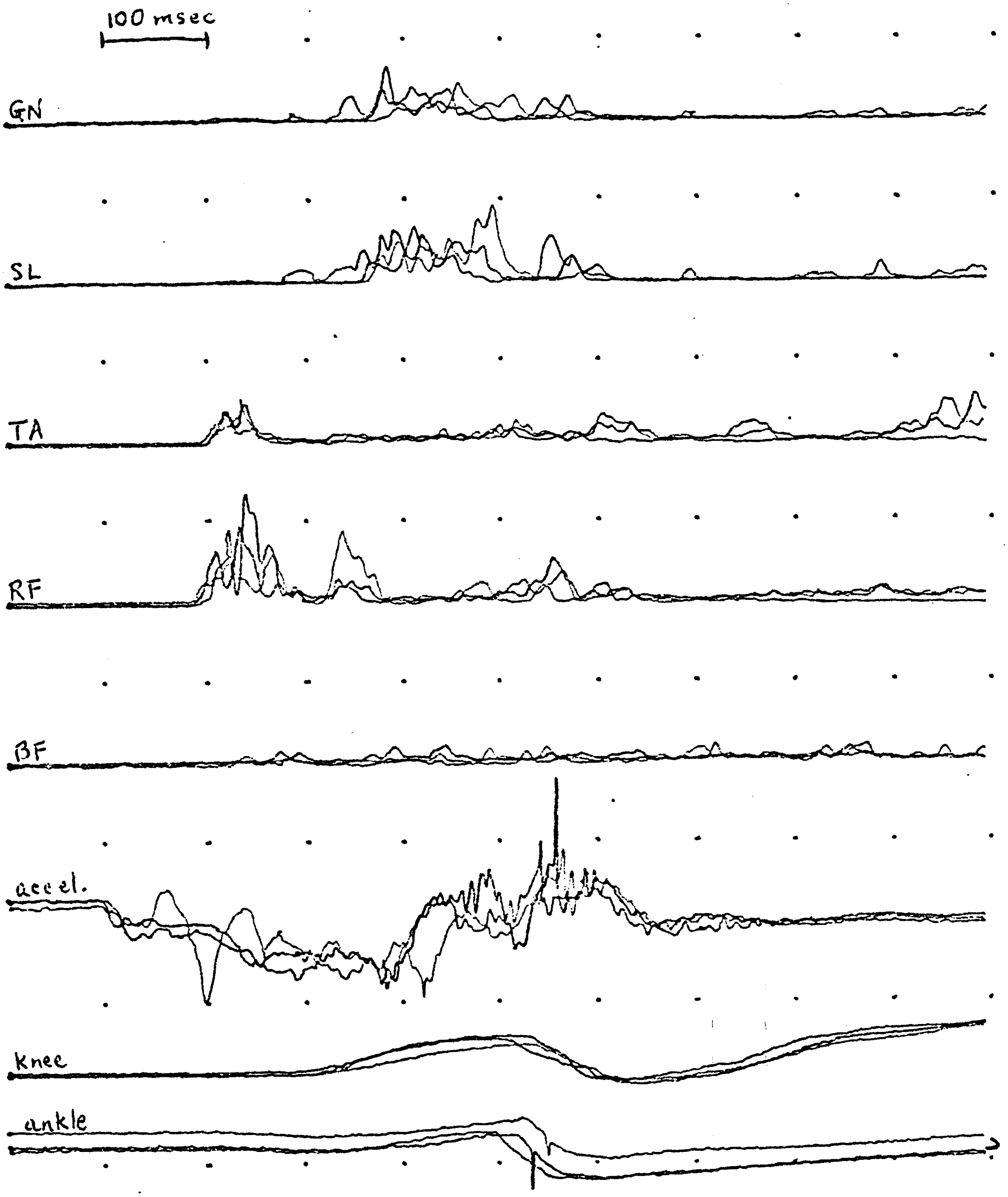


Figure 4.3.7. Subject LLA, tests 0.5G/N/B2/1-3.

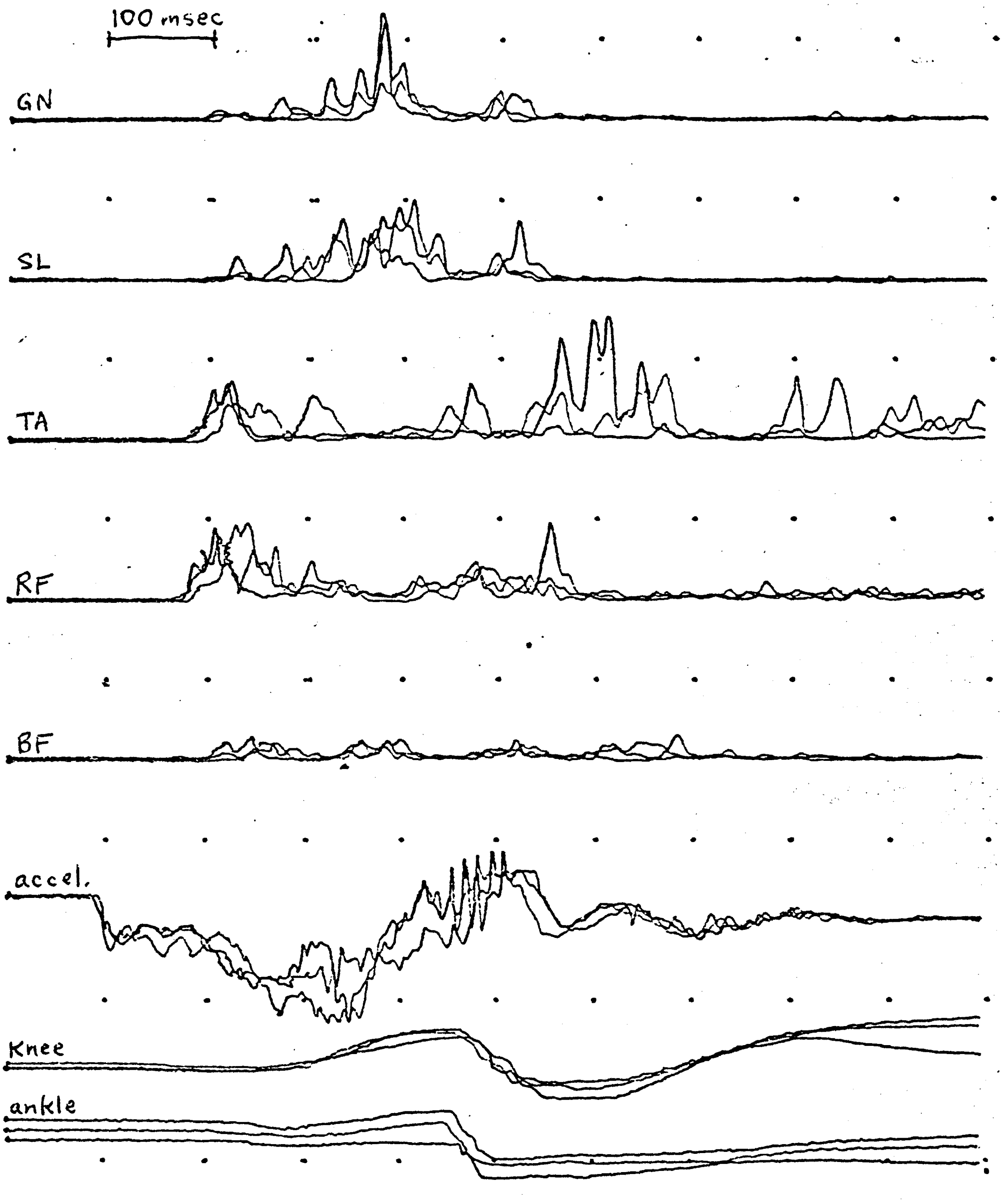


Figure 4.3.8. Subject LLA, tests 0.85G/N/B2/1-3.

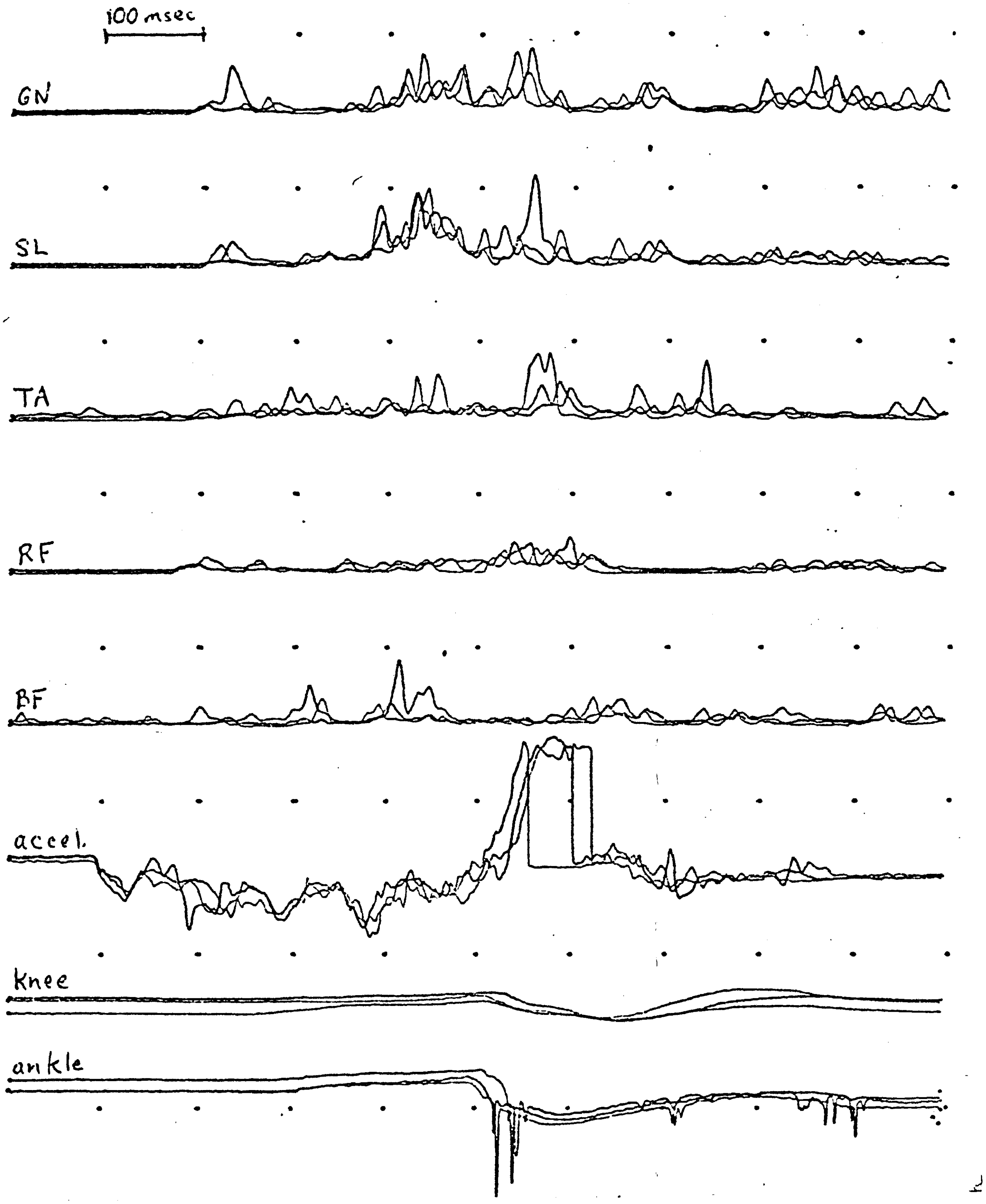


Figure 4.3.9. Subject TWA, tests 0.5G/N/B2/1-3.

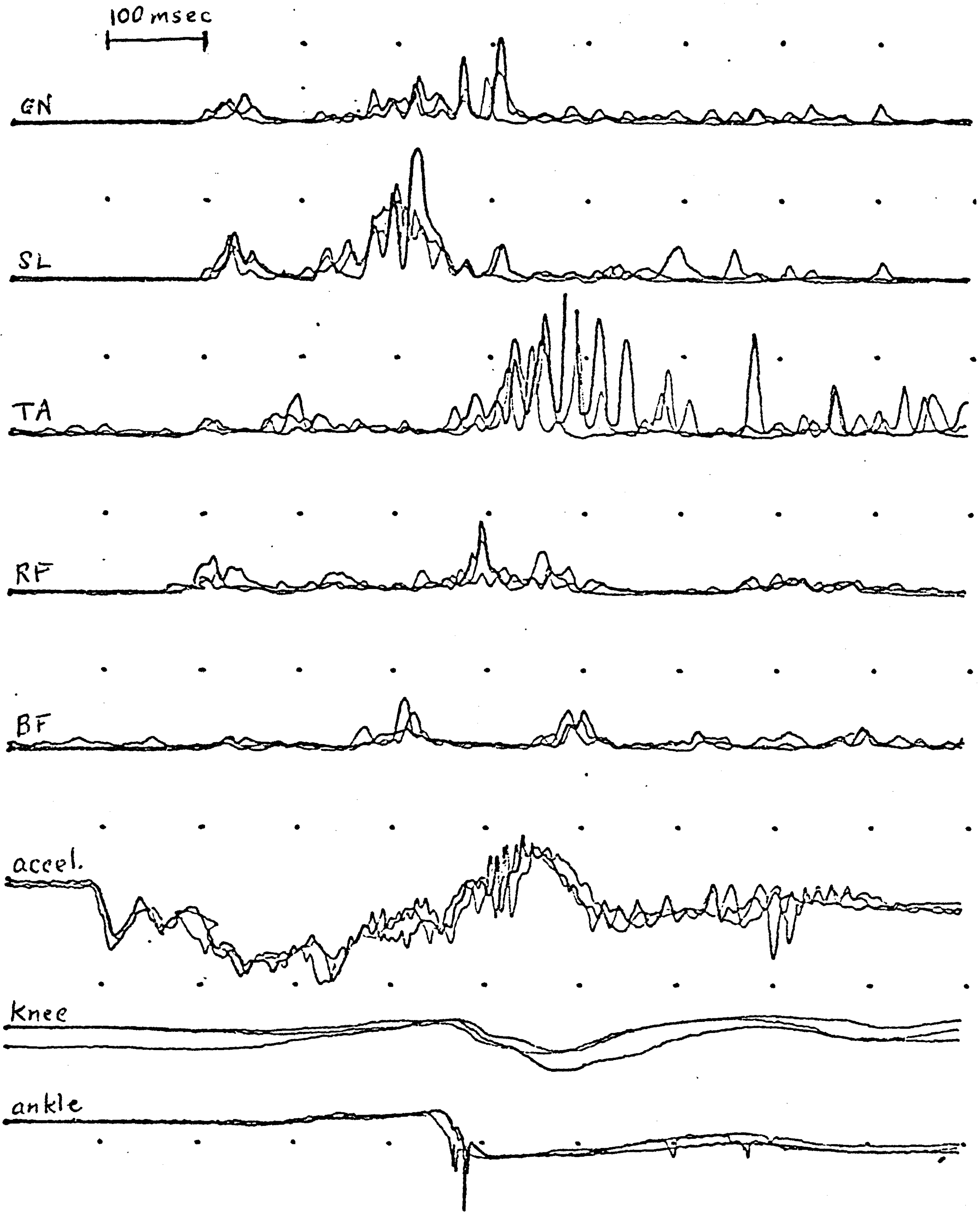


Figure 4.3.10. Subject TWA, tests 0.85G/N/B2/1-3.

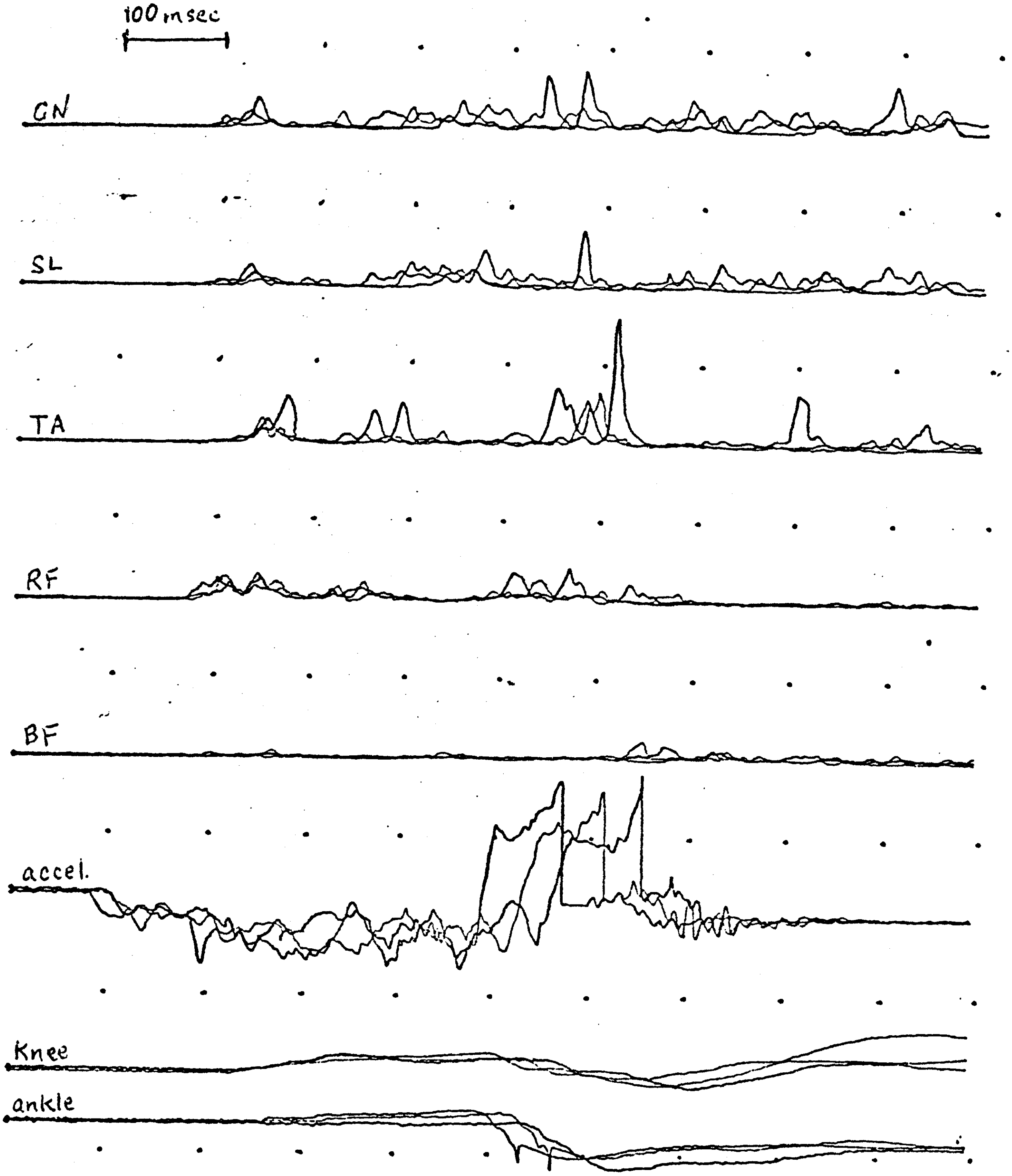


Figure 4.3.11 Subject PPE, tests 0.5G/N/B2/1-3.

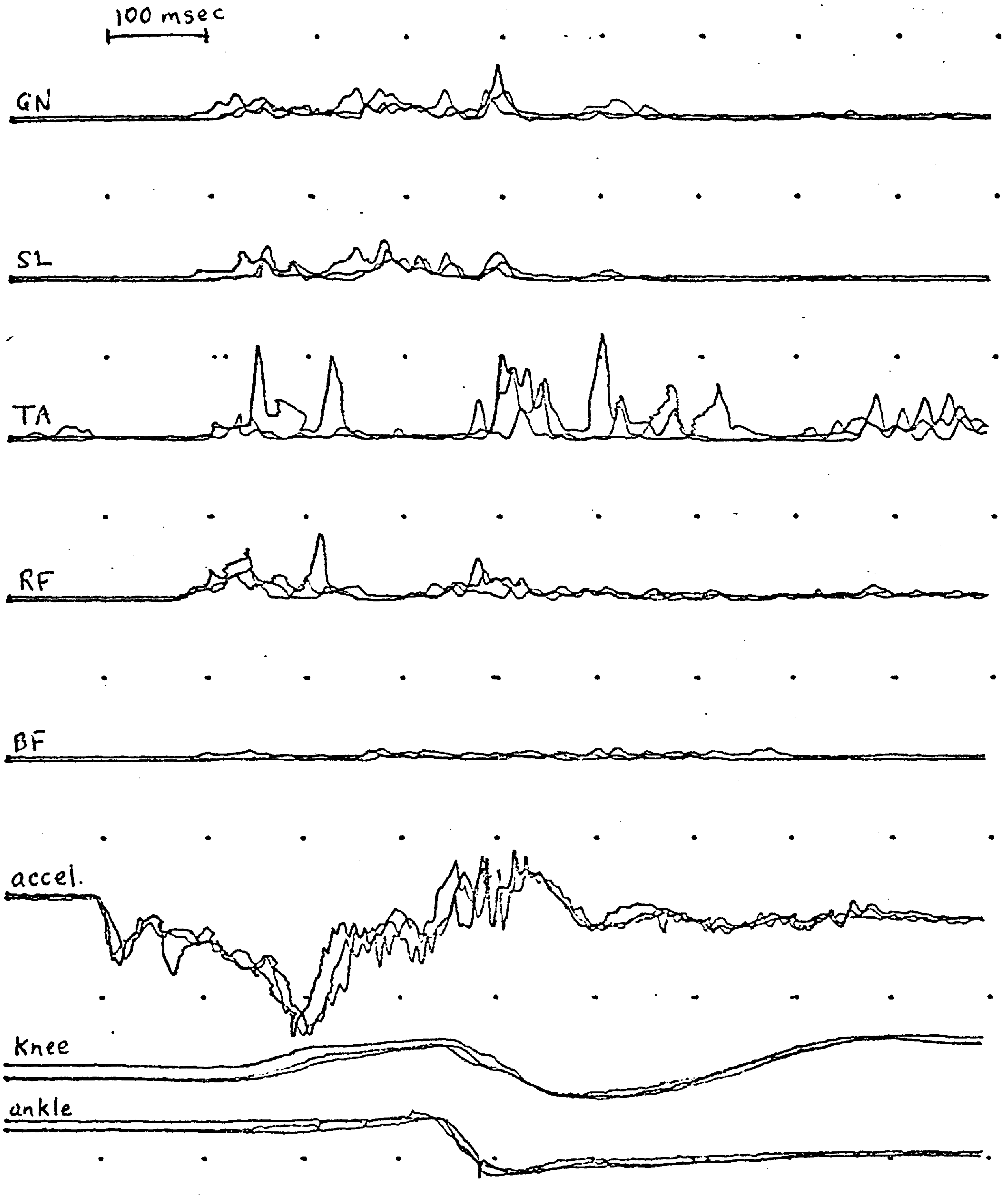


Figure 4.3.12. Subject PPE, tests 0.85G/N/B2/1-3.

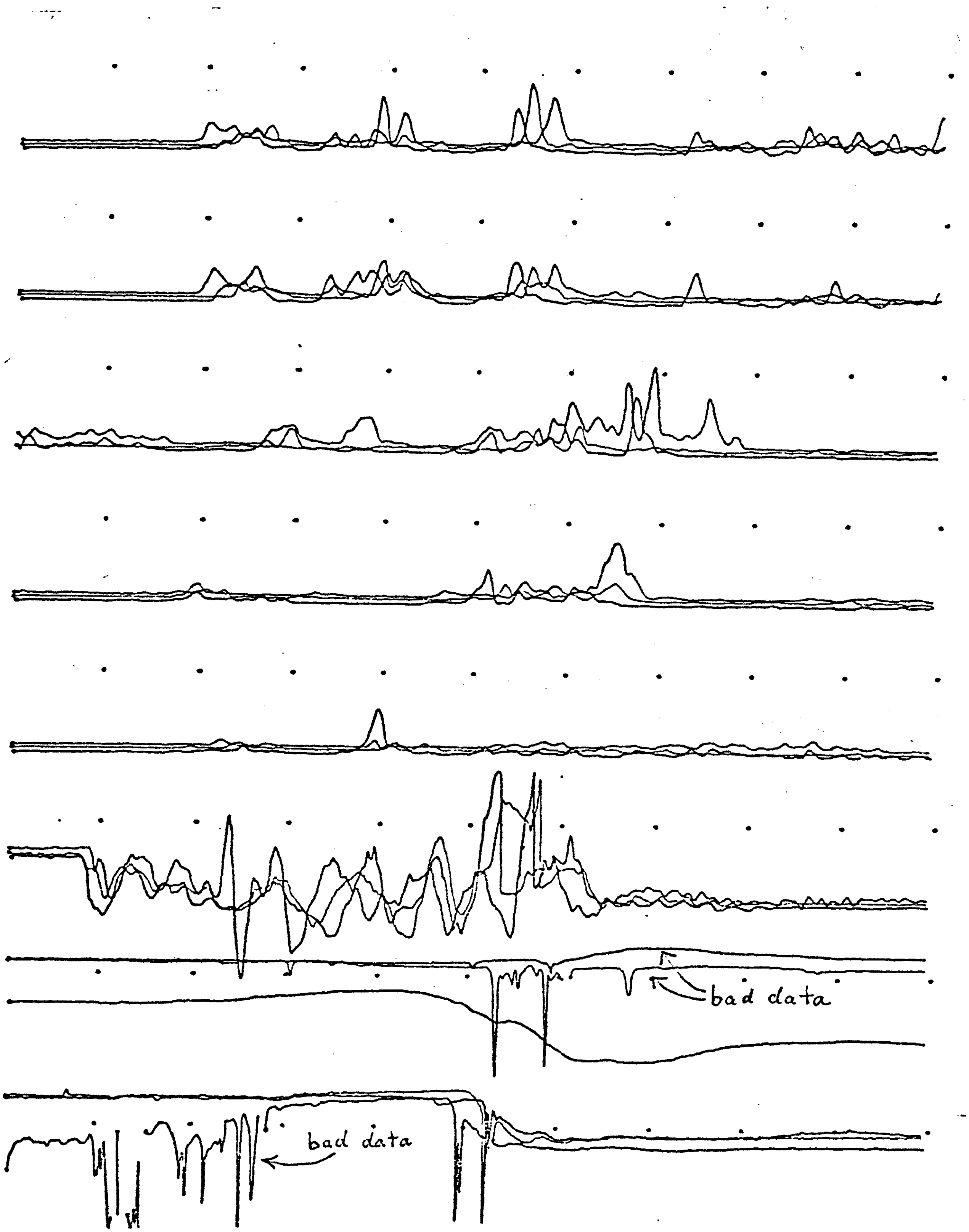


Figure 4.3.13. Subject PNE, tests 0.5G/N/B1/1-3.

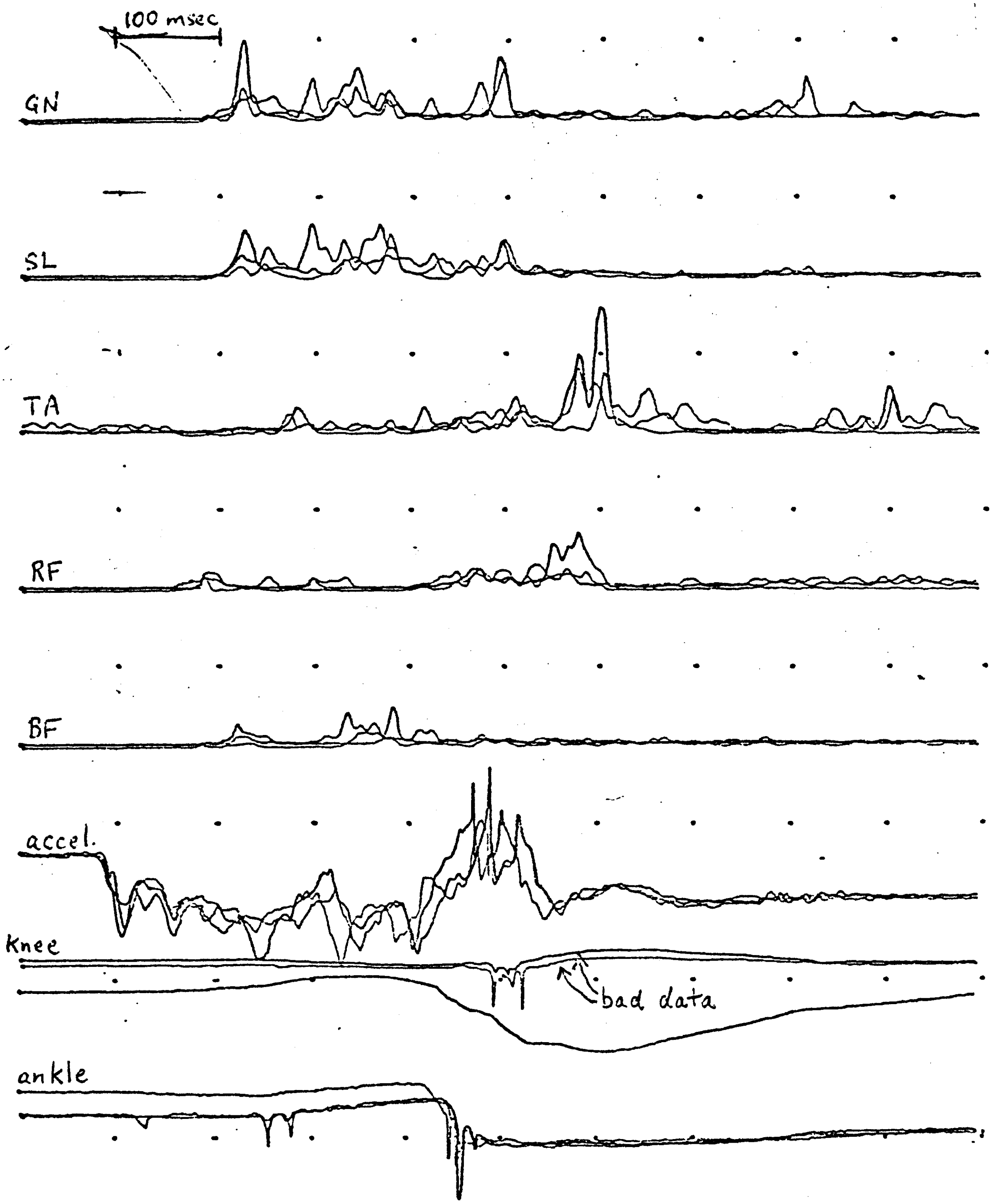


Figure 4.3.14. Subject PNE, tests 0.85G/N/B1/1-3.

specifically to electrode leads, rather than the muscles themselves. This distinction should be kept in mind because of the possibility that a given pair of electrodes may also detect EMG signals from adjacent muscles. This might result in significant crosstalk between pairs of electrodes which are adjacent, such as the GN and SL leads, specifically.

The first EMG response following release generally occurs with a latency of about 100 msec, where the latency is defined relative to the moment at which the acceleration reaches a value of 0.05g. The gastrocnemius (GN), soleus (SL), tibialis anterior (TA), and biceps femoris (BF) all respond with a latency of about 120 msec. The earliest rectus femoris (RF) reaction precedes these with a latency of only 100 msec. Within individuals, these latencies are relatively constant, but they vary between individuals by up to 10%. The RF response may precede the initial response of the other muscles by 10 to 40 msec.

The amplitude of these initial reactions, which will be referred to as the early response, is roughly a function of the acceleration transient upon release. Other factors may afffect the amplitude, and these will be discussed later. The amplitudes vary considerably for a given subject and set of test conditions, suggesting that factors such as expectation and level of apprehension may significantly affect the response. The very first drop for each subject invariably elicited large responses in all of the recorded muscles. The second drop and all subsequent drops rarely showed such elevated responses, indicating that substantial habituation had occurred immediately following the first drop.

Many of the soleus EMG records (analog-processed) manifested a double-peaked early response, consistent with the findings of Lacour et al. (1978) and Vidal et al. (1979) in the baboon. The double peaked structure was highly variable, though, and could not be seen in all of the recordings. The presence or absence of such a double-peaked structure was independent of test condition; during repetition of a test condition for a given subject, both types of structure could often be seen. The 10-msec rise time of the averaging filter should be fast enough to allow resolution of EMG bursts separated by 25 to 35 msec, which is the separation of the two components as reported by Vidal.

The period preceding the landing but following the early response generally consists of a variable length quiescent period followed by another reaction. This latter reaction has characteristic features and timing for each of the five muscles and depends upon the acceleration and the actual contact time. It will be referred to as the late reaction. Qualitatively, the reaction to the 0.85G falls is similar to the reaction to slower falls, except that the sequence of events is compressed in time and the amplitudes are generally higher. Quantitative differences will be discussed in the statistical analysis section. The quiescent periods in the GN and SL tend to be the longest, with a late response consisting of a large burst of activity just preceding contact. The GN and SL responses are highly corellated during the entire drop; this is reasonable, considering that both muscles act as plantar flexors of the foot. (However, some of the corellation may be due to electrical cross-coupling because of the anatomical proximity of the two muscles.) BF responses tend to coincide with the GN and SL timing, but the details of the response are more variable. Immediately following the early response in the TA and RF, another EMG burst may occur following a very short quiescent period, and preceding the late response of the GN and SL. Thus, during the late response period, GN, SL, and BF are usually coactivated, with RF reactions suppressed; RF activity tends to be maximal during quiescent periods of GN, SL, and BF. This agonist-antagonist pattern probably assures adequate knee flexion. Depending upon the subject, TA may be coactivated with either GN and SL or with RF, but tends to be relatively consistent within the reactions of a given subject.

Interpretation of the functional significance of the RF and BF reactions is difficult because of the many other muscles acting at the hip joint. The knee angle data actually indicates gradual extension of the knee prior to contact, although the knee never reaches full extension during the fall. (This may be a result of the knee angle limiter required as a safety device; perhaps the normal degree of knee flexion during a fall is less than that caused by the device.) Ankle angle data indicates gradual plantarflexion during the fall, as expected. While the SL and GN activity is consistent with the plantarflexion indicated by the ankle angle, the gastrocnemius muscle also acts to flex the knee.

The fact that the knee actually begins to extend suggests that action of the quadriceps is responsible. Because RF activity in the early response preceeds all other recorded reactions, it is possible that hip flexion (which is also an action of the rectus femoris) is assured by the CNS prior to the reactions of the lower leg. Significant hip flexion was observed to occur during falls, but without quantitative information it is not possible to make conclusions about the interaction of hip flexion with leg reactions. This is an interesting issue, though; increased hip flexion might result in a diminished need for knee flexion, especially if active ankle plantarflexion is adequate to cushion the landing. The fact that RF activity precedes all other recorded activity during the early response suggests that the CNS may adjust the proximal musculature prior to sending commands to the more distal muscles.

Immediately after contact, RF becomes active, presumably to counteract the passive flexion of the knee on contact due to the weight of the body. The GN and SL continue to be active for a short time to counteract the passive dorsiflexion of the ankle on contact. The actions of the RF, GN, and SL would all act to bring the person into an upright position. TA activity is extremely variable following contact. An extended TA response after contact often occurs when the person begins to lean backwards on contact; both a large RF and TA response would be expected in this case in order to dorsiflex the ankle, extend the knee and bring the person forward into an upright position from the backward leaning position.

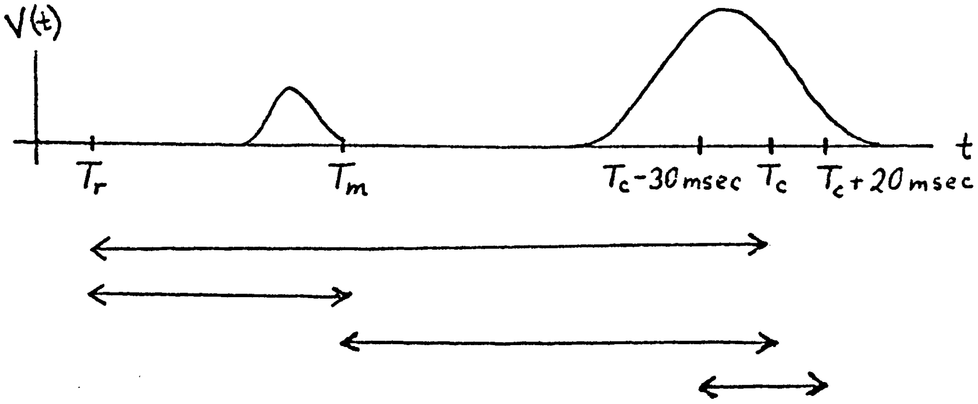
To summarize the more salient features of EMG reactions during the fall, all five muscles studied react to a drop with approximately simultaneous short latency early responses, followed by activation of the RF, coactivation of the GN, SL, and BF, and a more variable reaction of the TA.

During the trials in which the subject was not dropped, but the visual field was moved unexpectedly (OG/U and OG/D), few EMG reactions of any significance were detected even during the first occurrence. In the few trials in which certain subjects showed small twitch reactions, the latency of the twitch was about 300 msec and generally occurred in all five of the recorded muscles. This pattern is characteristic of a generalized startle reaction, although startle reactions typically have shorter latencies. See figure 4.3.4 on page 88. For subject EMA, the first trial of this test condition elicited a substantial response. The second repetition shows no response, and the third repetition shows only a slight twitch in RF. Most subjects never reacted at all to these stimuli; the EMG recordings were flat throughout the test. Because of the lack of a significant response, the OG/U and OG/D cases are not shown in the graphs of the data. However, the simple result of these tests should be remembered when interpreting the effects of visual field motion in reactions during falls; it is clear that this visual stimulus alone is not sufficient to elicit the characteristic EMG patterns seen during falls. However, this does not preclude the possibility of subthreshold phenomena at the segmental level.

4.5 Statistical analysis of the data

Because of the natural temporal separation of the EMG responses into an early component and a late response, the EMG was separated into two time segments for analysis in order to determine possible trends for each response individually. The moment of release was defined to be the instant at which the acceleration reached a value of 0.05g. This usually resulted in detection of release within one sample period of the release time as judged by visual inspection. For the purpose of interpreting EMG latencies, the 40-msec time constant of brake deactivation should not be overlooked. Contact time was defined to be the moment of toe contact, determined from the ankle angle measurements as the time at which the foot begins to rapidly dorsiflex. Both the moment of release and moment of contact, as well as all other measures of the data, were determined with the aid of a computer program and threshold detection schemes. The computer values were spot checked for accuracy, and all values were scanned to ensure that no gross errors occurred due to artifact detection. Values could be entered manually in the few cases where artifacts interfered with the automated detection.

Four separate integrations were performed on the EMG waveforms from each of the five muscles. The following diagram illustrates the time intervals over which these integrations were performed. A typical GN reaction is shown.



First, the filtered data was integrated from the moment of release, T_r , to the moment of contact, T_c . Next, the waveform was integrated from T_r to a time just after the early response, T_m . T_m was chosen to be equal to T_r + 175 msec, because in almost all cases in which early and late responses were clearly separated by a quiescent period, T_r + 175 msec fell in this quiescent period. The third integration was performed from T_m to T_c . These three values provide relative measures of net muscle activation during the fall, activation attributable to the early response, and activation due to the late pre-contact response, respectively. Again, the computed values were scanned and compared to plots of the original waveforms. Integrations over the specified time intervals were actually approximated by summating the sampled data over the appropriate sample periods.

In addition to separating the early response from the late response, the EMG activity occurring at the moment of contact was obtained by integrating the EMG from T_c - 30 msec to T_c + 20 msec. These integrated values should reflect the ability to adjust effective joint stiffness in preparation for contact and not reflex reactions to contact, since 20 msec is less than the shortest latency for spinal reflexes.

Before performing analysis of variance tests on the measures of integrated EMG activity, the values for each subject were normalized such that the average normalized values over all 45 drops for each subject were equal to a constant, K (arbitrarily chosen to equal 100):

$$X'_{crb} = \left(\frac{K}{\sum_{c=1}^{45} X_{crb} / 45} \right) X_{crb}$$

where X'_{crb} is the normalized value of the measure. Differences in the characteristics of the electrode sites and the relation between the electrodes, skin, subcutaneous fat and underlying muscle may be responsible for large differences in recorded EMG amplitude. Subcutaneous layers of fat, which can be a problem in female subjects, substantially reduces the recorded EMG amplitude because of the insulating properties of the fat overlying the muscle. Since these differences introduce gain factors which vary between subjects, and because the analysis of variance assumes variance homogeneity, the above normalization scheme seemed reasonable. Comparisons of EMG reactions between different treatments was the main concern, and not overall differences in activation levels between subjects.

Figures 4.4.1-20 on pages 108-127 present the normalized, integrated EMG data for each of the four periods chosen for integration. Each page displays the data for one muscle. The top graph on each page shows six bars for each drop condition; the first three bars represent the average

(cont. on p. 128)

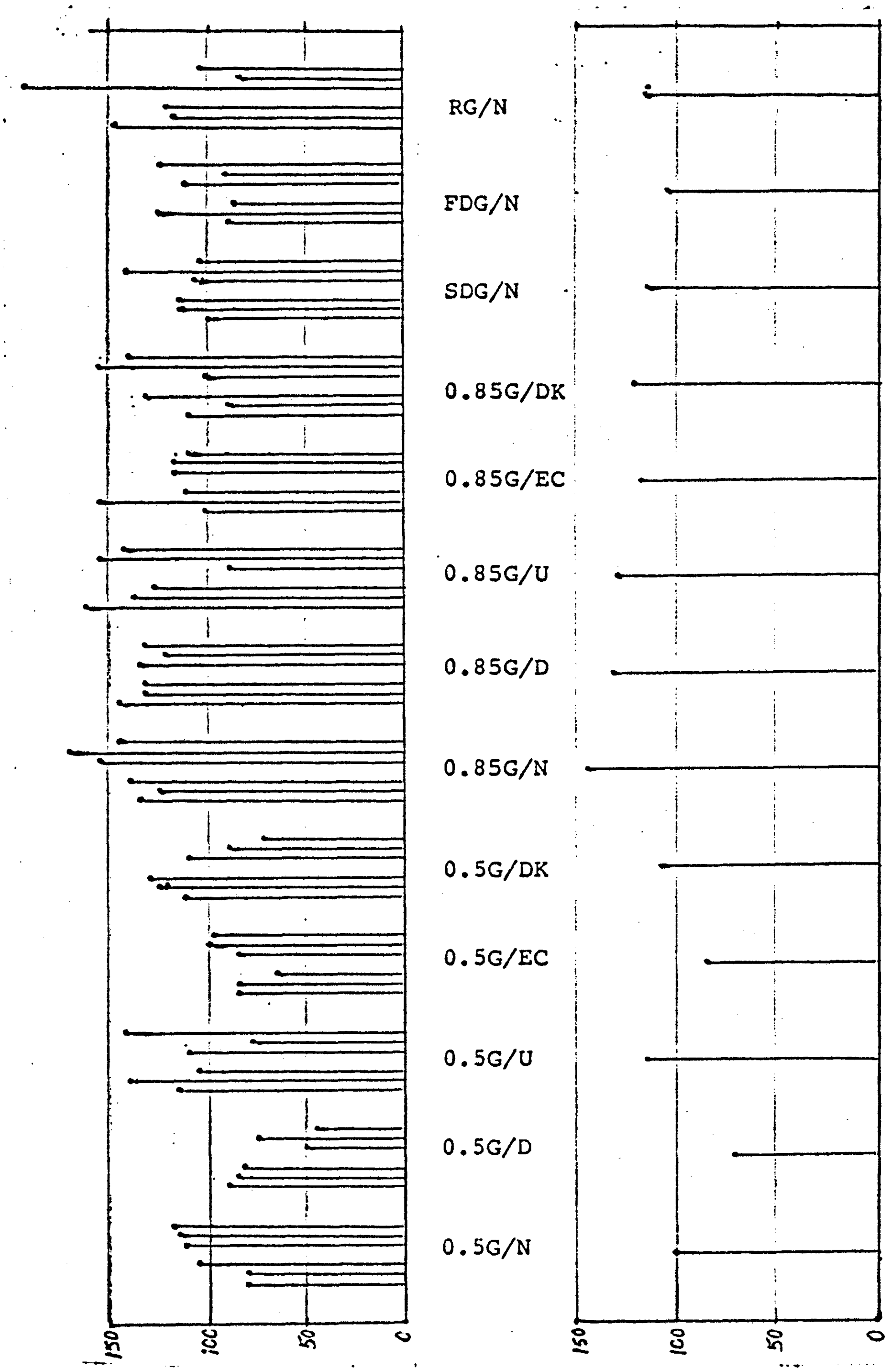


Figure 4.4.1. Gastrocnemius, integrated EMG during entire fall.

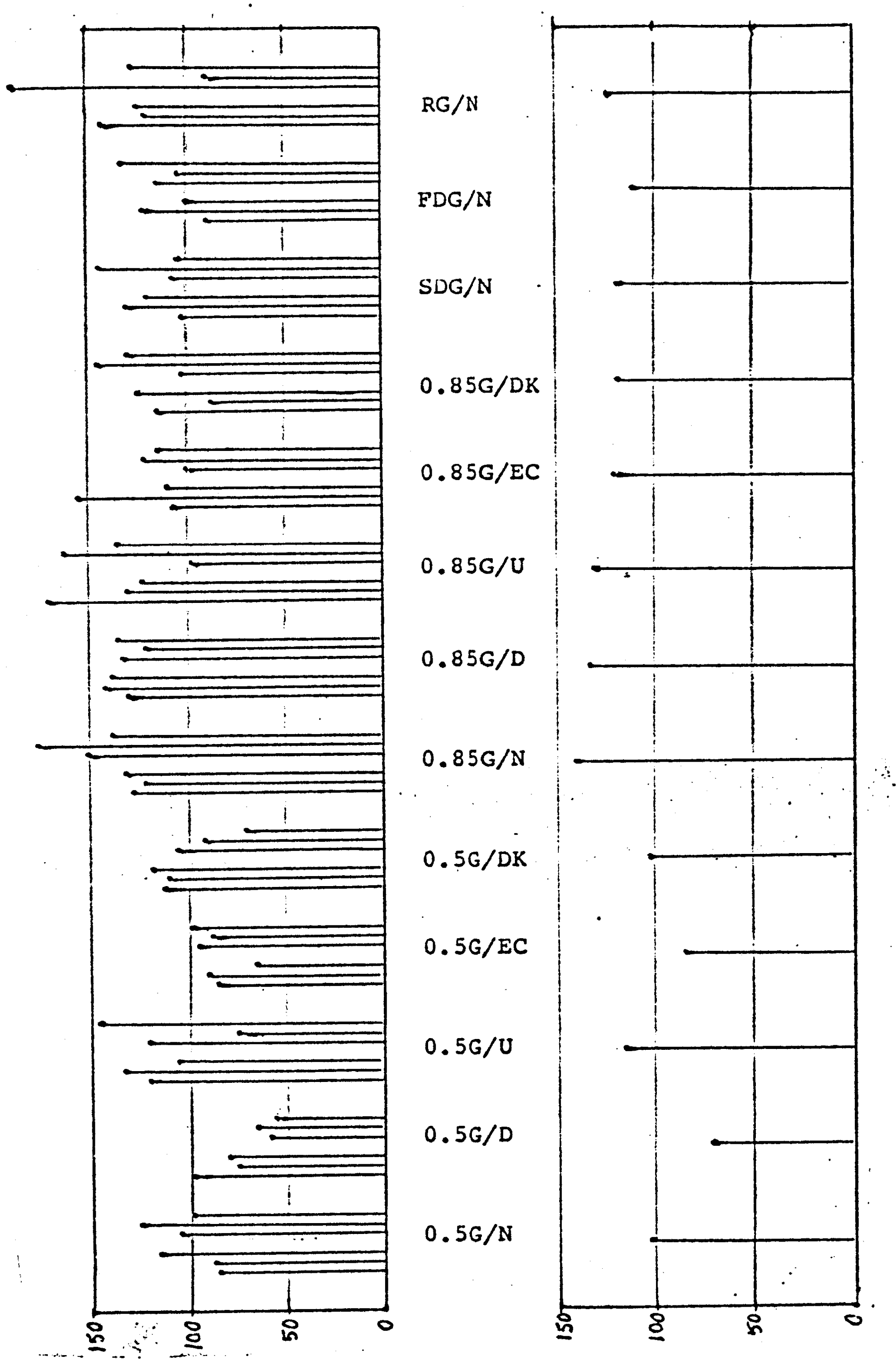


Figure 4.4.2. Soleus,
integrated EMG during entire fall.

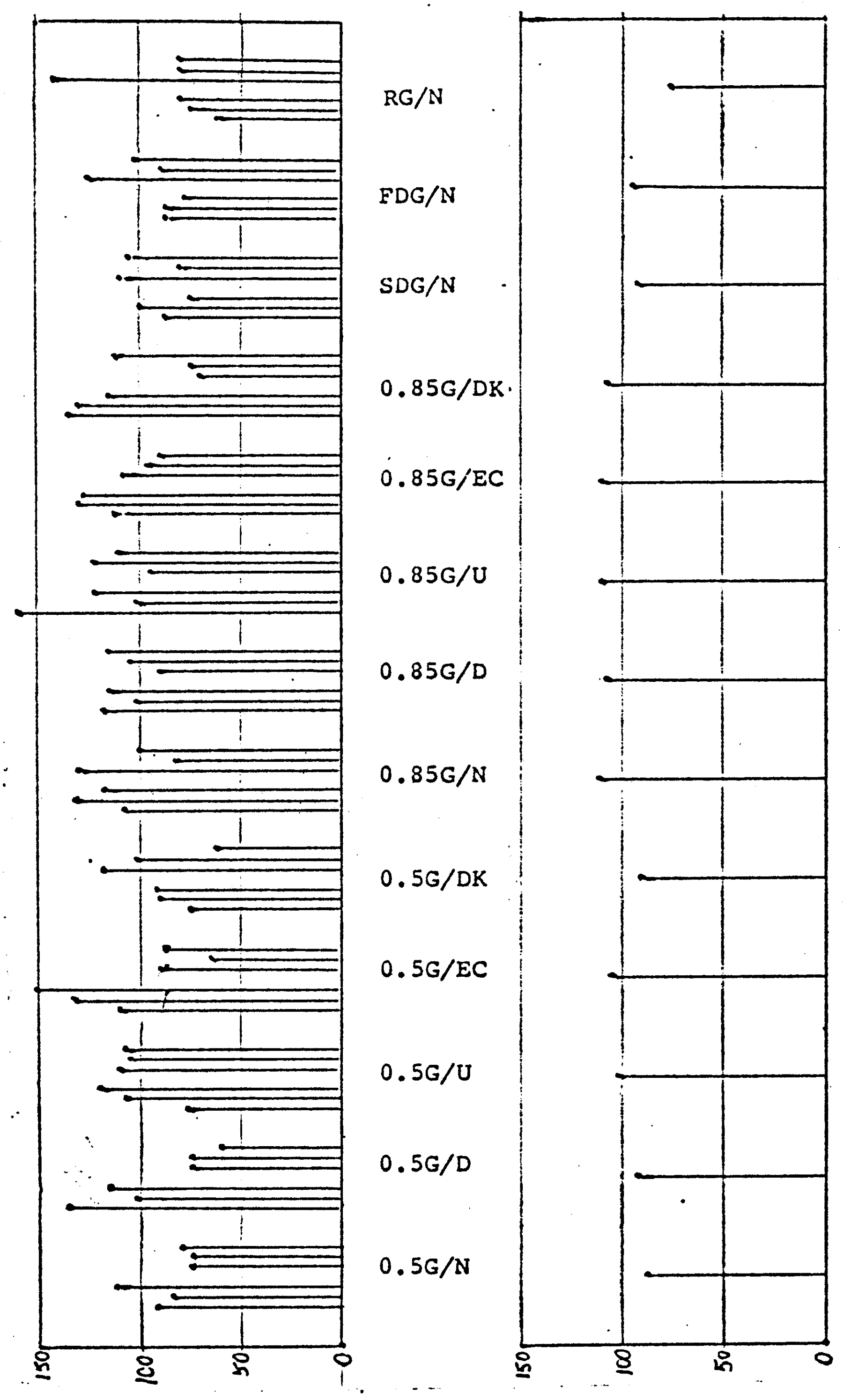


Figure 4.4.3. Tibialis anterior,
integrated EMG during entire fall.

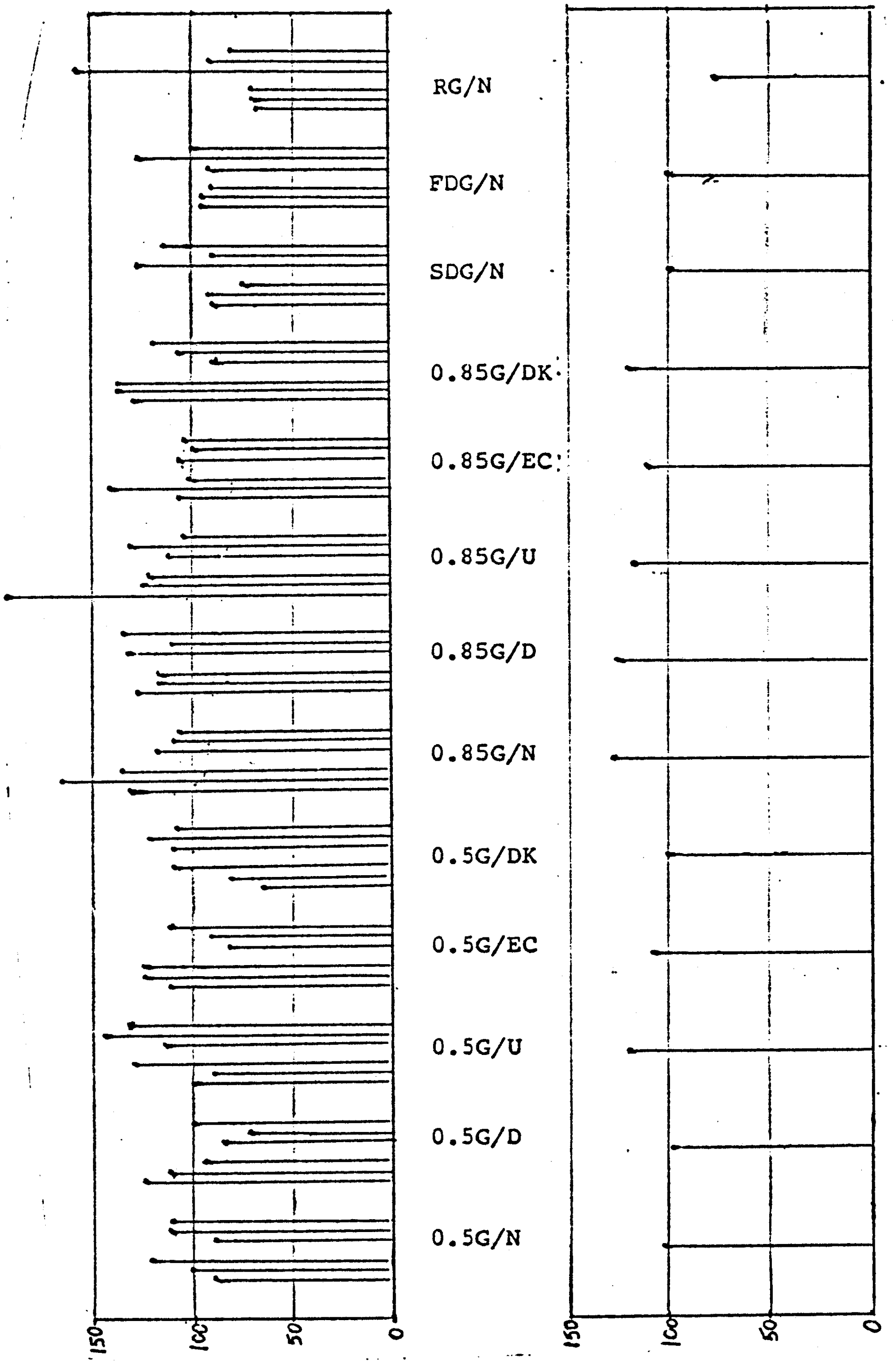


Figure 4.4.4. Rectus femoris, integrated EMG during entire fall.

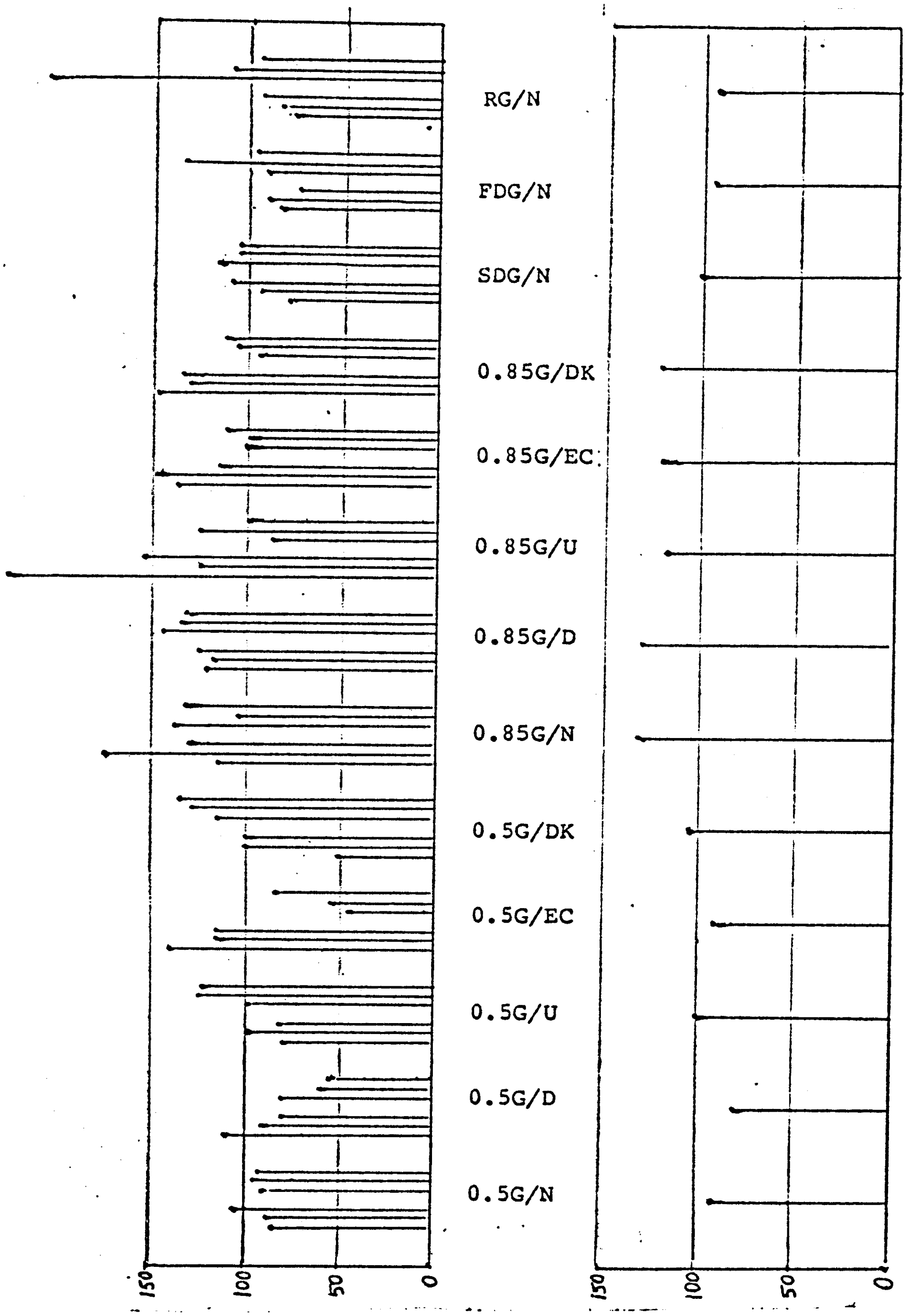


Figure 4.4.5. Biceps femoris, integrated EMG during entire fall.

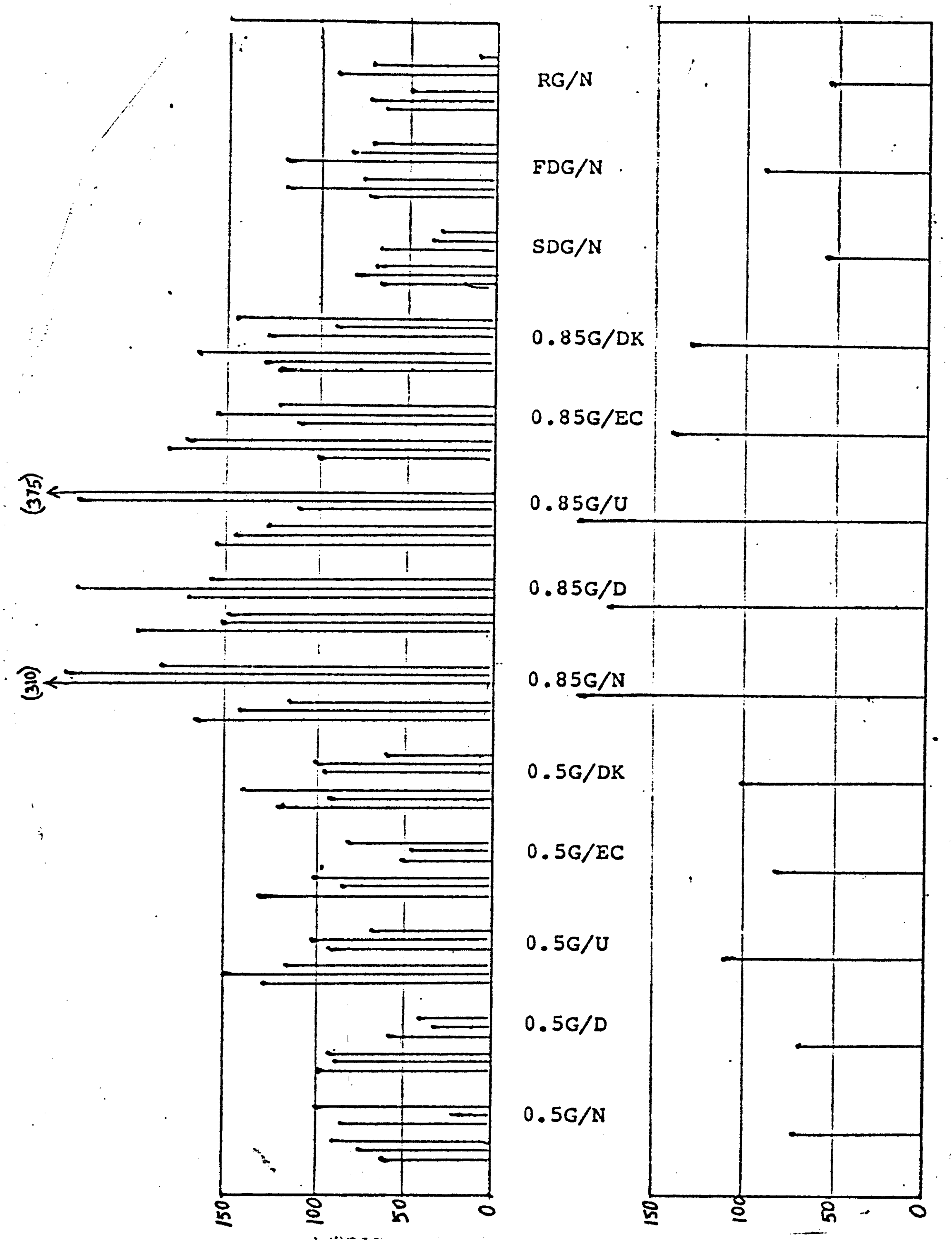


Figure 4.4.6. Gastrocnemius,
integrated EMG during early response.

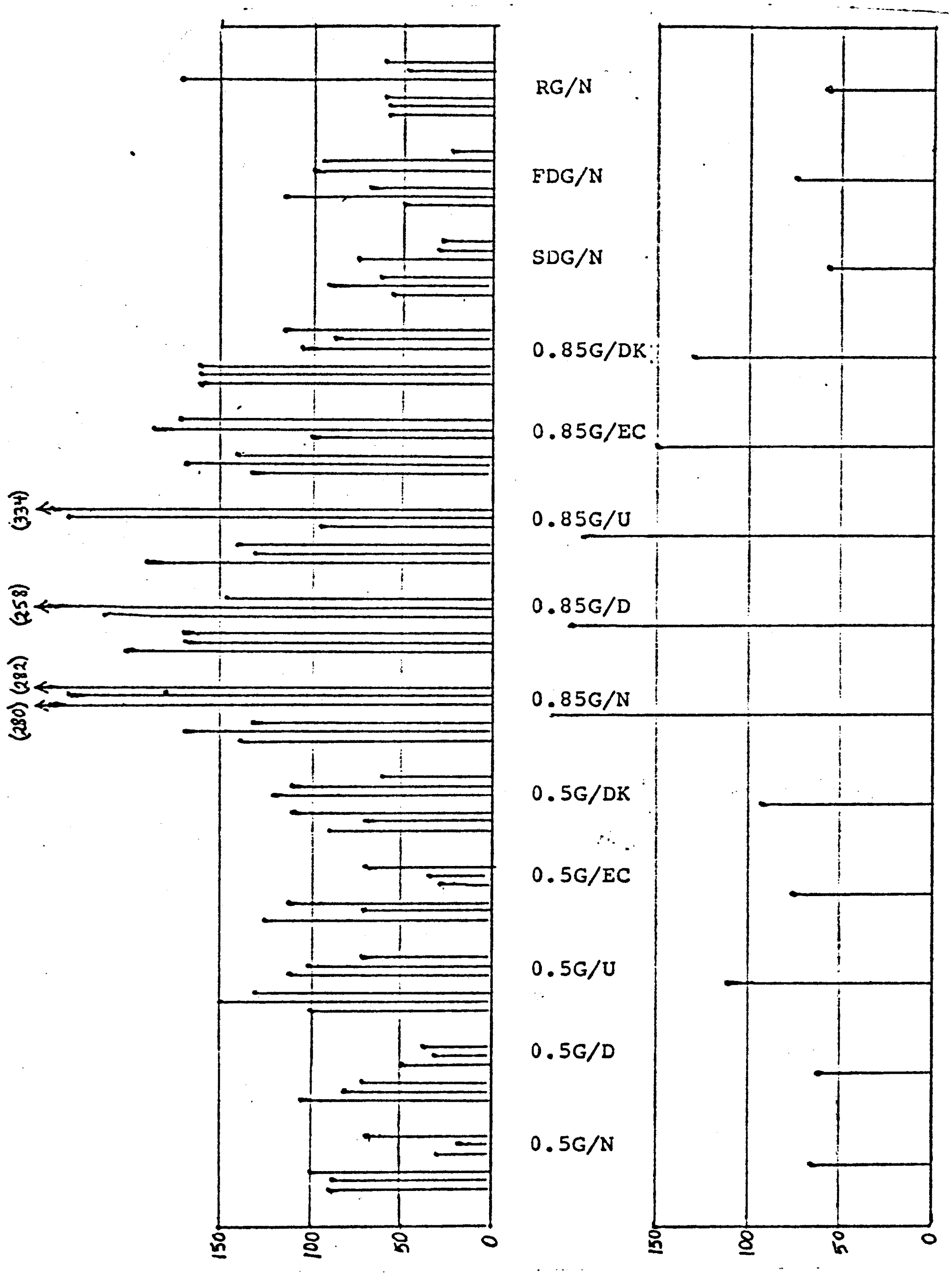


Figure 4.4.7. , Soleus, integrated EMG during early response.

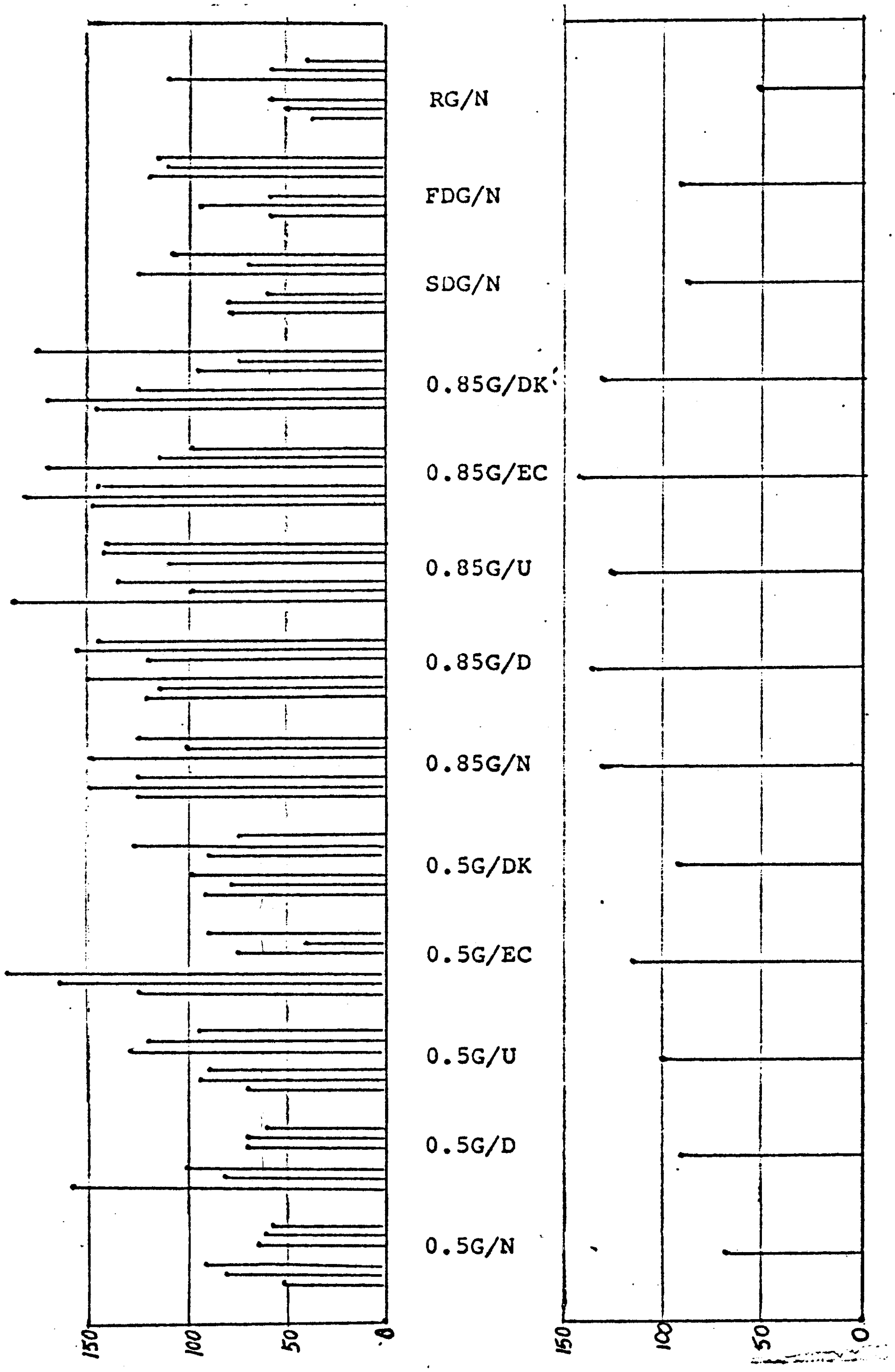


Figure 4.4.8. Tibialis anterior, integrated EMG during early response.

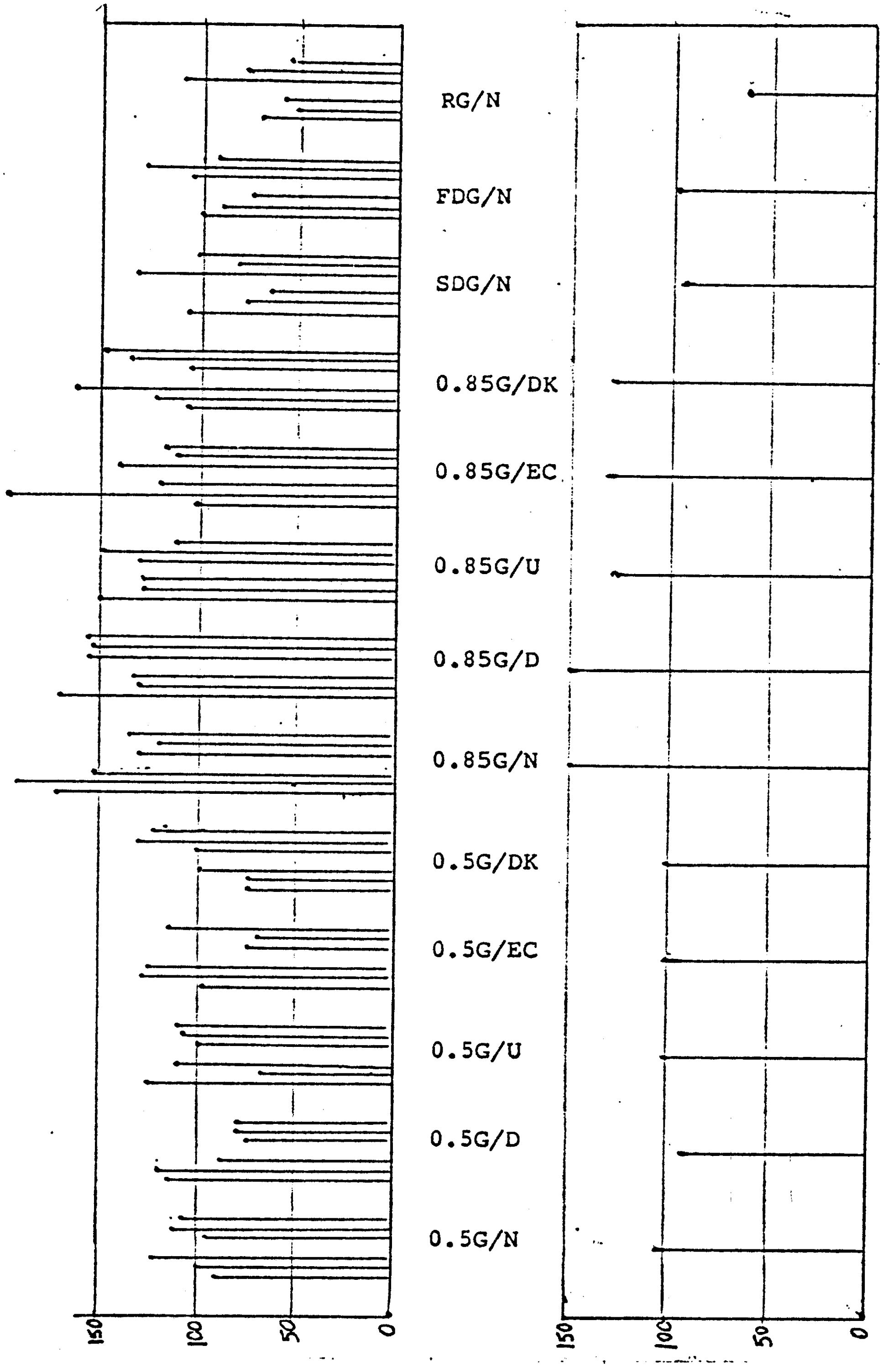


Figure 4.4.9. Rectus femoris, integrated EMG during early response.

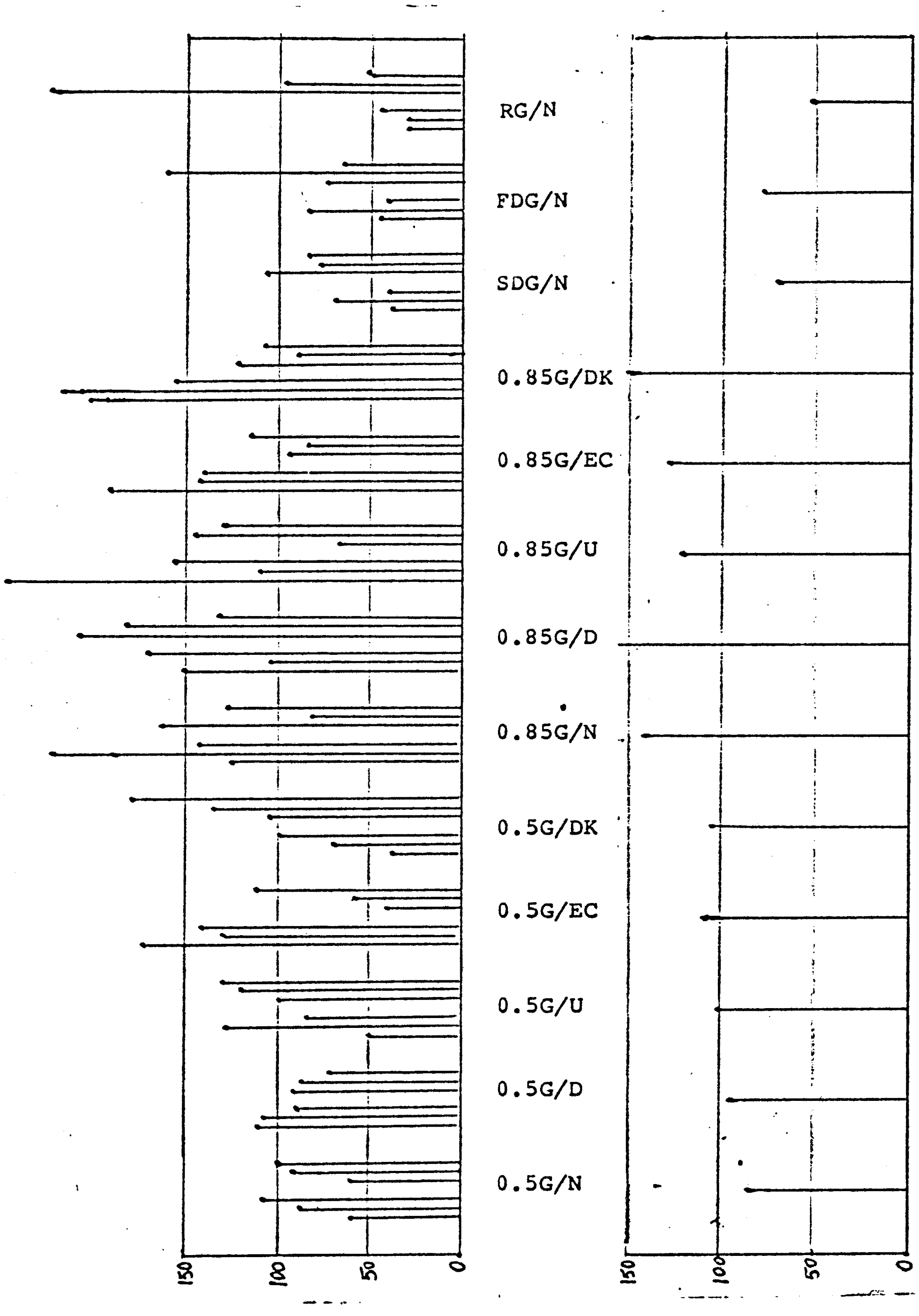


Figure 4.4.10. Biceps femoris, integrated EMG during early response.

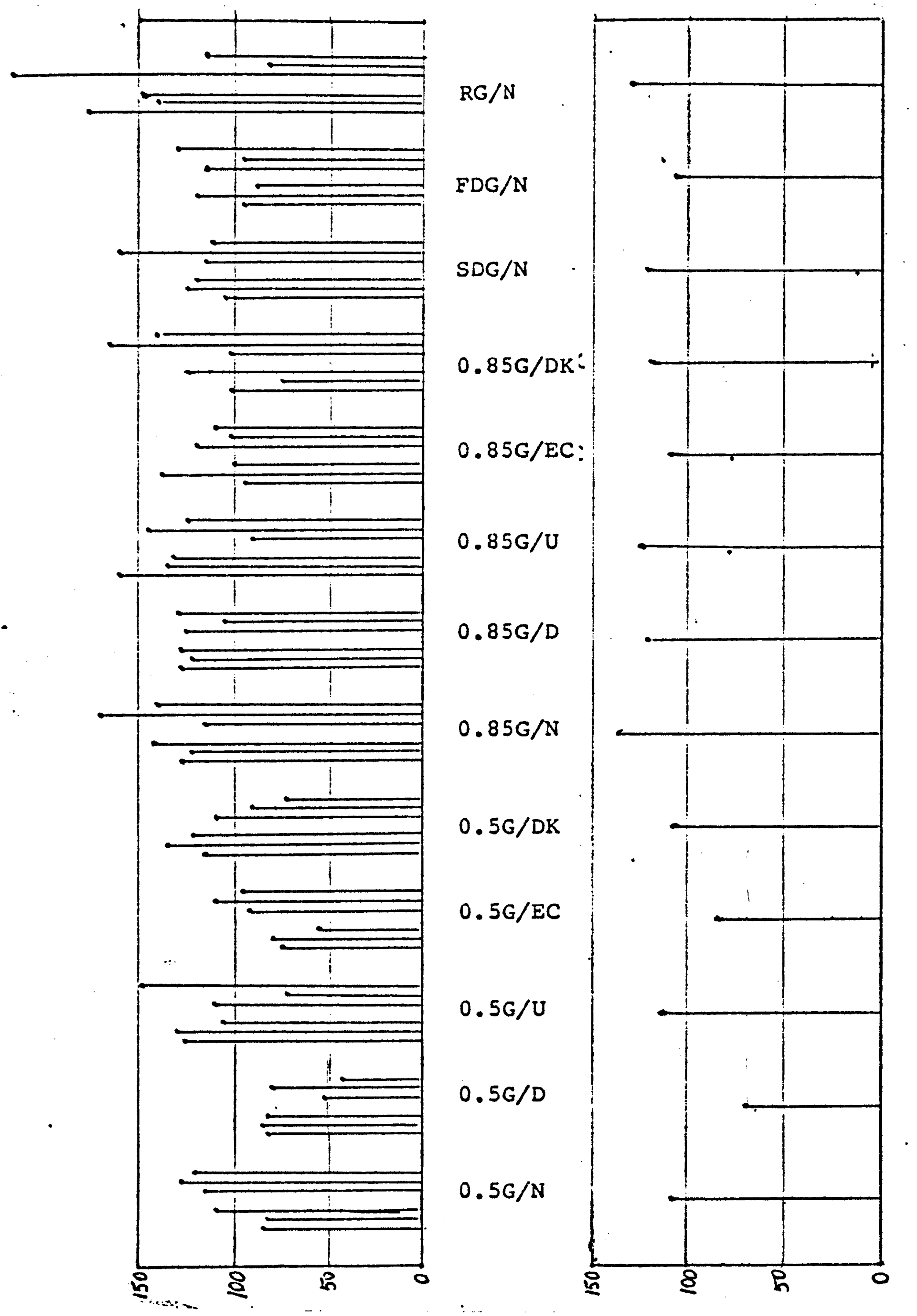


Figure 4.4.11. Gastrocnemius, integrated EMG during late response.

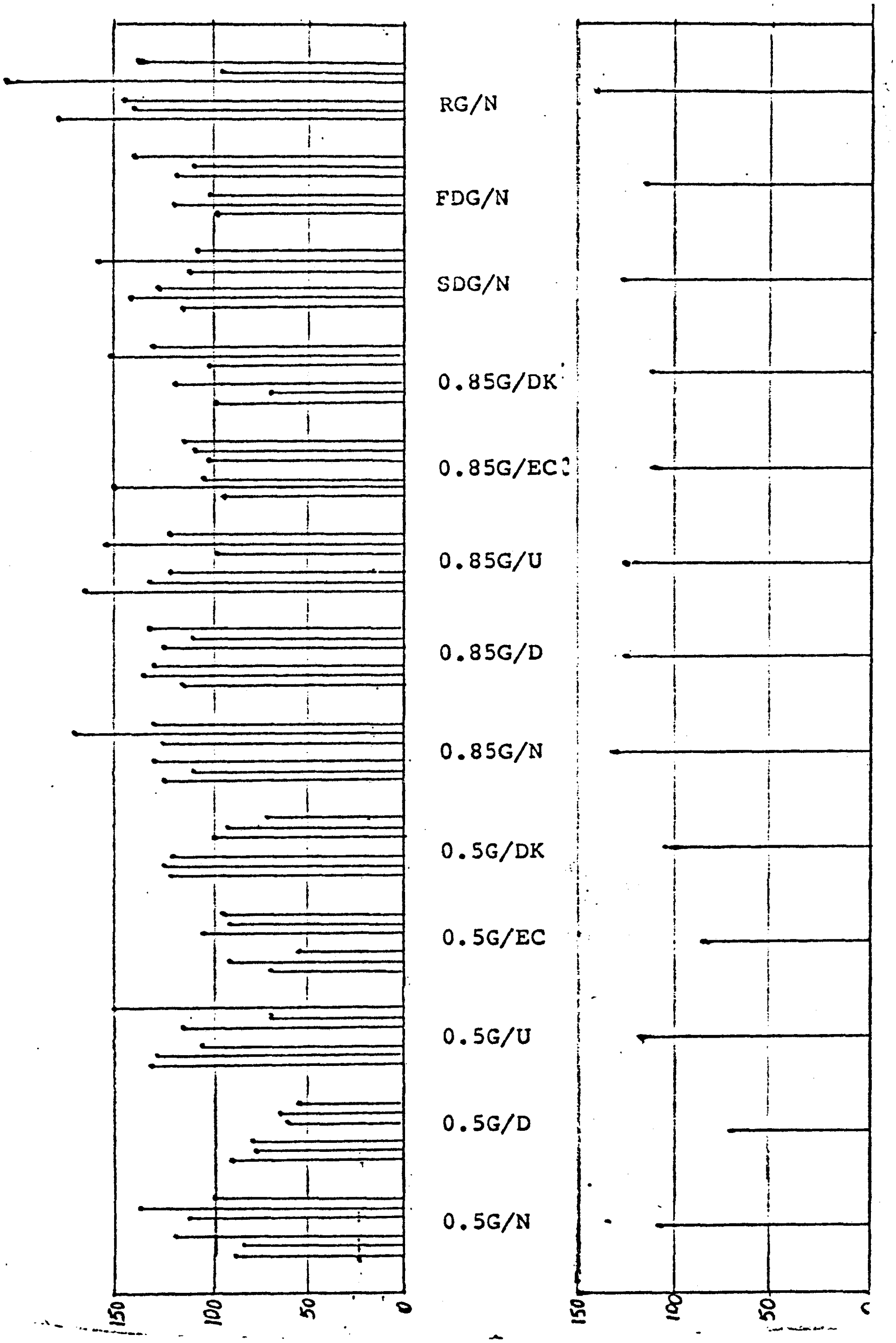


Figure 4.4.12. Soleus, integrated EMG during late response.

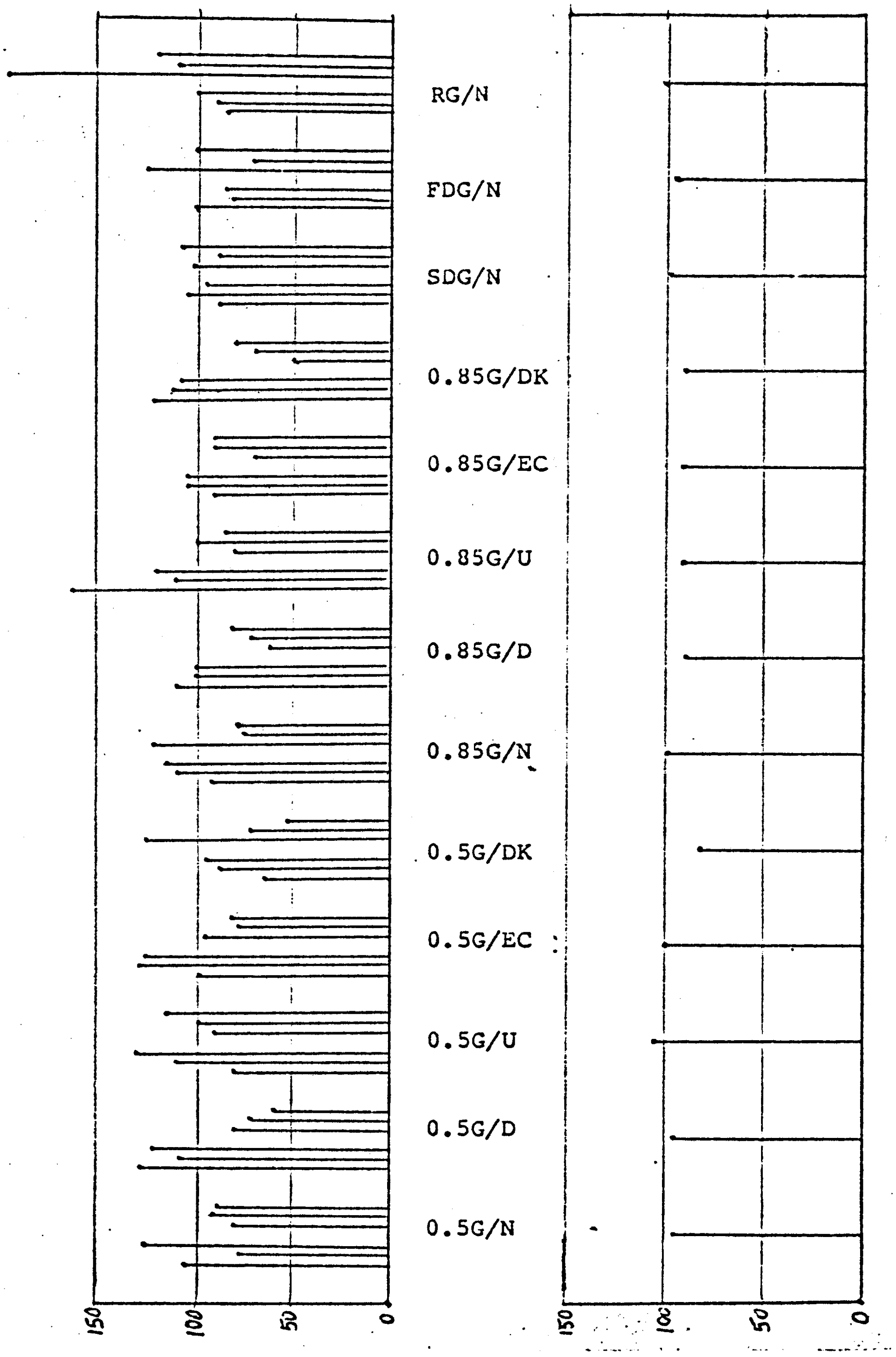


Figure 4.4.13. Tibialis anterior, integrated EMG during late response.

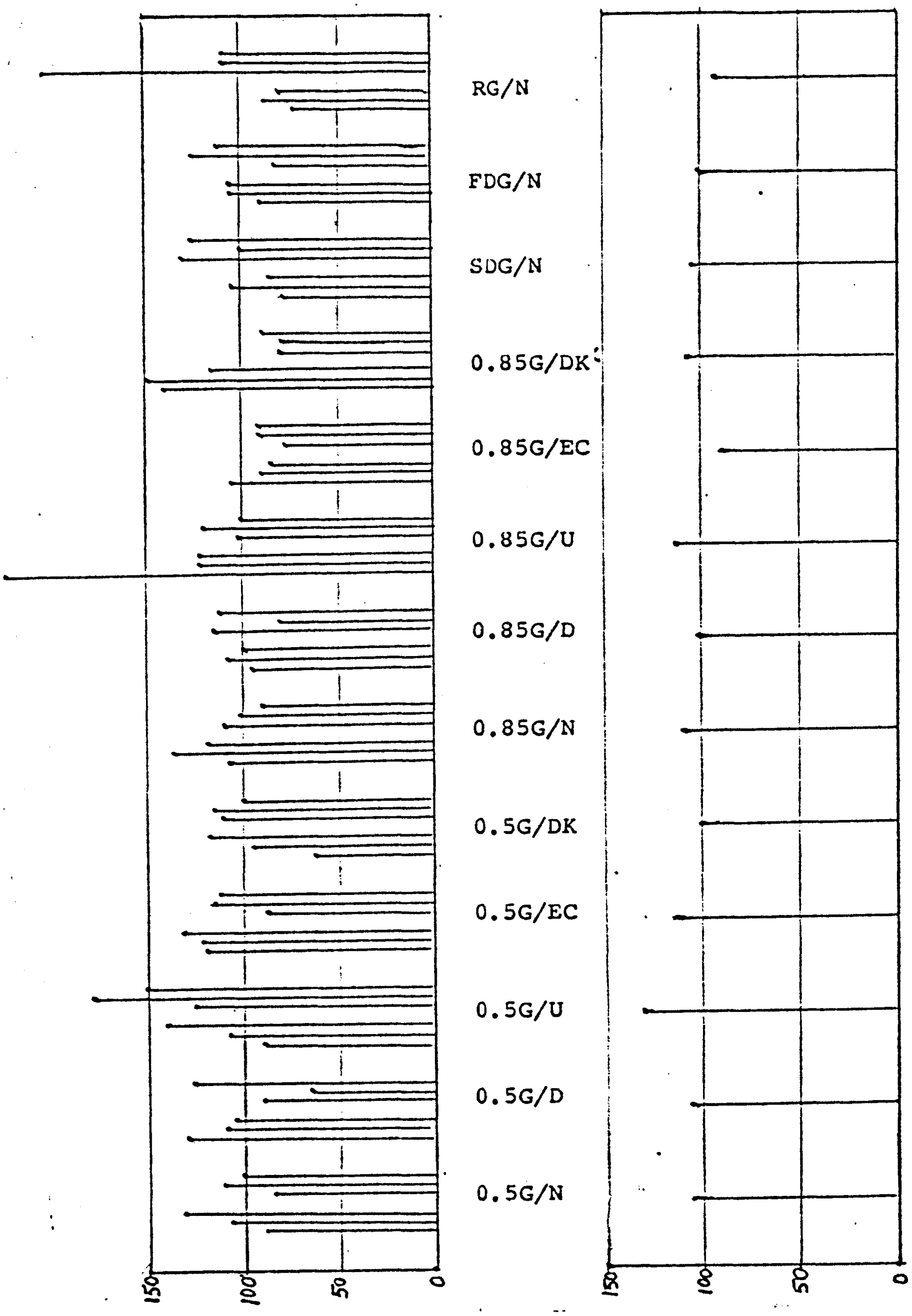


Figure 4.4.14. Rectus femoris, integrated EMG during late response.

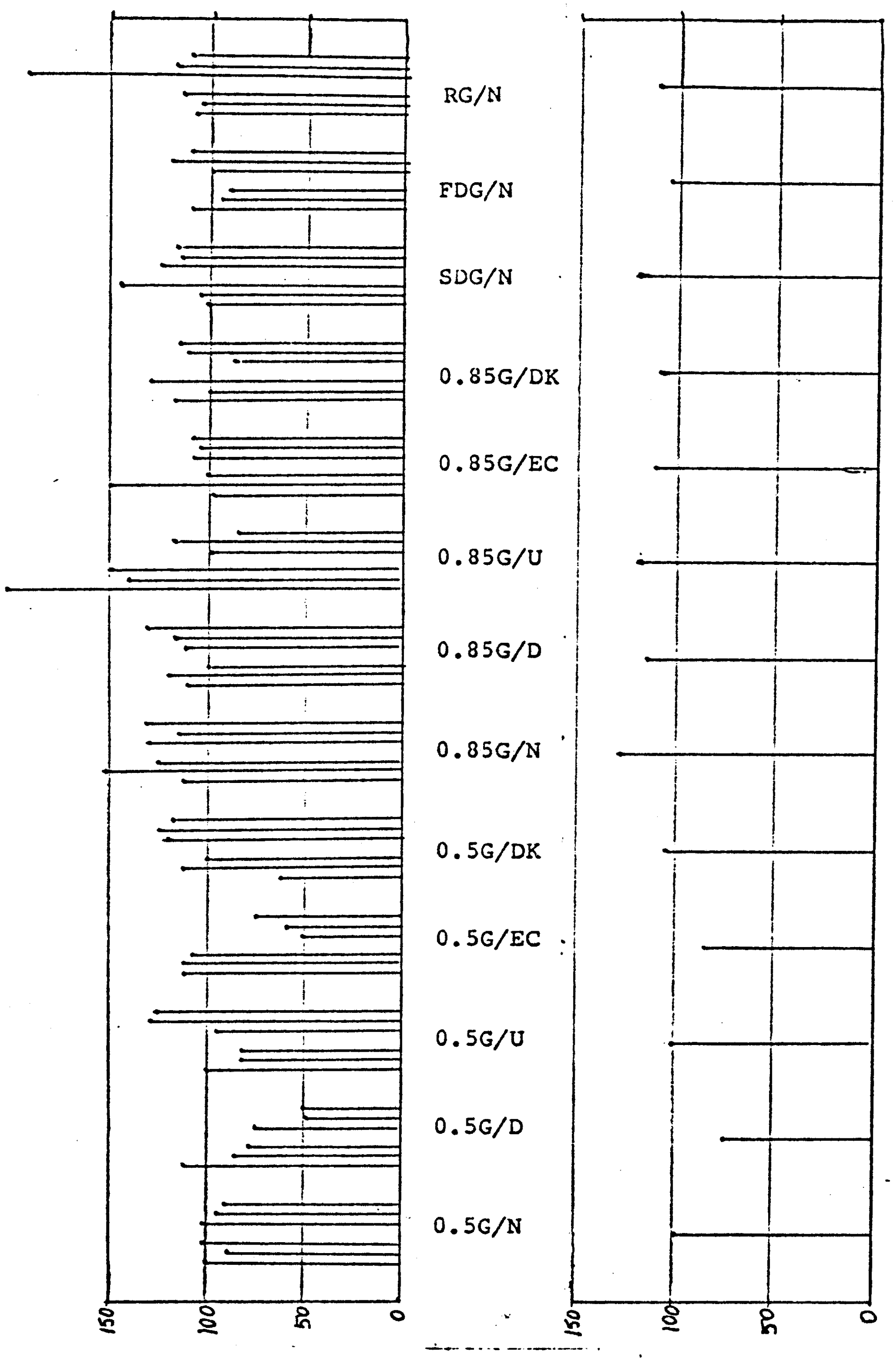


Figure 4.4.15. Biceps femoris, integrated EMG during late response.

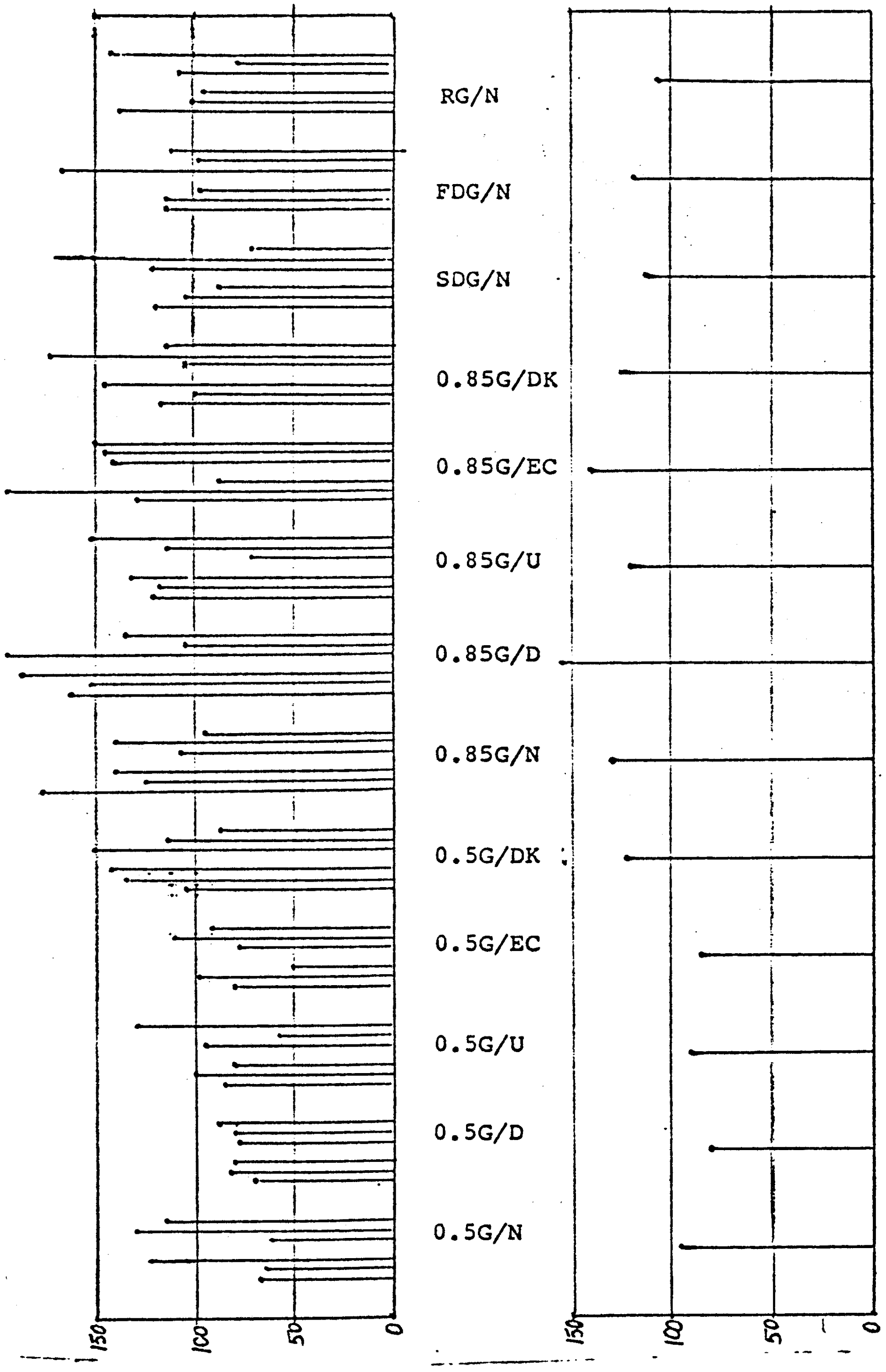


Figure 4.4.16. Gastrocnemius, integrated EMG during contact.

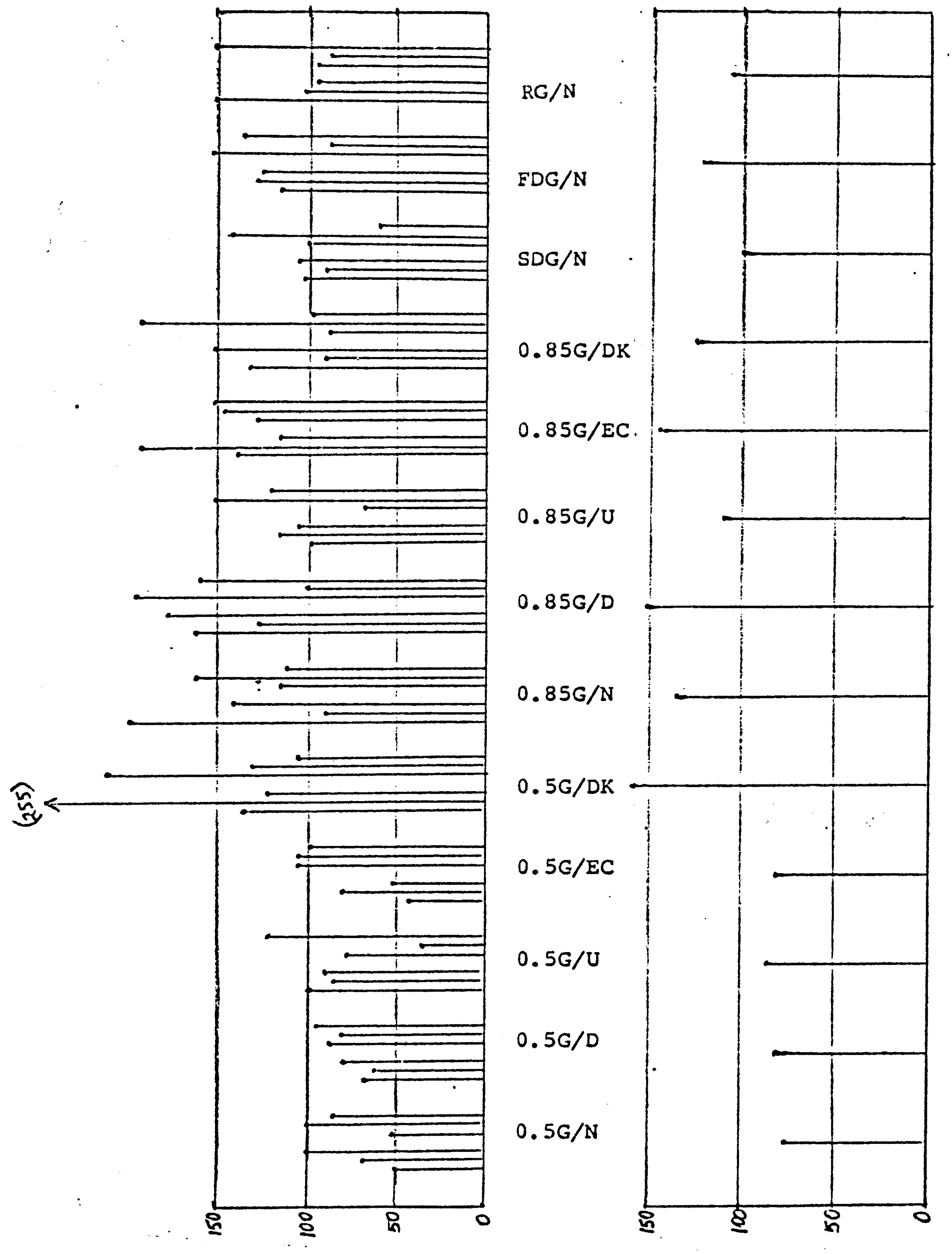


Figure 4.4.17. Soleus, integrated EMG during contact.

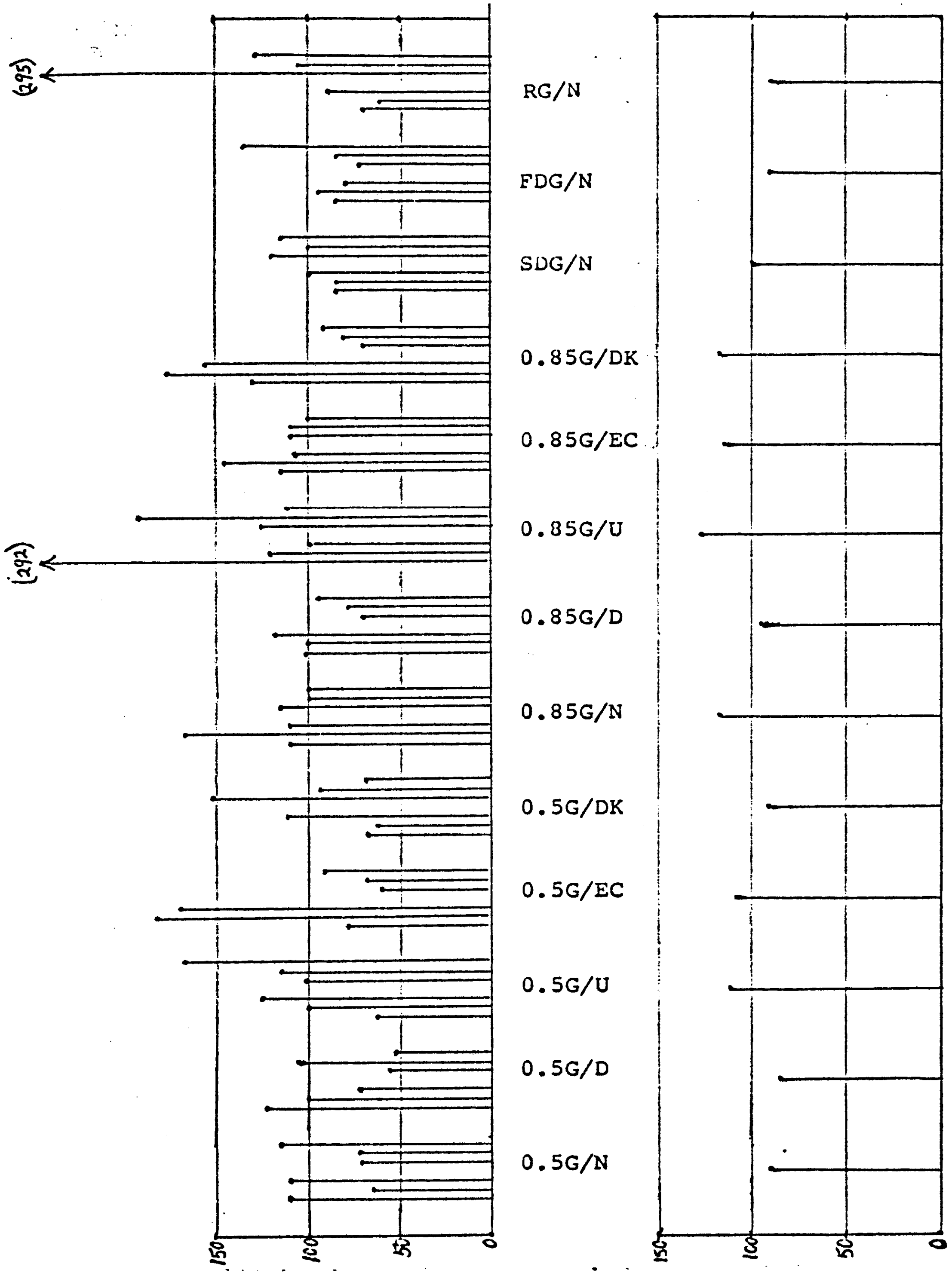


Figure 4.4.18. Tibialis anterior, integrated EMG during contact.

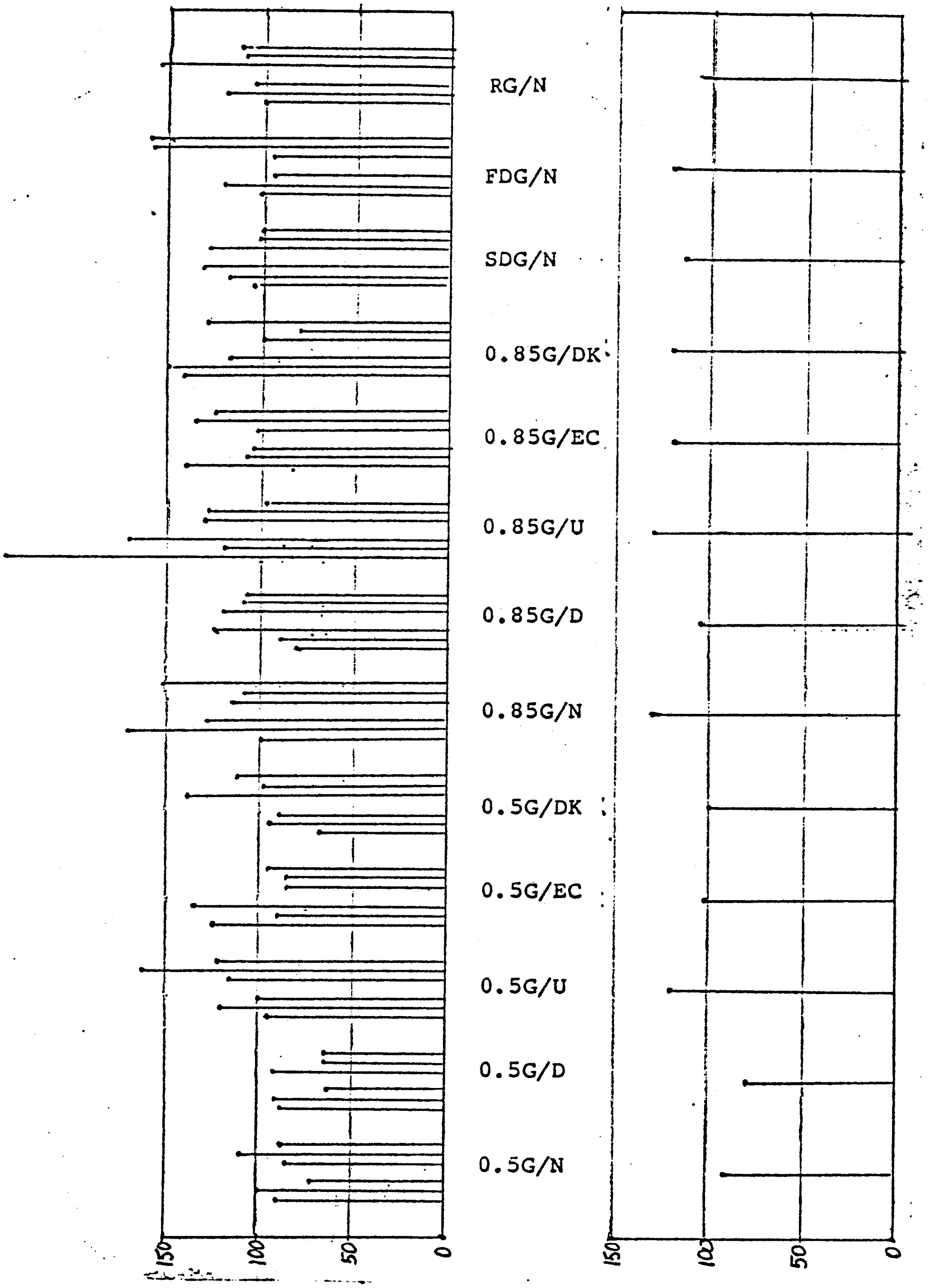


Figure 4.4.19. Rectus femoris, integrated EMG during contact.

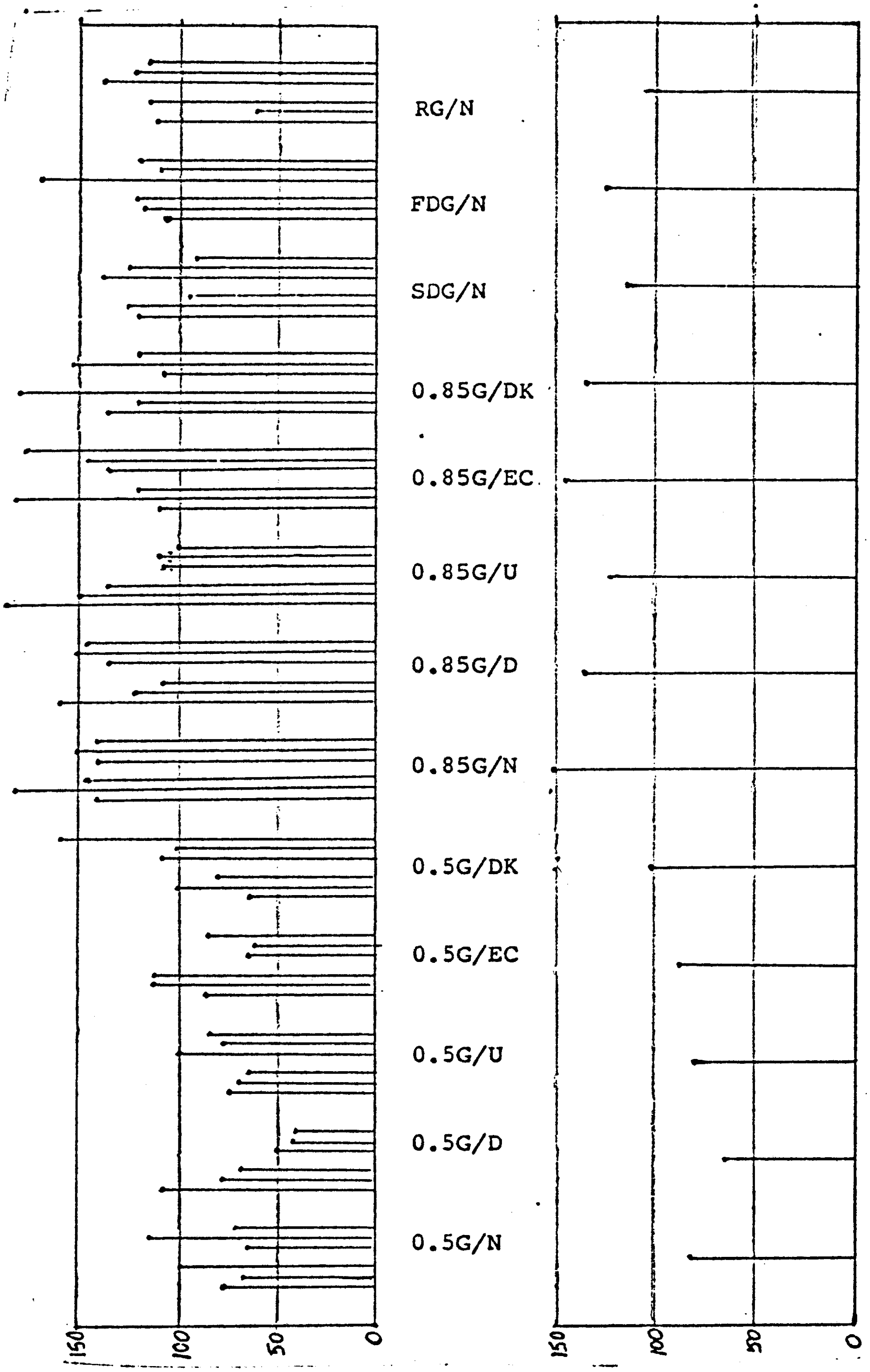


Figure 4.4.20. Biceps femoris, integrated EMG during contact.

normalized values across all five subjects for each of the three repetitions in block 1, and the second three bars correspond to the repetitions in block 2. The lower graph shows the average value over both blocks and all repetitions of a given test condition. Because the very first drop for each subject showed significantly elevated response magnitudes, the first drop for each block was eliminated from the statistics. In block 1, the first test was 0.85G/U/B1/1 and for block 2, the first test was RG/N/B2/1. In the graphs in figures 4.4.1-20, these two drops are shown in the top graph, but are eliminated from the group for the purpose of averaging in the lower graph.

Early response latencies relative to release time were determined for each muscle using threshold recognition techniques similar to the procedure for recognizing release and contact times. Computed values were compared with the original plots. In cases where the early response was absent or very small, the value for the latency was treated as a missing datum.

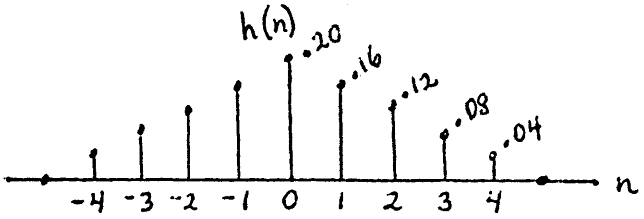
In order to quantify synergistic relationships between pairs of muscles, corellation coefficients were calculated for the following three time periods: T_r to T_c , T_r to T_m , and T_m to T_c . The corellation coefficient was calculated as follows:

$$r = \frac{E\left[\left(V_1' - E(V_1')\right)\left(V_2' - E(V_2')\right)\right]}{\left[E\left[\left(V_1' - E(V_1')\right)^2\right] + E\left[\left(V_2' - E(V_2')\right)^2\right]\right]^{1/2}}$$

where

$$E(V_1') = \sum_{n=n_1}^{n_2} V_1'(n) / (n_2 - n_1 + 1)$$

and similarly for all other expectations. n_1 and n_2 are the sample periods defining the desired interval over which the corellation was calculated. V_1' and V_2' represent digitally filtered versions of the original sampled, analog filtered EMG, V_1 and V_2. $V'(n) = h(n) * V(n)$, where the impulse response is shown below:



This digital filtering reduced high frequency oscillations in the EMG and increased the computed correlation coefficient when coactivation actually occurred.

It must be noted that the probability distribution of the filtered EMG values is not Gaussian. Instead, the distribution is one-sided and skewed toward values near zero due to the nature of rectified signals. A corellation coefficient, as such, assumes a Gaussian distribution. However, if the computed values are interpreted as relative measures of coactivation, the analysis of variance techniques can be applied to these derived measures in order to test for differences and trends among treatments as with any other derived measure.

Another difficulty in the interpretation of the coactivation coefficients arises from the possibility of significant cross-coupling between the GN electrodes and the SL electrodes, specifically. Much of the corellation of the signals from these muscles may result from the fact that the gastrocnemius and soleus are both attached to the Achilles tendon and lie very close together. Again, because this factor is probably constant throughout the testing, analysis of variance should yield valid comparisons between test conditions.

4.6 Reactions to different acceleration profiles

Before considering the effects of altered visual field motion, differences in the main effects of acceleration profiles will be analysed. From the data shown in figures 4.4.1-20, it is evident that as a first approximation, the faster the fall, the larger the reaction. In figure 4.5.1 on page 132, integrated EMG activity during the early response is plotted as a function of velocity at the end of the first 100 msec following release. The data points in these figures are taken directly from figures 4.4.6-10. Because of the relatively slow time constant of the brake, the first 100 msec of acceleration effectively consists of a curve with an average slope which is different for each acceleration profile. The velocity at 100 msec is a convenient measure of the suddenness of release.

Trends for all muscles are significant ($P<0.001$) over the entire range of velocities at 100 msec, but comparisons between only the slowest four velocities shown do not reach a significant level ($P>0.05$) for GN, SL and TA. Instead, these three muscles seem to manifest a plateau in activity as a function of suddenness of release, until a certain level is reached; the average response during 0.85G falls is definitely much higher, especially for GN and SL. It must be emphasized that the data do not allow conclusions to be made about absolute values of muscle force; only relative changes

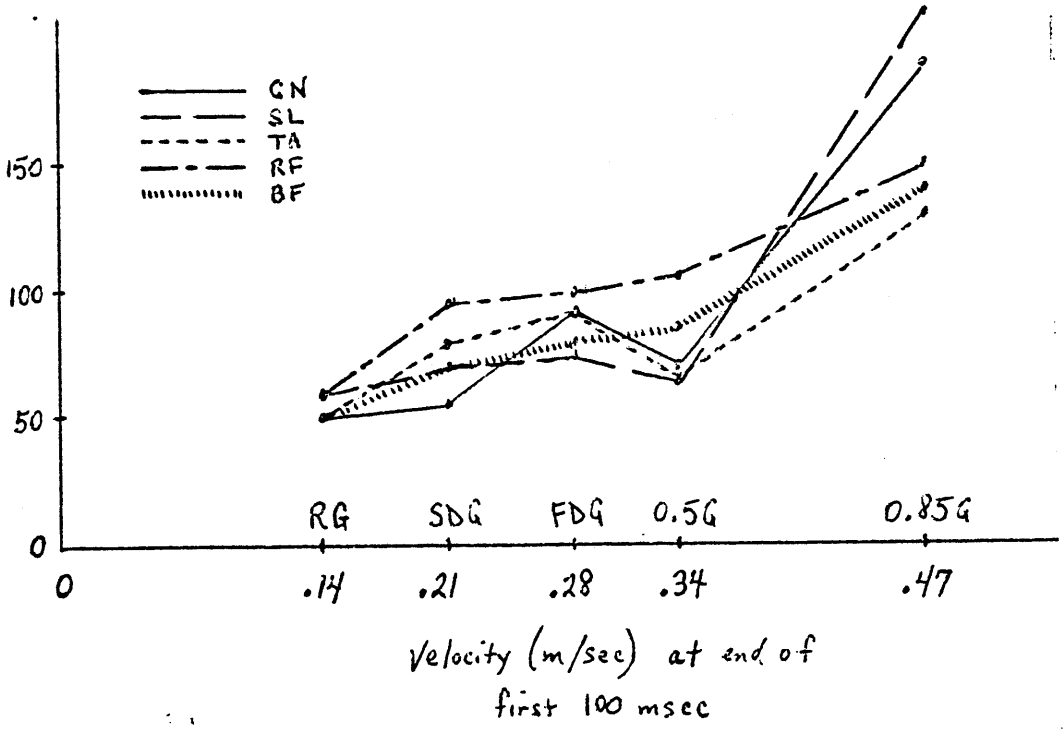


Figure 4.5.1. Integrated EMG during early response, normal visual field conditions.

among different drops can be compared.

The early response usually begins at about 100 to 120 msec and is over by 160 msec. Since the fibres of the vestibulospinal and reticulospinal tracts have average conduction velocities of 94 and 119 meters/sec, respectively (Wilson and Yoshida, 1969, in the cat), brainstem to gastrocnemius conduction time would be only about 15 msec, based on a conduction distance of 1.35 m and assuming a similar conduction velocity for the faster motor axons (Henneman, 1974e). Therefore, it seems reasonable that the early response signal which is sent as a result of processing in the brainstem and vestibular nuclei might incorporate information received from the vestibular receptors up to about 100 msec. The data indicate a strong relation between the velocity and the early response magnitude, as shown in figure 4.5.1. While the velocity at the end of 100 msec was chosen as the coordinate for the abscissa because it seemed reasonable, other interpretations are certainly possible. Acceleration at the end of a certain time could also be used, and a similar monotonic relationship would be observed. The important point is that the response magnitude is a function of the suddenness of the release.

The following table presents average latencies of the early response during 0.5G and 0.85G falls for all muscles recorded. (Visual conditions have no significant effect on latencies; therefore, the following values represent averages for all visual conditions.)

(latencies in msec)

	0.5G	0.85G
GN	106 ± 11	99 ± 7
SL	110 ± 12	104 ± 9
TA	99 ± 13	95 ± 10
RF	83 ± 12	78 ± 6
BF	99 ± 11	87 ± 8

Using analysis of variance, the trends for both GN and SL are statistically significant ($P<0.05$), but the differences are not large. Deterministic differences due to acceleration profile characteristics cannot be ruled out as a possible reason for the variation.

GN and SL early responses typically account for only 10 to 20% of the total integrated EMG during the entire fall. On the other hand, TA and RF early responses represent 40 to 50% of the total for these muscles, and BF, 25 to 35%. While relative comparisons of absolute muscle force are not possible from EMG data, these figure do indicate the relative functional significance of the early response for each muscle. GN and SL early response is, therefore, probably not a major contributor to the total force developed in these muscles.

Figure 4.5.2 is relevant not because of the small differences which are present, but rather, because of the striking similarity of the integrated activity values for all acceleration profiles. It must be remembered that these values were obtained by integrating the filtered EMG data from a fixed time to the moment of contact. Since the faster falls result in a shorter fall time, this implies that the average EMG level must increase in order to achieve the same total integrated value. For example, compare the original data of figures 4.3.1 vs. 4.3.2 and figures 4.3.5 vs. 4.3.6; these comparisons are between the 0.5G/N and 0.85G/N conditions in two different subjects. The normalized average EMG levels for the late response period are shown in figure 4.5.3 on page 137.

The integrated EMG during the late response period, as shown in figures 4.4.11-15, shows much less variation with acceleration profile than during the early response. The 0.85G/N drops elicit somewhat greater late responses than the other /N cases for all five muscles. It must be remembered that these values were obtained by integrating the analog filtered EMG from a fixed time to the moment of contact; since the fastest falls result in a shorter fall duration, this implies that the average EMG level must increase in order to achieve the same total integrated value.

Integrated EMG during contact, as shown in

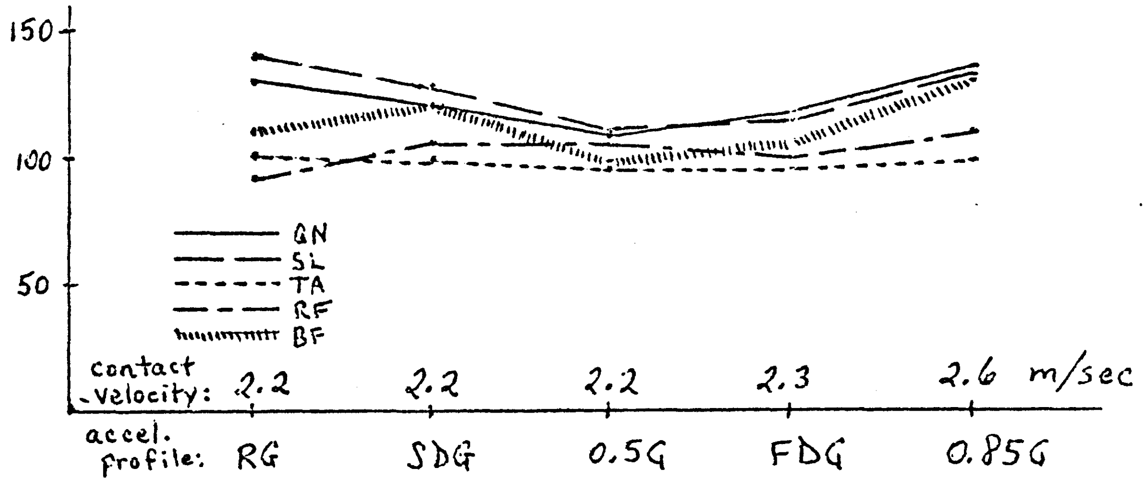


Figure 4.5.2. Integrated EMG during late response, normal visual field conditions.

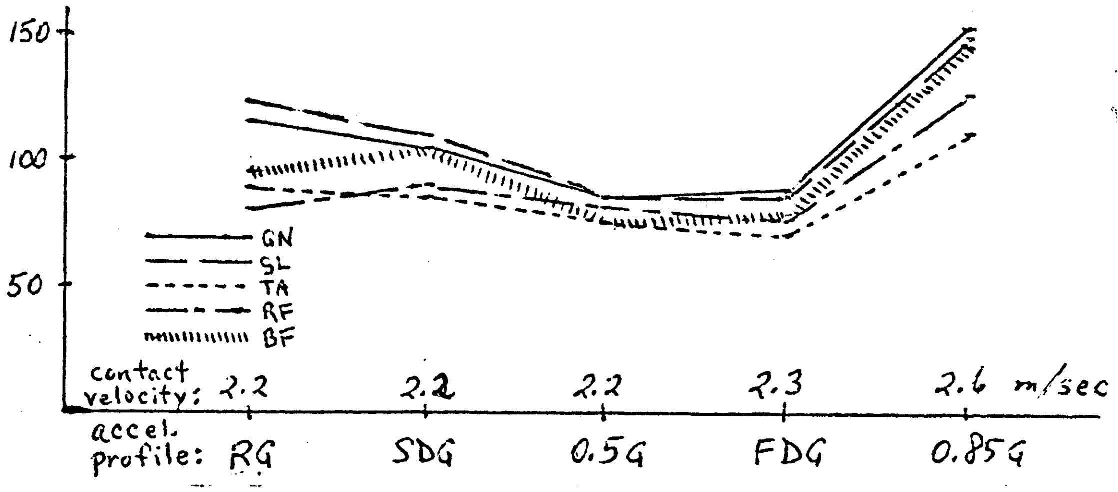


Figure 4.5.3. Average integrated EMG (per unit time)
during early response,
normal visual field conditions.

figures 4.4.16-20, indicates consistent increases of muscle activation in all muscles during contact as the speed of the fall increases. The degree of muscle contraction might reasonably be expected to correspond to the velocity at contact; in figure 4.5.4, the integrated EMG during contact for the /N falls is plotted for all muscles as a function of contact velocity. Differences between pairs of drops for a given muscle do not reach a statistically significant level, except for the difference between the 0.5G/N and 0.85G/N drops for all muscles (P<0.01).

Timing differences between 0.5G/N and 0.85G/N falls for the late response are evident in the original data from most of the subjects. Compare the following figures of the original data: 4.3.5 vs. 4.3.6, 4.3.9 vs. 4.3.10, 4.3.11 vs. 4.3.12, 4.3.13 vs. 4.3.14, and to a lesser extent in 4.3.1 vs. 4.3.2. In figures 4.3.5 and 4.3.6, the late response demonstrates a relatively constant relationship to the contact time, which differs by about 80 msec. In other words, the contact time for the 0.5G fall occurs about 80 msec later than the 0.85G fall; the late response is shifted by a similar amount and the quiescent period following the early response is lengthened. Similar patterns can be seen in the other pairs. It is important for the purpose of comparison to ignore any activity following contact, since reflex activity following contact will obviously be related to the moment of contact.

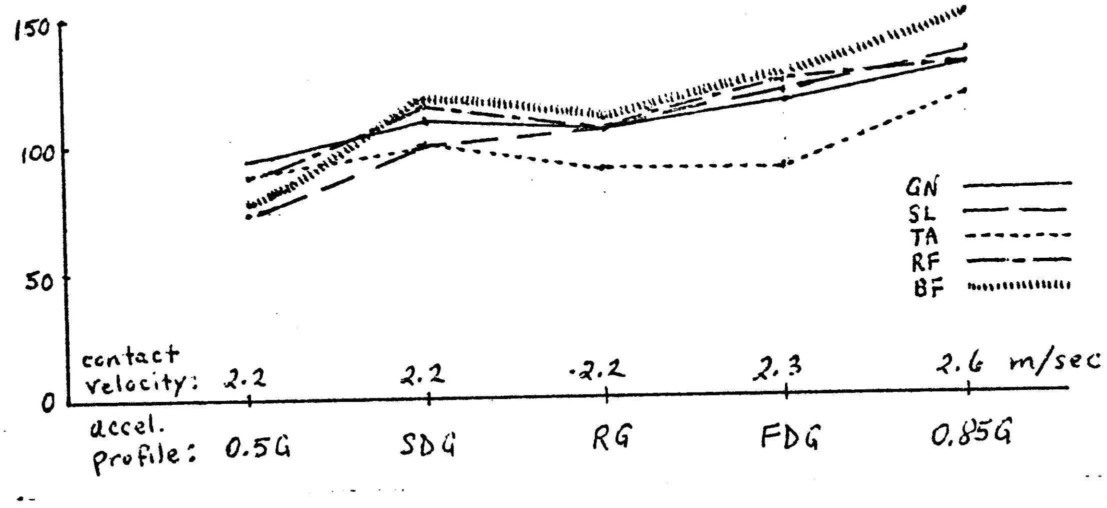


Figure 4.5.4. Integrated EMG during contact, normal visual field conditions.

The fact that almost all points for the SDG, RG, and FDG drops fall in the range between the 0.5G and 0.85G drops for all muscles, may suggest a trend. The only exception to this is the point representing TA during the FDG fall. All of the falls which have a contact velocity of 2.2 m/sec are plotted in the order 0.5G, SDG, and RG, because the characteristics of the acceleration profiles are such that acceleration changes occur progressively later in the waveforms. For example, during the 0.5G falls, the only acceleration transient occurs during the initial release; however, for the RG and SDG falls, the ramp in acceleration does not end until late into the fall, as can be seen in figure 4.1. Therefore, any internal mechanisms which may attempt to predict final contact velocity would have to make adjustments for this fact later in the reaction.

The results are consistent with the prediction that acceleration changes during the fall induce reactions later in the fall, although the differences do not reach the level of significance for each muscle separately. EMG reactions during contact for the SDG falls are greater than during contact for 0.5G falls, even though the contact velocity is the same. Another result which can be deduced from this data is that the subject successfully accounts for these acceleration increases during mid-fall. For the SDG drop, in particular, if the mid-fall acceleration increase were not taken into account, the projected contact velocity would be about 1.8 m/sec instead of 2.2 m/sec; contact EMG levels would then be expected to be less than for the 0.5G case, not greater.

4.7 General habituation

In the test sequence of block 1, test 0.85G/U/B1/1 is the first test; in the test sequence of block 2, test RG/N/B2/1 is the first test. In figures 4.4.1-20, almost all of the measured reactions during these tests are significantly greater than reactions during the second and third repetitions of the same test, sometimes by as much as 200%. However, the second and third tests of the sequence for both blocks elicited EMG responses which were within the range of values for all subsequent tests. No significant reduction or increase in general EMG amplitude was found throughout the remainder of the tests in the session, indicating that almost all of the habituation had occurred before the second test.

The pattern of habituation of the integrated EMG during the late response and contact should be noted in particular. The GN and SL reactions even during the first fall are not far outside the range of reactions for the remainder of the session. The TA, RF, and BF do show considerably elevated late response EMG during the first trial, and TA and RF also show considerably elevated values during contact. This pattern is strikingly diferent from that of all subsequent reactions. Possible reasons for this peculiar pattern of coordination during the first trial will be discussed in the next chapter.

4.8 Main visual effects

Drops during modified visual field motion indicate numerous significant effects on the response pattern, but the details of the changes are complex and do not allow a simple linear model of the influence of visual field velocity on EMG reaction magnitude.

Visual effects are most clearly seen in comparing the different 0.5G falls. GN, SL, and BF show the most dramatic differences in integrated EMG during the entire fall. (See figures 4.4.1-5.) While certain comparisons may not reach significant levels in all of these muscles, the following general trends may be seen: compared to the drops with normal (/N) visual condition, reactions are diminished in the /D and /EC cases, increased in the /U cases, and not significantly affected by darkening the room (/DK). The diminishing of the response in the /D cases is the most significant effect. Significance limits as determined by analysis of variance are shown in the following table for comparison between the different cases for 0.5G falls (integrated EMG during entire fall). A blank entry in the table indicates that the comparison did not reach the 0.05 level.

	GN	SL	TA	RF	BF
0.5G/N vs. /D	<.01	<.001			<.01
/N vs. /U		<.05	<.01		
/N vs. /EC	<.01	<.01			

By examining the integrated EMG values for the early and late responses for the different 0.5G falls (figures 4.4.6-10 and 4.4.11-15), the early reaction appears largely responsible for contributing increased reactions for the /U cases. The GN and SL values for the /U case is significantly elevated above that for any other visual condition, although the GN and SL values for the /DK condition are also elevated relative to the /N case. While the various non-normal visual fields cause bidirectional modulation of the total response magnitude during the fall compared to the normal case, the early response is increased by any kind of unusual visual field motion which differs from the normal, eyes open case. Significance values are tabulated below for cases where the early response is significantly greater than the response to a normal fall:

	GN	SL	TA
0.5G/N vs. /U	<.05	<.01	<.01
/N vs. /EC			<.05
/N vs. /DK	<.05	<.05	<.05

During the late response period, the GN, SL, and BF all show similar patterns in the comparison between different 0.5G visual conditions. Since the late response accounts for the major portion of the total response during the fall, the patterns seen in the integrated EMG for the entire fall are very similar. In contrast to the patterns observed for the early response, the abnormal visual field conditions tend to consistently diminish, rather than increase the late response magnitude. The only exception to this occurs in the RF late response; if any differences are observed, the response is increased relative to the normal case. Significance values are shown below for cases in which the late response is significantly different from the late response during a 0.5G/N fall:

	GN	SL	TA	RF	BF
0.5G/N vs. /D	<.001	<.001			<.001
/N vs. /U				<.05	
/N vs. /EC	<.001	<.001			

During the contact period, few major differences between the various visual conditions for 0.5G falls are evident. The most striking difference occurred for the /DK case; SL integrated EMG during contact is significantly greater than during a normal fall ($P<0.001$). GN EMG is also greater, but does not reach the 0.05 level of significance. RF contact EMG demonstrates some modulation with respect to visual field motion; it increases during the /U case and decreases during the /D case. However, only the /U case compared to /N is significant (P<0.05).

The effects of different visual field conditions on the 0.85G falls are not nearly as dramatic as for the 0.5G falls. In fact, the most notable result is the lack of significant differences between the various visual field conditions compared to the wealth of effects observed during 0.05G falls. During the early response period, the only significant main effect is that for the 0.85G/EC and /DK falls, the GN and SL response magnitudes are reduced relative to the /N case (P<0.05). Note that this is exactly the reverse of the result obtained for 0.5G falls, in which the /DK and /EC conditions elicit an <u>increased</u> early response relative to the 0.5G/N condition.

During the late response period of 0.85G falls, as in the early response, the main significant effect is that GN and SL responses during /EC and /DK falls are reduced (P<0.01 for GN during /EC and P<0.01 for SL during /DK). EMG during the contact period presents a number of interesting differences. The SL values for the 0.85G/D case has slightly elevated values relative to the /N case, and the /U case shows significantly lower (P<0.05) values than the /N case. GN and SL typically show large bursts of EMG activity prior to and during contact. This result indicates that the upward moving visual field may fool the person into believing that he is falling faster than in reality, causing him to prematurely activate SL. If the reaction is already on its decline during contact, the contact EMG measure would then indicate a reduced response. The TA response during contact clearly suggests a pattern of reciprocal innervation when compared to the SL response. The TA response is decreased for the 0.85G/D case and increased for the /U case ($P<0.05$), which is just the opposite of the pattern observed in SL contact reactions.

To summarize the main effects, the early response varies significantly with differences in the initial acceleration transient, whereas the late response shows more variation with respect to visual field conditions. Visual field conditions significantly affect both the early and late responses for 0.5G falls but do not have as much effect on 0.85G falls. The fact that the late response shows less variation with respect to the initial acceleration transient is not surprising; if the late response is a more volitional preparation for landing, its parameters should be determined by the expected velocity at contact with the floor. Since the corresponding range of contact velocities tested (2.2 to 2.6 m/sec) was considerably less than the corresponding range of initial acceleration transients, the results are consistent with this hypothesis.

4.9 Interaction effects

Except for the drastic reduction of the EMG magnitude following the very first fall, few other habituation or adaptation effects were seen. Observation of the subjects during the falls indicated that they were able to control their landings quite well. The few subjects who lost their balance upon contact usually did so only during the first trial, and learned almost immediately the correct method for landing without losing balance.

This experiment was designed with the intention of allowing immediate sequential effects to be analysed. However, no consistent patterns were observed. While it might be reasonable to suspect that the immediately preceding test may influence the reaction, the data here indicate only that any possible effects do not reach the 0.05 level of significance. The main effects of acceleration and vision were the predominant factors affecting all tests.

Certain longer term interactions were noticed, however. For the purpose of analysing these effects of sequence order, table 4.4 on page 84 also shows the average sequence position for each set of three tests of a given condition. For example, since the two blocks have exactly the reverse sequence of the other, if the average sequence position of test 0.5G/N is 17 in block 1, then it must be 29 (46 minus 17) in block 2. If the comparison of two tests is significantly different between block 1 and block 2, an interaction effect exists, and may be due to the possibility that the reaction may vary with the number of drops previously experienced.

During the late response period, the comparison of GN and SL for 0.5G/N and 0.5G/U and also for 0.5G/N and /DK reveals what seems to be an increased sensitivity of the reactions to /U and /DK conditions later in the testing sequence. This effect is surprising since it indicates that visual effects are not ignored as the testing proceeds, but may actually be enhanced. The significance values of the block by test condition interactions for the above comparisons are listed below (see figures 4.4.16-17):

block x test condition interaction during late response

	GN	SL
0.5G/N vs. /U	<.05	<.001
0.5G/N vs. /DK	<.05	<.01

Tibialis anterior responses also show a few significant interaction effects, but most of the significant comparisons are among the 0.85G drops. Here, TA responses generally tend to decrease with experience. Refer to table 4.4 on page 84 to verify the actual sequences for block 1 and block 2; the significance values for significant block by test condition interactions are shown below:

block x test condition interaction during late response

	TA
0.85G/N vs. /U	<.05
/N vs. /DK	<.05

These are the same visual field conditions which show the most significant interactions for GN and SL during 0.5G falls. Other interactions did not reach a significant level.

While the interaction effects do not indicate direct linkage between the GN and SL and the TA responses, the overall trends indicate a diminution of the importance of TA response with time and an increase in the importance of GN and SL. This would be reasonable considering the antagonist relationship betweeen these muscles. Though statistically significant, the effects are not great, as can be seen in figures 4.4.16-18.

4.10 Coactivation coefficients

Table 4.5 on page 150 presents the coactivation coefficients, as defined previously, for all pairs of muscles recorded. Several results are of interest here. The fact that all of the muscles respond simultaneously during the early response is reflected in the high values of the coactivation coefficients for the early response. GN and SL show consistently high values, but much of this may be due to electrical crosstalk as mentioned previously. While

Table 4.5. Coactivation coefficients for 0.5G/N and 0.85G/N falls.

muscle pair	early response 0.5G	0.85G	late response 0.5G	0.85G
GN-SL	.80	.85	.75	.71
GN-TA	.58	.65	.23	.09
GN-RF	.43	.45	-.06	-.18
GN-BF	.44	.66	.31	.38
SL-TA	.57	.62	.27	.14
SL-RF	.34	.37	-.12	-.26
SL-BF	.45	.70	.39	.36
TA-RF	.45	.47	-.04	-.02
TA-BF	.44	.51	.18	-.05
RF-BF	.56	.48	-.09	-.14

....

Table 4.6. GN-TA and SL-TA coactivation coefficients for 0.5G and 0.85G late responses: all visual conditions.

	0.5G					0.85G				
	/N	/D	/U	/EC	/DK	/N	/D	/U	/EC	/DK
GN-TA	.23	.23	.36	.17	.32	.09	.28	.23	.06	.27
SL-TA	.27	.30	.36	.19	.32	.14	.26	.28	.10	.33

most of the early response values for the 0.5G and 0.85G falls are not significantly different, the GN-BF and SL-BF values are increased for the 0.85G falls ($P<0.001$). This probably is due to the tendency to increase the degree of knee flexion simultaneously with ankle plantar flexion early in the fall in order to cushion the landing; knee flexion is more crucial during faster falls.

Likewise, the level of TA co-contraction with GN and SL decreases during the late response period ($P<0.01$). This would allow a given level of GN and SL contraction to be more effective in plantar flexing the ankle.

Table 4.6 on page 150 presents the coactivation coefficients during the late response for GN-TA and SL-TA for all visual conditions during 0.5G and 0.85G falls. These coefficients were the only ones which varied significantly with visual conditions. Note that for both accelerations, all of the non-normal visual conditions except /EC tend to induce increased co-contraction of TA with GN and SL.

CHAPTER 5

INTERPRETATIONS AND CONCLUSIONS

The experimental design of this study allows comparisons of the main effects of different rates of acceleration with results reported by other researchers, and also allows comparisons of visual effects with previously reported data. The testing procedure differs in several important respects from previous studies and the results have made a critical reexamination of previous results necessary.

Melvill Jones and Watt (1971b) performed the first detailed examination of human responses to sudden, unexpected falls. (See Chapter 1 for a more extensive review of this and other related studies.) The Melvill Jones and Watt procedure differed from the procedure in this study in that their subjects held onto a bar overhead which was unexpectedly released. The release into zero-g occurred nearly instantaneously, whereas in the present experiment, the brake time constant for deactivation was 40 msec. Melvill Jones and Watt reported an early response latency in TA and GN of 75 msec, which was relatively invariant with height of the fall. This is consistent with the 99 msec latency in GN obtained in this study for 0.85G falls, if it is assumed that an acceleration threshold Δg of about 0.2g must be reached before the early response is triggered (Greenwood and Hopkins, 1976a). For the ramp acceleration case, GN and SL responded with average latencies of 108 and 112 msec, respectively. Again, this is consistent with a threshold Δg of 0.2g before an early response is initiated by otolith-dependent brainstem mechanisms.

Greenwood and Hopkins (1976a) reported that the threshold for eliciting a detectable early response is about 2 m/sec^2 (about 0.2g). They used a system which required the subject to be suspended in a harness, and released him following deactivation of an electromagnet. Since they used a system of counterweights, the acceleration transient at release was relatively rapid, similar to that of Melvill Jones and Watt.

To further determine the sufficient parameters of the stimulus, it would be useful to use carefully controlled acceleration ramps of varying slopes. It is conceivable that the hypothesized threshold Δg of 0.2g applies only within a certain time limit. If the total cumulative Δg occurs over a long period of time, it would seem likely that no "early response" would ever manifest itself. Ramp accelerations of sufficiently gradual slope to determine threshold specifications were not tested in this study.

The magnitudes of the integrated EMG activity during the early response are also consistent with the findings of Greenwood and Hopkins (1976a), who determined that the magnitude of the GN early response was a linear function of the acceleration transient. Figure 4.5.1 on page 132 indicates a monotonic function of early response magnitude versus velocity at the end of the first 100 msec. This data does not provide enough information to make conclusive statements about the linearity or non-linearity of response with respect to various measures of initial acceleration transient, as discussed in the previous chapter. If these data differ in any respect from the results of Greenwood and Hopkins, it is in the result that GN and SL responses increase more that the TA, RF or BF responses for the higher acceleration drop condition, 0.85G. Watt (1980, personal communication) has confirmed that the GN response for one-g falls is greater than would be indicated by a linear relationship between early response magnitude and initial acceleration transient.

Both Melvill Jones and Watt (1971b) and Greenwood and Hopkins (1976a) clearly determined that if subjects knew the height of the fall beforehand, they could accurately and consistently adjust the timing of the late response such that maximal activity preceded contact by 40 to 140 msec. Subjects in Greenwood and Hopkins' experiment reported sensations of surprise at being dropped from different heights with blindfolds on. Their expectations seemed to be that contact would occur sometime between the range of contact times actually occurring. The timing of the late response and subjective sensations were consistent with a preparation for landing which was either too early or too late.

The first three subjects in the current study were tested at heights of 28 and 43 cm, and the results indicate almost perfect ability to adjust the late response timing. In addition, for normal visual field conditions, subjects never reported a sensation of surprise after falls which included acceleration changes after the initial release. If subjects are capable of adjusting the late response timing contingent upon incoming vestibular information during the fall, then the absence of subjective sensations of surprise suggests that the more automatic mechanisms involved in the late response do not require the level of conscious awareness which is triggered by a situation where expectation differs significantly from reality.

Both the early response and late response did not habituate significantly, with the exception of the very first trial, confirming the results obtained by Melvill Jones and Watt and by Greenwood and Hopkins. The fact that the very first drop elicits much larger responses suggests that there are some similarities to a general startle reaction. This analogy is also suggested by the fact that no early response occurs when the person initiates a fall himself. As mentioned in the previous chapter, the RF, BF, and TA muscles all manifest greatly elevated early responses compared to those during subsequent falls, whereas GN and SL do not present such dramatic differences. This fact suggests that the nature of the early response during the first fall may include a component which is qualitatively different. An increased emphasis on EMG activity in the thigh musculature and tibialis anterior suggests that the action might be more similar to a crouching or withdrawal reaction, rather than an enhanced preparation for an antigravity reaction. The latter would be characterized by increased GN and SL activity. (Refer to section 1.3 which discusses the action of these muscles.)

However, a typical startle reaction to auditory and visual stimuli quickly habituates and disappears with repetition, and is usually not gradable with respect to stimulus intensity. Because the early reaction during unexpected falls persists even after numerous repetitions, any further comparison to a startle reaction would be misleading. Rather, the early response seems to be a reflexly triggered reaction of predominantly vestibular origin of functional significance in the organization of preparation for landing (Greenwood and Hopkins, 1976b; Lacour et al., 1978). In addition, its presence in decerebrate cats (Watt, personal communication) is not characteristic of a startle reaction.

The effects of different visual field conditions requires more careful interpretation, since the results are not simple. They certainly do not support the naive idea that a linear weighted sum of visual field velocity estimate plus vestibular velocity estimate is internally generated and used to control the landing response.

The only previous study of the effects of visual field conditions on rapid motor reactions during falls was completed by Vidal et al. (1979) on baboons. A number of differences between their experimental procedures and the procedures in this study will make comparison difficult, in addition to the fact that baboons were used rather than humans. They tested the baboons by dropping them at one g in a seated position; being in a seated position obviates the need for a late response in the leg extensor muscles, and, indeed, they found that any late response was rapidly extinguished with repetition.

Vidal tested only three visual field conditions: falls in the dark, with a normal laboratory environment, and with a lighted box surrounding the baboon's head. One difficulty with the comparisons of these different visual field conditions is that the normal case and the stabilized vision case involve completely different visual environments; more variables than relative visual field velocity are being changed. Their results indicate that the early response is slightly reduced by a darkened visual environment and even more by the stabilized field. However, placement of a box around the baboon's head presents a completely different kind of visual environment which may induce the baboon to preset the gain of the early response to a reduced level. Thus, rather than testing the effect of reflex reactions to the combination of vestibular input and visual field velocity, it is possible that the Vidal experiments tested the ability of the baboon to preset the gain of the reflex depending upon conditions of which the animal was aware well before the fall commenced. The results do not allow any definite conclusions to be made concerning the role of visual field motion cues, specifically, in rapid motor responses.

The current study differs significantly from the Vidal paradigm in the visual conditions used. The /N, /D, and /U cases described in the previous chapter correspond to different relative visual field velocities, of which the subject was completely unaware before the fall commenced. During the setup period prior to the fall, care was taken to prevent the subject from detecting cues which might allow him to deduce which relative visual velocity was selected. Thus, all differences between the /N, /D, and /U cases must be due solely to visual field velocity effects during the fall, since the visual field pattern was exactly the same, otherwise.

The results of this study are comparable to those of

Vidal, but only if his test conditions are reinterpreted. First, for 0.85G falls, both the /EC and /DK conditions significantly reduce GN and SL early responses compared to the /N case. The /DK condition reduces the responses slightly more than the /EC condition, but is not significantly different (P>0.05). In this respect, the current findings agree with Vidal's results. For 0.85G falls, though, the means for the /N, /D, and /U cases are all quite similar for all of the muscles recorded. This indicates that visual field velocity does not significantly alter the early response for 0.85G falls. It seems more likely that the stabilized vision case in Vidal's experiment is similar in effect to the act of closing the eyes. The baboon possibly interprets the placing of a box over his head as a signal that visual information concerning the environment is being eliminated; the same phenomenon would occur during voluntary eye closure. Therefore, if the "stabilized vision" case is interpreted as being analogous to the /EC condition of the current study, the results are perfectly consistent.

The current study, however, does reveal significant effects of visual field velocity on the early response, but primarily for the 0.5G falls. The 0.5G/N and /D conditions are not significantly different, but the /U case elicits a 60% increase in GN and an 80% increase in SL activity relative to /N. The /EC and /DK conditions actually increase the magnitude of the early response in GN and SL, with /DK causing the greater increase of 50%.

Although the current paradigm involving unexpected falls differs from the Nashner and Berthoz paradigm (1978) of induced antero-posterior sway, the visual field conditions are quite analogous. (See Chapter 1 for a description of these experiments.) The normal (N), stabilized (S) and enhanced (E) conditions are analogous to the /N, /D, /U conditions tested here. The results for the 0.5G and 0.85G falls are not directly comparable to the Nashner and Berthoz results, since the /U condition enhanced, rather than slightly diminished, the early response during 0.5G falls. For 0.85G falls, which could be construed as more normal vestibular stimuli than 0.5G falls, the /D and /U conditions did not enhance the early response. If anything, they diminished it, although not to a statistically significant degree. In this respect, the 0.85G falls are comparable to the Nashner and Berthoz paradigm, since their subjects were induced to sway in a one-g environment. It would be interesting to see these sway experiments repeated on subjects who have just entered a reduced-g environment, such as can be produced during parabolic aircraft flight patterns.

5.1 Proposed model for early response generation

In order to make some sense of the seemingly disparate trends observed for the early response magnitude under different acceleration and visual field conditions, one possible model is proposed which accounts for the differences. A diagram of the model is shown in figure 5.1 on page 163.

The acceleration sensor portion of the model incorporates results of other investigators which indicate that the saccules are probably responsible for generating the signals for triggering the early response. Watt (1980, personal communication) has reported that by placing subjects in a reclining position, the early response magnitude is diminished considerably when unexpected falls are simulated with the use of bungee cords to replace the gravitational force. The physical setup is comparable to the vertical situation, but simply rotated 90 degrees into the horizontal position. Data obtained in zero-g conditions during parabolic flights also indicate similar findings. In both the horizontal and zero-g conditions, the saccules are no longer biased with a one-g gravitational force toward the feet, which is apparently responsible for diminishing vestibulospinal reflexes.

Other reports indicate that the vestibulospinal reflexes are also depressed when the neck is in an off-center

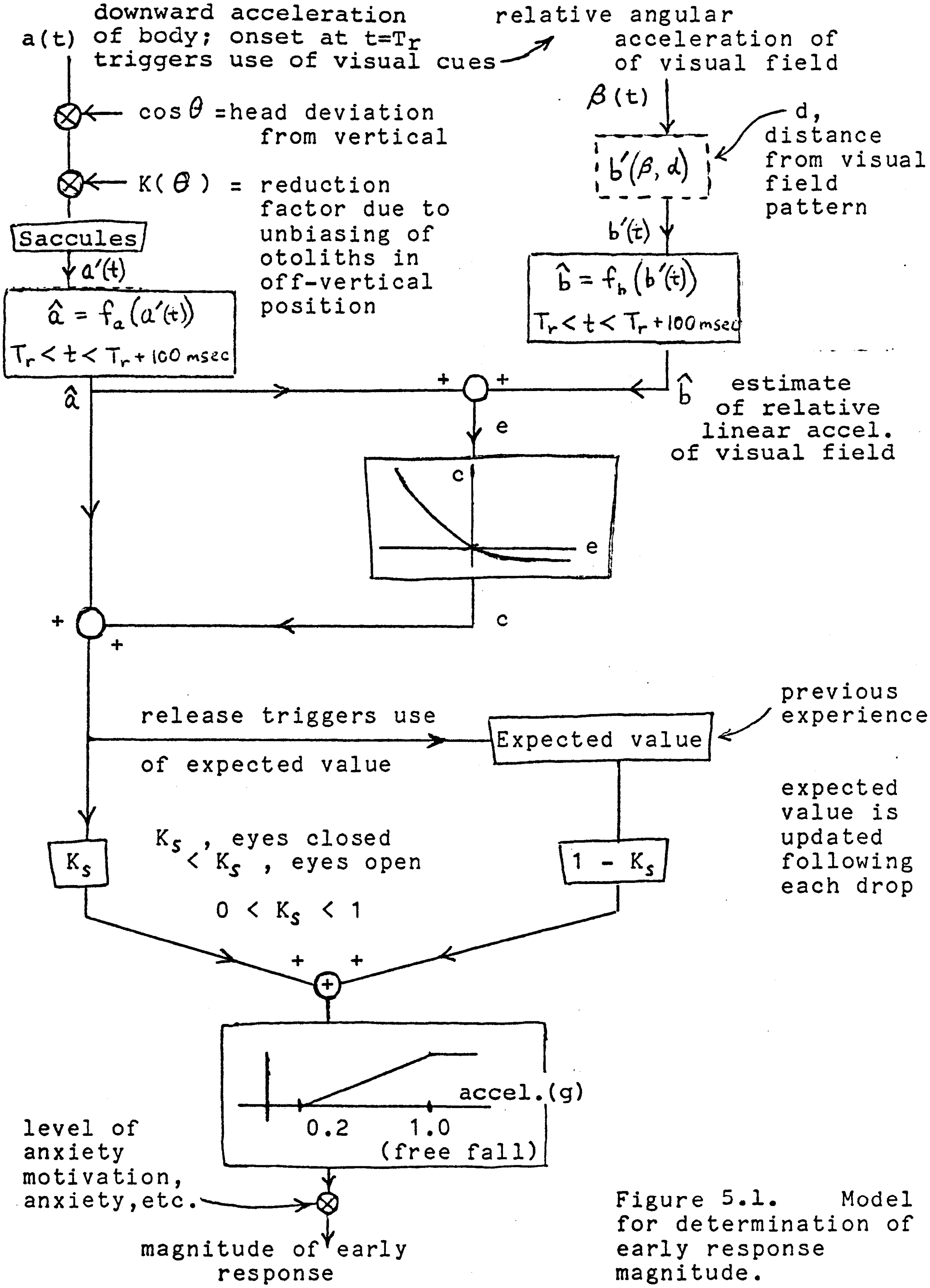


Figure 5.1. Model for determination of early response magnitude.

position. Therefore, it is possible that the reduction may be due to two factors. First, simply tilting the head such that the predominant sensitivity vectors of the saccules are no longer oriented in the direction of motion, will reduce the signal by cos θ, where θ is the angle of tilt from the vertical. Secondly, tilt relative to the vertical will decrease the one-g bias of the saccules, and, thus, will additionally reduce the gain by the factor, $K(\theta)$, as shown in figure 5.1. Such a saccular nonlinearity has been described by Fernandez and Goldberg (1976a,b). The downward acceleration is estimated by the otolith apparatus prior to the early response and this quantity is labelled as $\hat{a}$ in figure 5.1.

The visual portion of the model represents a strategy for increasing the estimate of downward acceleration if the relative visual field velocity indicates a higher acceleration than indicated by the otoliths. Prior to a fall, the subject is aware of his distance from the pattern or from objects in the environment. The transformation from relative angular field velocity to relative linear velocity is shown in dotted lines as a reminder that it is not known whether such a transformation actually occurs in the pathways involving fast visual processing. More experimentation with pattern spatial frequency and pattern-to-subject distance during unexpected falls would be required in order to verify this possibility. Implicit in the model is the assumption that both retinal slip velocity and information about current eye velocity can be added to provide an estimate of total visual field motion with respect to the head.

Circularvection experiments by Wist et al. (1977) seem to indicate that such an angular-to-linear transformation occurs for perception of self-rotation even though it is inappropriate in these circumstances. It was reported that "with the angular speed of a visual surround held constant, the perceived speed of rotary self-motion increased linearly with increasing perceived distance of the surround." These results are of significance in analyzing perceptual effects, but their relevance to rapid reflex-type reactions is uncertain.

Note that the values represented by $\hat{a}$ and $\hat{b}$ are single values rather than functions of time. The inclusion of the f functions symbolizes the assumption that only sensory information from the moment of release to the early response onset is used to calculate inertial and visual field acceleration estimates for the immediate purpose of determining early response magnitude.

The next stage of processing involves comparing the acceleration estimate from the saccules to the visual estimate. If a difference arises, an error signal, e, is generated. In a normal fall with head erect, the estimate of downward acceleration, $\hat{a}$, should exactly cancel the estimate of relative visual field acceleration, $\hat{b}$, in the upward direction, providing no error signal. This argument does not specifically address the issue of otolith dynamics; however, if the otoliths are modelled as a second order, overdamped system with a step rise time of only several msec, the dynamics should not significantly affect the reasoning. The dynamics of central neuronal processing of otolith input is not known in any detail.

The nonlinear function which provides the compensation signal, c, accounts for the result that a stabilized visual field (/D condition) does not decrease the early response as much (if at all) as an upward moving field increases it, at least for the 0.5G falls. In the /U condition, the visual acceleration estimate, $\hat{b}$, is twice the saccular estimate, $\hat{a}$. This generates an error signal equal to $-\hat{a}$, which causes a large compensation signal. This compensation signal is then added to the saccular estimate prior to further processing. A nonlinear function for generating the compensation signal insures that any conflicts between the visual and vestibular estimates of acceleration are resolved such that the adjusted estimate, $\hat{a} + c$, may be increased relative to $\hat{a}$, but not decreased significantly. This is reasonable since the factors cos θ and $K(\theta)$ will always act to reduce the estimate relative to the true value, a.

In the model shown, the compensation function does not depend on $K(\theta)$, but this may be likely. To test this possibility, the same set of visual field conditions could be tested on subjects lying on their backs or in zero-g as in the Watt studies. Such a series of tests may indicate whether the compensation process occurs prior to the stage at which the $K(\theta)$ factor reduces the signal. If this is the case, the effective gain of the compensation would be reduced.

The next stage of processing accounts for the observed differences between the /N, /EC, and /DK condition. Recall that for 0.5G falls, the early response in GN and SL is increased whereas for 0.85G falls, the /EC and /DK conditions cause a decreased early response compared to the /N condition. These results suggest that prior to the fall, the subject determines that the acceleration estimate will not be sufficiently reliable and decides to provide his own estimate based on past experience. Then, the release triggers the use of this stored value in determining the early response magnitude; following the fall, the expected value is updated to include the most recent event. A continuous range of relative weighting is allowed by the K_s factor in figure 5.1. Because the early responses for 0.5G/EC and /DK are not exactly the same, the K_s factor is probably adjusted to a value somewhere between 0 and 1, rather than completely ignoring either the current estimate or past values.

In the final stages of processing, the acceleration estimate passes through a function which includes threshold and saturation levels. No dynamics are shown in the diagram, but are certainly possible, considering that the threshold may be a function of some combination of rate of acceleration, da/dt, and the total acceleration change, Δa, within a certain time period. As mentioned previously, the accelerations tested in this study did not allow a threshold to be determined. For rapid transients as in sudden steps of acceleration, the threshold is probably around 0.2 m/sec^2. The saturation level of one g (9.8 m/sec^2) accounts for the observed result that 0.85G/U falls did not elicit a significantly increased early response. For this condition, the adjusted acceleration estimate, $\hat{a} + c$, would be much greater than one g. Considering that downward accelerations greater than one g (free fall) rarely occur in nature, it makes sense for any neurophysiological mechanisms to regard acceleration estimates greater than one g with suspicion.

Since other factors such as level of attention, anxiety, and motivation may also affect the response, a final gain is included which depends on these factors. While the multiplicative interpretation should not be taken too literally, it seems more reasonable than an additive model, since both the variance and the magnitude of the early response increase as a function of acceleration. Refer to the upper graphs of figures 4.4.6-10 on pages 113-117; although individual variance is not shown, note the variation of average values with repetition number for a given drop condition. The variation for 0.85G/N falls is greater than for 0.5G/N falls, which can readily be seen.

In terms of the proposed model, the results obtained here are consistent with the general idea proposed by Nashner and Berthoz (1978) that short latency postural reactions may be diminished by visual cues if those visual cues indicate a situation which is sufficiently different from the expected inputs. The concept of sensory conflict has also been embodied in a model of circularvection during visual field rotation and actual rotation of the subject (Zacharias and Young, 1977).

5.2 Possible physiological explanations for visual-vestibular interactions during early response

Although previous physiological experiments unquestionably indicate visual-vestibular interactions at the level of the vestibular nuclei, the Keller and Precht (1978, 1979a,b) results are difficult to compare and reconcile with the results of this study. These authors found that the rolloff frequency for visual angular velocity influence on the vestibular nuclei neurones during horizontal rotation is about 0.25 Hz, (τ =0.64 sec). Such slow dynamics would hardly be consistent with the rapid effects of visual field velocity on the early response during falls.

One difficulty with making such a comparison is the fundamental difference in the way visual field motion must be processed during linear translations and rotation. During rotations of the body around any axis, a knowledge of retinal slip velocity and eye velocity is sufficient to deduce relative rotation of the visual surround. On the other hand, the analogous problem during linear motion is more complex. In order to deduce relative linear motion of the visual surround, retinal slip velocity and eye motion are insufficient; The eye-to-visual surround distance must also be known. Since the person is presumably aware of the distance, it is not inconceivable that this information could be continually supplied to any neural mechanisms which are involved in the combination of visual field velocity and vestibular cues.

In the rotational mode, the slow dynamics of visual influences on vestibular units is consistent with the idea that the semicircular canals provide accurate information at higher frequencies, but need to be supplemented with visual information at lower frequencies where their gain is reduced. The situation may be different in the linear mode; while the otolith organs are certainly not limited by their frequency response, with a time constant of only several msec, there may be a limitation in the accuracy of the transformation from head linear acceleration to body linear acceleration.

Such teleological speculation does not alter the observed results. The existence of rapid visual influences on early motor reactions during falls should provide motivation to perform physiological searches for these effects. Daunton and Thomsen (1979) determined that vestibular neurons which responded to otolith input also responded to relative linear visual field motion. Only steady state responses during 0.59 Hz sine wave stimulation were obtained; although more data must be taken to determine response dynamics, these units appeared analogous to the units recorded by Keller and Precht during horizontal rotations.

For purposes of comparison, note that for 0.85G/U falls in this study, the relative angular visual field velocity is 120 deg/sec at the end of the first 100 msec of the fall. Assuming no eye movements occur in this time (which may not be true) this would result in a maximum retinal slip velocity of 120 deg/sec, which is well above the saturation range of 3 to 10 deg/sec that Keller and Precht found for their vestibular nuclei units. However, Brandt et al. (1973) reported that perception of circularvection saturates at 180 deg/sec. While it is unlikely that visual information at 100 msec has much effect on the early response at 100 to 160 msec, the absence of any great difference between the 0.85G/N and 0.85G/U cases might be due to the possibility that visual velocity perception saturates. This would be unlikely if, for example, the early response parameters were already determined based on sensory input during the first 30 msec. The best way to eliminate potential saturation would be to increase the distance between the subject and the visual field so that a given linear velocity would not result in such high angular velocities across the visual field. Unfortunately, the laboratory room used here did not allow a more spatious display.

The search for a physiological basis for fast visual influences on the early response should not be restricted to the vestibular nuclei. It is possible that visual influences are transmitted independently of the vestibulospinal system and interact with vestibularly triggered responses at the segmental level. Most of the recent physiological data, including the results of Keller and Precht, and Daunton and Thomsen, indicate visual-vestibular interactions at the vestibular nuclei which are consistent with known oculomotor control strategies, visual perception, and slow postural reactions observed during vection stimuli. Convincing evidence for rapid visual control of postural reactions via the vestibular nuclei has not been forthcoming, though. The nonlinearities inherent in the results of the current study indicate a much higher degree of processing than that seen in the relatively linear visual-vestibular interactions in the vestibular nuclei. In addition, the nature and complexity of the nonlinearities suggest that vestibular and visual influences are highly interdependent, which would diminish the likelihood that visual influences are transmitted to the segmental level independently of vestibular influences.

Tectospinal pathways might provide another possible route for rapid visual inflences on the spinal cord. While Maeda et al. (1977) showed that stimulation of the frog tectum and optic tract induced IPSP's and EPSP's in spinal motoneurones, it would be useful to determine if similar effects could be seen using visual field motion rather than electrical stimulation. The dynamics of the responses to natural visual input would be extremely valuable information. However, because of the difficulty of intracellular recording at the spinal level with unanesthetized animals, such experiments may not be possible. Given the current knowledge about high frequency visual information in the superior colliculus, it is possible that the superior colliculus may be involved in rapid visual-spinal influences rather than the vestibulospinal pathways. However, because of the many differences between the frog and human visual systems, such a proposal is only speculative. The tectospinal pathway is relatively more important in frogs than in humans.

Maeda also showed that the tectal and optic tract stimulation summated algebraically with vestibular stimulation at the level of the motoneurones. Since the result of Nashner and Berthoz and the results presented here indicate much more complex interactions between visual and vestibular information, such interactions must occur prior to the spinal level. This suggests that if the tectospinal tract is the pathway which conveys rapid visual influences on posture, then it must transmit information which already reflects the complex combination of both vestibular and visual cues. In terms of the model, perhaps the compensation signal, c, could be interpreted as the command signal which is sent via the tectospinal pathway.

5.3 Additional experiments suggested by the early response model

The proposed scheme for the generation of the early response suggests a number of additional experiments which might verify the nature of particular elements in the model. The most crucial test would be to conduct experiments analogous to those of Watt in zero g and horizontal positions using the visual field motion conditions tested in this study. Because the acceleration estimate, $\hat{a}$, would be significantly reduced in these cases relative to the actual acceleration, a, the saturation value of one g for the final estimate would result in greater range for potential enhancement by an upward moving visual field. Therefore, in these cases an upward moving field (/U condition) might be expected to significantly increase the early response magnitude for fall accelerations greater than 0.5 g.

As mentioned previously, the possible presence of an angular-to-linear visual field velocity (or acceleration) estimator could be tested by altering the distance of the pattern from the subject. If such a transformation successfully occurs, the results should be independent of distance. While extreme distances may result in a loss of visual velocity cues simply because the visual velocity threshold is not reached, it is unlikely that this would become an issue in a normal environment where nearby objects are usually present in the visual field. This idea has been invoked to explain the phenomenon of height vertigo, which is characterized by increased low-frequency postural sway (Brandt et al., 1977).

All of the experiments of the current study were obviously performed in a normal one-g gravitational field, and the hypothetical saturation level for the final estimate is also one g. By repeating these tests in hyper-g and hypo-g environments, it might be possible to determine if and how quickly the saturation value adapts to the altered gravitational field.

The effects of head tilt on the early response were not tested in the present study because it was judged too hazardous to test on humans. Similar tests with monkeys would reveal the effect of various amounts of head tilt on the early response, and might verify the appropriateness of the cos θ and $K(\theta)$ factors involved in the estimation of $\hat{a}$.

The expected value mechanism which seems to operate in the /DK and /EC conditions was hypothesized on the basis of only the current set of experiments. Further tests are necessary to verify that an expected value determination actually occurs. For example, if the 0.85G falls were eliminated from the testing sequence, the early response during the 0.5G/DK and /EC conditions should be less. The time course of the decrease would depend upon the amount of previous experience which is required as input to the expected value determination.

5.4 Synthesis of the late response

An analogous model of the late response would probably not provide as much insight as the early response model, since the processing involves higher level CNS functions which are not known in great detail. Both the visual and vestibular senses obviously contribute significant information for the synthesis of the late response, as shown by the data.

Comparisons of the responses to the five acceleration stimuli indicate that the timing of the late response consistently precedes the moment of contact. Apparently, the subject is capable of successfully monitoring the acceleration well into the fall, since the initial transient during the first 100 msec would provide inadequate information in the SDG, FDG and RG conditions where acceleration continues to change after the first 100 msec. The advantage of using the SDG, FDG, RG, and 0.5G stimuli was that they all have comparable fall durations. It is clear from even the original data that late response timing is quite different for 0.5G and 0.85G falls. If only the initial 100 msec of acceleration were monitored, the subject's projected estimate of contact time would be much different than in reality, especially for the RG and SDG profiles. Since the total integrated EMG responses to the SDG, 0.5G and RG falls are similar, the person probably monitors the changes well into the fall. Timing differences which are evident in the original data also support this idea. Compare figures 4.3.1-3. However, because the actual range of contact velocities and contact times is not great (refer to figure 4.1 on page 73), it would be difficult to determine at what time prior to contact information arrives too late to affect the response.

Visual influences on the late response tend to be quite different than visual influences on the early response. Since the early response latency is relatively constant, and the response is manifested simultaneously in numerous muscles, the effect of visual field velocity as a modulator of the amplitude can be simply characterized. However, the late response does not occur simultaneously in these muscles;

the coordination and timing are important aspects of the response. Visual influences may manifest themselves as any number and combination of parameters of the late response, including amplitude, timing, and coordination between muscles.

For example, for 0.85G falls comparison of the /U and /D conditions reveals a timing difference which causes more of the GN and SL activity to shift later into the contact period for the /D case. The fact that no noticeable habituation to these visual influences occurs suggests that vestibular information alone may not be considered sufficiently reliable as to preclude the use of other sensory modalities. If vestibular information were accurate, the subject might be expected to eventually ignore the abnormal visual information. Perhaps with longer periods of testing, subjects might eventually learn to ignore it. No indication of such habituation occurred in this study, though.

Visual effects on the late response during the 0.5G falls generally cause a reduction of the response, which is exactly the opposite of the effect on the early response. The /D condition causes a large reduction of the late response. Here, the general effect seems to be on the amplitude rather than timing. One possible explanation for the tendency to reduce the amplitude in abnormal visual conditions may be that any detection of visual motion which conflicts with the vestibular signal is recognized as a true motion of the external world. Such recognition may then reduce the influence of the vestibular cue, since it then becomes the signal whose accuracy is doubted. The possible role of cognitive processes in the late response greatly increases the number of strategies available, and any such post hoc explanation must not be taken too seriously.

5.5 Significance of results in terms of models of internal feedback during intended movement

The fact that no early response is seen during falls in which the subject initiates the release himself (Greenwood and Hopkins, 1976b) suggests that the early response may reflect the discrepancy between expected sensory input and actual input. In the present study, the subjects knew that they would be dropped within several seconds, yet even this knowledge is not sufficient to suppress the early reaction. This would be consistent with a mechanism which actually constructs the expected sensory input at the time it is expected; if the actual event occurs at the predicted moment, the actual sensory input would agree with the expected input, and any compensatory motor strategies which had been predetermined based on the expected input would proceed unchanged. In the case of falls, this latter process would correspond to the pre-contact reaction seen during self-initiated falls.

Such a concept of comparison between predicted and actual sensory input has been invoked to explain a variety of perceptual phenomena occurring during voluntary movement. The most frequently cited example is that normal voluntary eye movements do not result in apparent movement of the visual world, yet externally imposed eye movements and intended eye movements during induced oculomotor paralysis do cause apparent movement of the visual field relative to the subject. Internal feedback models to account for such phenomena have been proposed by Sperry (1950), von Holst and Mittelstaedt (1950), and Teuber (1966). Various terms have been used to describe the process, including internal feedback, efference copy, and corollary discharge. Physiological and anatomical evidence for the existence of internal feedback pathways at various levels of the CNS have been reported by Oscarsson (1967, 1970), Thach (1970a,b), and Evarts (1970a).

MacKay (1966) pointed out that perhaps the process of comparison between expected and actual sensory input should be interpreted as an evaluation rather than a simple cancellation or subtraction as had been commonly assumed. Cancellation would need to be extremely accurate in order to prevent apparent motion during voluntary eye movement and other tasks such as tactile exploration.

These internal feedback models are equally applicable to interpreting both the perceptual consequences and further motor commands arising from discrepancies between predicted and actual sensory inflow. In the present study it is a motor command in the form of the early response which may be a manifestation of the hypothetical internal feedback. The nonlinear manner in which visual and vestibular cues are combined to determine the early response magnitude suggests that MacKay's idea of evaluation rather than cancellation may be a more appropriate interpretation. In other words, both visual and vestibular cues are each evaluated conditionally upon the other, rather than estimated independently and algebraically summated. It is perhaps noteworthy that the kinds of complex evaluation of multiple sensory modes that operate in perception may also apply to certain reflexes.

To further test the idea of the internal feedback model, it would be interesting to make only certain aspects of the sensory cues unpredictable. For example, what might happen if the subject initiated the release himself, but would not know the nature of the visual field motion and/or acceleration during the fall? How would the early response be affected during unexpected falls if the subject were informed of the nature of the visual field motion and/or acceleration stimuli prior to the fall?

CHAPTER 6

SUMMARY

The results of this thesis clearly demonstrate the existence of visual influences on EMG reactions during unexpected falls. This is consistent with studies of visual influences during induced postural sway in humans (Nashner and Berthoz, 1978). It also confirms the expectations of Vidal et al. (1979) in baboons. However, the experimental conditions of this latter study did not allow definite conclusions about rapid visual effects on motor responses, since the results could be explained by the possibility that the baboon subjects could alter their responses based on visual cues detected prior to release.

During the falls, both acceleration profile and relative visual field motion were altered. EMG from surface leads over the gastrocnemius (GN), soleus (SL), tibialis anterior (TA), rectus femoris (RF), and biceps femoris (BF) was recorded and analyzed.

Most of the statistically significant effects were observed in the lower leg muscle reactions (specifically, the GN and SL leads). The major findings of the present study are outlined below:

1) EMG patterns in GN and SL leads are consistent with the patterns observed by Melvill Jones and Watt and by Greenwood

and Hopkins. The early response was found to occur to some degree in all of the muscles recorded. The late response was more variable and was generally timed to correspond to the moment of contact.

2) The early response magnitude an all five muscle leads is an increasing function of the suddenness of release (as measured by the slope of the acceleration during the first 100 msec).

3) Differences of visual field motion did affect the magnitude of the early response, but not in a manner consistent with the results of Vidal et al. (1978). It is maintained that the stimulus conditions in the present study are methodologically consistent, and therefore the interpretation of the rapid visual influences on the early response are more straightforward. The major effect seen here was that for 0.5G falls, the early response magnitude is generally increased when upward visual field motion is increased relative to the subject (compared to the normal case). This effect was not observed for 0.85G falls. Downward visual field motion (visual field stabilized relative to body) did not significantly alter the early response magnitude relative to the normal visual field condition. Late response magnitudes were diminished in the case of 0.5G falls, however.

4) Visual field motion also significantly affected the amplitude of the late response. Again, the effect was much

greater for 0.5G falls than for 0.85G falls.

5) During falls in which the eyes were closed or the room was darkened, the early response in GN and SL leads was increased for 0.5G falls and decreased for 0.85G falls compared to the normal, eyes open visual field condition. The late response was not significantly affected by these conditions. This result suggests the operation of a mechanism which uses a neurally stored, expected pattern in cases where visual information is missing.

A model for the synthesis of the early response was developed to account for the complex interactions of visual and vestibular cues. Because the early response has been shown to be primarily otolith-dependent and reflexive in nature, such a model may aid in understanding the physiological corellates of such interactions, presumably at the brainstem level. The absence of the early response in self-initiated falls further suggests that it may provide a significant clue regarding the organization of movement control.

The rapid dynamics which are necessary to account for the effect of vision on the early response are not compatible with the relatively slow dynamics of observed vestibular nuclei neurons in response to visual input, in cases where the animal is held stationary. (It is possible that these dynamics are somewhat faster when visual-vestibular conflict is reduced.) In addition, the complexity of the interactions indicate that a simple algebraic summation of visual field acceleration and gravireceptive estimates of acceleration cannot account for the results either. This precludes the possibility that visual and vestibular information are independently conveyed to the spinal motoneurone level. On the other hand, because visual and vestibular information converges in the tectum as well as in the vestibular nuclei, it is possible that units in the tectospinal tract represent a pathway for mediating rapid visual influences on spinal cord motoneurones.

By altering the acceleration profile, it was possible to determine that the early response is a function of the magnitude of the acceleration transient prior to the early response. The late response is more complicated, and both its amplitude and timing can be adjusted prior to contact in order to anticipate requirements during contact. Acceleration appears to be monitored well into the fall and incorporated into the late response, although it was not possible to determine beyond what time further information was not incorporated into the pre-contact response.

Differences in visual field conditions also significantly affected the late response. Many of the effects observed during the late response were different from those seen during the early response, and suggest that the late reaction is compensatory in nature, and is under a greater degree of voluntary control. Because of this, any interpretations of the late response from a physiological perspective are much more difficult. Instead, the results must be interpreted phenomenologically.

APPENDIX A

REVIEW OF POSTURAL TESTS OF VESTIBULAR FUNCTION

Note: Specific references with special relevance to a particular section are listed at the beginning of that section. See table B.1 on page 196 for abbreviations used in this appendix.

A.1 Advantages and disadvantages of behavioral tests

Vestibular dysfunction has long been tested by relatively simple techniques which either require the subject to maintain his balance during a number of standing and walking tasks, or involve observation of the subject's response to an externally applied disturbance to the vestibular senses. While such tasks are of value because of their simplicity, evaluation of the results is complicated by the involvement of other sensory systems in such tasks, the possibility of learning, and the complexity of the motor systems involved in making the responses. Visual, tactile, proprioceptive, and even auditory cues are important, and if subjects have disorders of any of these senses, this must be known. Humans are adaptable, clever creatures who may respond to an experimentally designed disturbance with strategies that totally obviate the need to use the particular sensory or motor capability that the experimenter is attempting to test. All of these difficulties must be considered when devising a test and interpreting the results. Another problem is that the subject's response to a particular disturbance may not be representative of "natural" strategies employed during normal activities, and, therefore, should only be used with caution to derive a more general model.

A.2 Common stimuli used to provide gross disturbances to the vestibular system

Graybiel (1974)
Kornhuber (1974a)

Rotatory, galvanic, and caloric stimuli are commonly used to induce disturbances of the vestibular system. The most common procedure for the rotation method requires rotating the subject about the vertical axis, such that the horizontal canals are approximately aligned with the plane of rotation. Since the canals act as integrating accelerometers with a finite time constant, the response decays after about 30 seconds. If the rotation is suddenly stopped, a sense of rotation will be induced in the opposite direction. Nystagmus and postural asymmetries occur, which can be recorded as a function of time. Such postural asymmetries include, for example, the tendency to rotate the torso and arms in the direction of perceived rotation.

Galvanic stimuli involve current injection into an electrode placed at or near the ear, which results in a gross discharge of the vestibular receptors. Because of the non-specific nature of the stimuli, the results are difficult to interpret beyond a simple phenomenological explanation.

Caloric stimuli allow the advantage of stimulating only one ear at a time. The stimulus strength can be adjusted simply by controlling the temperature of the water used to irrigate the ears. Water which is colder than body temperature causes convection currents in the canal fluid which are opposite to those produced by hot water. Since all three canals may be stimulated by this method, the actual direction of induced rotation is due to the combined effects of each canal, and cannot be readily deduced. Brief stimuli, however, tend to affect primarily the horizontal canals. As discussed later, many of the induced postural movements and nystagmus have predominant components in the horizontal direction.

A.3 Individual limb movements induced by vestibular stimulation

Peitersen (1974)
Fregly (1974)

Rotatory, galvanic, and caloric stimuli all result in detectable postural disturbances, but predictable, repeatable results are often difficult to obtain with many of these techniques. Often, the direction of observed postural tendencies depend on many other factors. Some of the more repeatable observations will be reviewed here.

As a general rule, laterotorsion (head-turning) in the direction of the slow phase of nystagmus accompanies nystagmus whenever it occurs, whether caused by rotatory, galvanic, or caloric stimuli. If the arms are extended forward, they also tend to drift in the direction of the slow phase. This is a less pronounced effect, and some variation occurs among subjects. Cold caloric stimuli result in lowering of the ipsilateral arm and raising of the contralateral arm as well as the lateral drifting tendency. Hot caloric stimuli cause the reverse phenomenon.

Trunk reactions must be tested while the subject is seated to eliminate the effects of the leg response. Cold caloric causes the trunk to lean ipsilateral to the stimulus, whereas hot water causes contralateral leaning.

Consistent patterns in the lower limbs have been the most difficult to obtain. During walking tests following caloric or rotatory stimuli, the speed of walking is an important parameter. During slow forward walking, a blindfolded subject drifts in the direction of the slow component of nystagmus. Fast forward walking results in a zig-zag pattern with no particular drift tendency toward a given direction. During slow backward walking, the drift is opposite to the slow component.

During in-place stepping tasks, subjects usually rotate slowly in the direction of the slow phase. However, care must be taken to eliminate a large number of other cues, which makes the test more tedious than it may seem initially. First, the subject must be securely blindfolded so that general illumination patterns in the room are not detected. Closing the eyelids is not sufficient. Then, the room must be made soundproof, or noise masking provided with headphones, to eliminate auditory directional cues. The subject must wear shoes, since a barefoot subject can detect his own thermal footprint on the floor. To test the effect on the legs, the arms should be at rest. If the arms are extended, the arm drift may cause the trunk and legs to follow.

A.4 Normal and induced sway during standing

Nashner (1970, 71, 73, 76, 77, 78)
Nashner and Wolfson (1974)

While standing, normal subjects sway predominantly in the anteroposterior plane, with some lateral sway, which can be reduced by isometrically tensing the leg muscles to provide greater stiffness. A cold caloric causes the subject to sway toward the irrigated ear whereas a hot caloric causes the opposite. Turning the head from the neutral position during standing can also alter or abolish these sway patterns.

Nashner and Wolfson (1974) used galvanic stimulation to initiate a disturbance to the vestibular system while the blindfolded subject stood on a servocontrolled platform. The platform allowed suppression of ankle proprioceptive feedback by keeping the ankle angle constant. Thus, corrective strategies were forced to rely on vestibular mechanisms. Transient postural sway in the antero-posterior direction resulted only when the head was turned and not when it was facing forward. This was construed as evidence for a head-body transformation of the descending motor commands.

EMG response in the gastrocnemius followed the onset of the galvanic stimulus with a latency of 100 msec. Torque produced by the muscle followed with a latency of 200 msec and lasted for 350 msec. In the case where no servo-control was employed, some corrective force began at 600 msec, probably due to ankle feedback. When ankle feedback was eliminated, the corrective phase did not begin until after 1100 to 1300 msec. It was concluded that ankle and vestibular information summate, instead of ankle feedback suppressing the vestibular information, since the initial phase (before 600 msec) was unaffected by the presence or absence of ankle feedback.

A.5 The tipping test

Peitersen (1974)

The tipping test requires the subject to maintain his balance on hands and knees while he is tilted head down on a platform. People with destroyed labyrinths cannot maintain their balance and will fall without the use of vision. In basal ganglia disorders, the tilt reaction is often lacking. A normal tilt response consists of an initial resistance, a passive phase during which the subject starts to fall, and a final steady state which arrests the fall and maintains stable posture. The first phase was hypothesized to originate from labyrinthine feedback of a transient nature, and the last phase was attributed to maintained otolith feedback. However, it seems more likely that the initial phase is simply due to increased muscle stiffness, or "stiction", which is characteristic of small amplitude changes of muscle length. As the stiction is overcome by gravity, muscle length rapidly increases until the final corrective phase arising from vestibular feedback. The tipping test is not used much clinically, because other tests are presumably simpler and more sensitive.

A.6 Effects of vestibular disturbances on segmental reflexes

Kots (1976)
Reschke et al. (1976)

Segmental reflexes are also affected by caloric stimulation, which is consistent with electrophysiological results demonstrating potentiation of the segmental reflexes following VST activation. Cold caloric increases the ipsilateral patellar reflex, induced by striking the tendon. Hot caloric increases the contralateral patellar reflex. The fact that the reflex response to stimulation of the posterior tibialis nerve is not increased indicates that the γ system is probably activated by the caloric stimuli, increasing the magnitude of the gastrocnemius reflex.

Prolonged exposure to weightlessness also has a significant effect on the strength of spinal reflexes. Soleus-spinal H-reflexes are potentiated during periods of zero-g and are inhibited during hyper-g (Reschke et al., 1976).

A.7 Tests of balance during walking

Fregly (1974)

Fregly has developed a series of tests requiring subjects to maintain their balance under circumstances of variable difficulty. The tasks include standing with feet in tandem heel-to-toe position (modified Romberg test), standing on one leg, walking heel-to-toe on a beam, and walking on a line on the floor. Some of the tasks were done both with eyes open and eyes closed. In addition to simplicity and objectivity of scoring, the tests were required to provide a wide range of difficulty and a high sensitivity to individual differences. By repeating the tests with eyes closed, the effect of vision can be estimated, but the presence of proprioceptive, tactile and auditory cues in addition to vestibular sensation still permits many complex interactions to occur. As a diagnostic technique, such a multidimensional analysis of a complex system may be of value, but as a research tool, it leaves too many variables unrestrained to allow an understanding of basic mechanisms. Performance in the walking tasks, especially, are susceptible to improvement by learning and depend significantly on motivation.

APPENDIX B

THE FUNCTION OF THE VESTIBULAR SYSTEM AND RELATED BRAINSTEM STRUCTURES IN THE CONTROL OF POSTURE

Note: Specific references with special relevance to a particular section are listed at the beginning of that section.

B.1 General structure and innervation of the vestibular nuclei

Brodal (1974)

Figures B.1-5 contain schematic representations of anatomical connectivity with the vestibular nuclei to which it may be useful to refer throughout the text in this appendix.

The vestibular nuclei include four relatively distinct nuclei on each side of the brainstem on the floor of the fourth ventricle. A number of smaller cell groups are also included. The term vestibular nuclei here includes the superior (SVN), lateral (LVN), medial (MVN), and descending (DVN) vestibular nuclei, the interstitial nucleus of the vestibular nerve, cell groups f, l, x, y, and z, and the nucleus supravestibularis. Of these, the LVN, MVN, and DVN are of the foremost interest for considering postural control, since these areas contribute significant descending

Table B.1. Abbreviations used in text

bvFRT	bilateral ventral flexor reflex tract
DSCT	dorsal spinocerebellar tract
DVN	descending vestibular nucleus
FRA	flexor reflex afferents
iFT	ipsilateral forelimb tract
LVN	lateral vestibular nucleus
lVST	lateral vestibulospinal tract
MLF	medial longitudinal fasciculus
MVN	medial vestibular nucleus
mVST	medial vestibulospinal tract
RST	reticulospinal tract
SVN	superior vestibular nucleus
VSCT	ventral spinocerebellar tract
VST	vestibulospinal tract

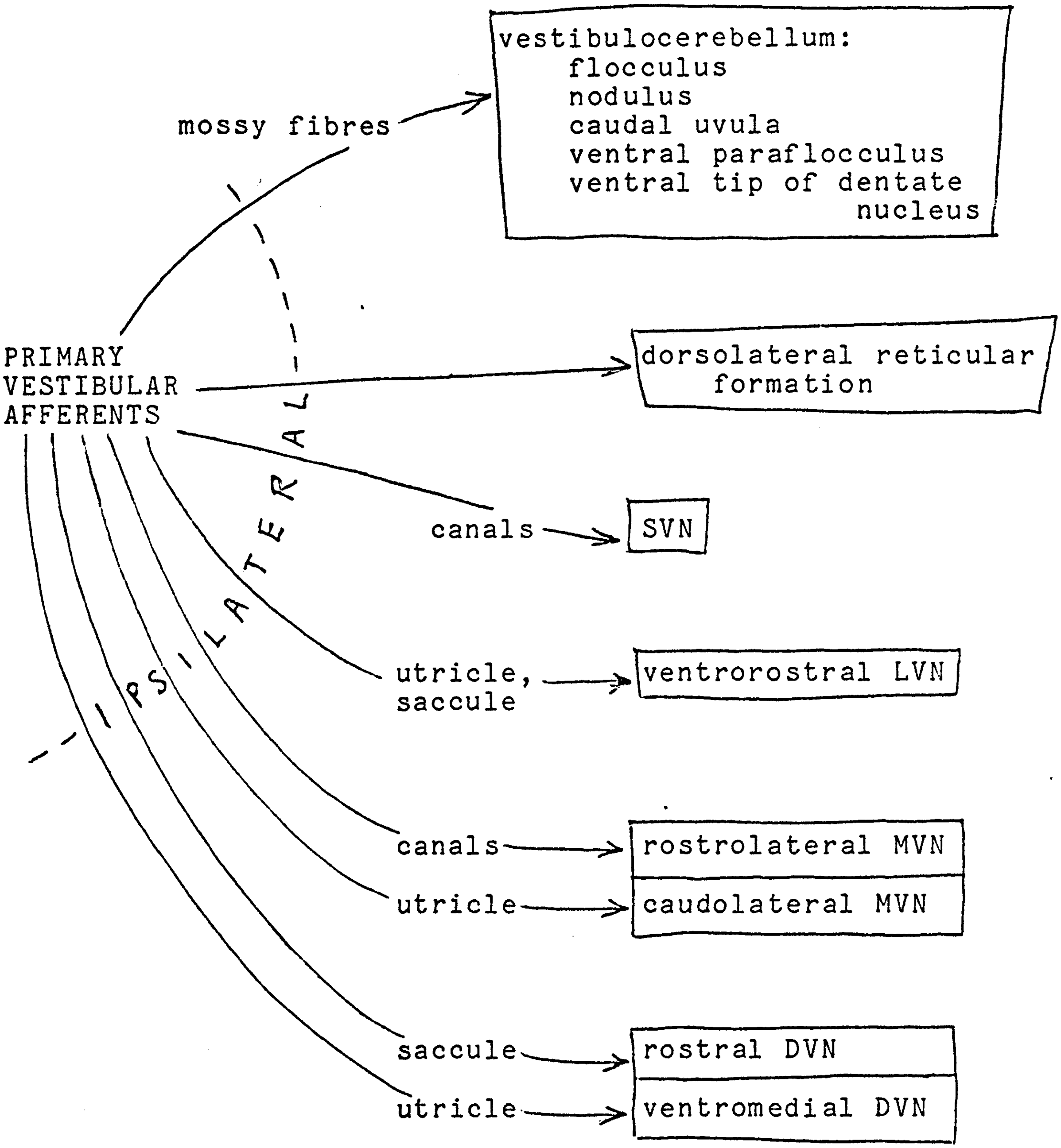


Figure B.1. Primary vestibular afferents to cerebellum.

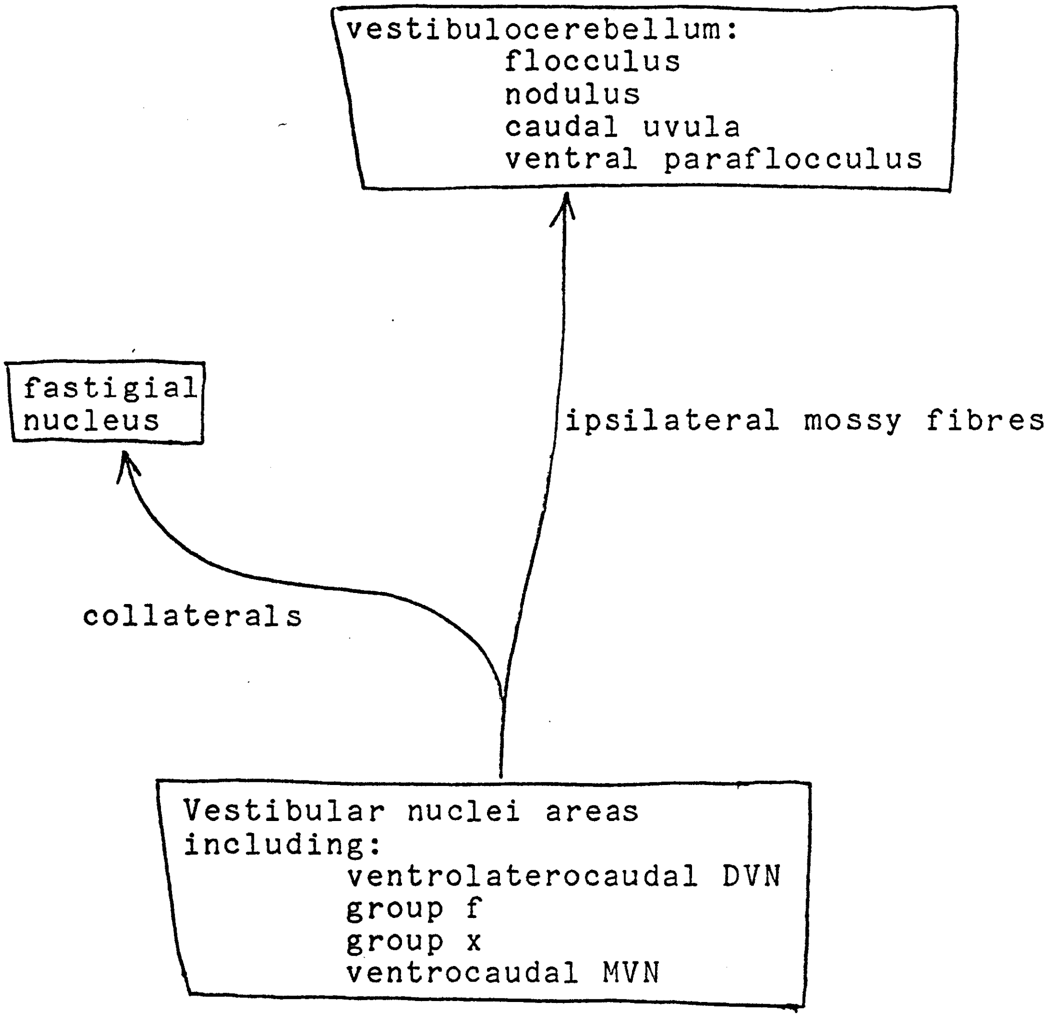


Figure B.2. Secondary vestibular afferents to cerebellum.

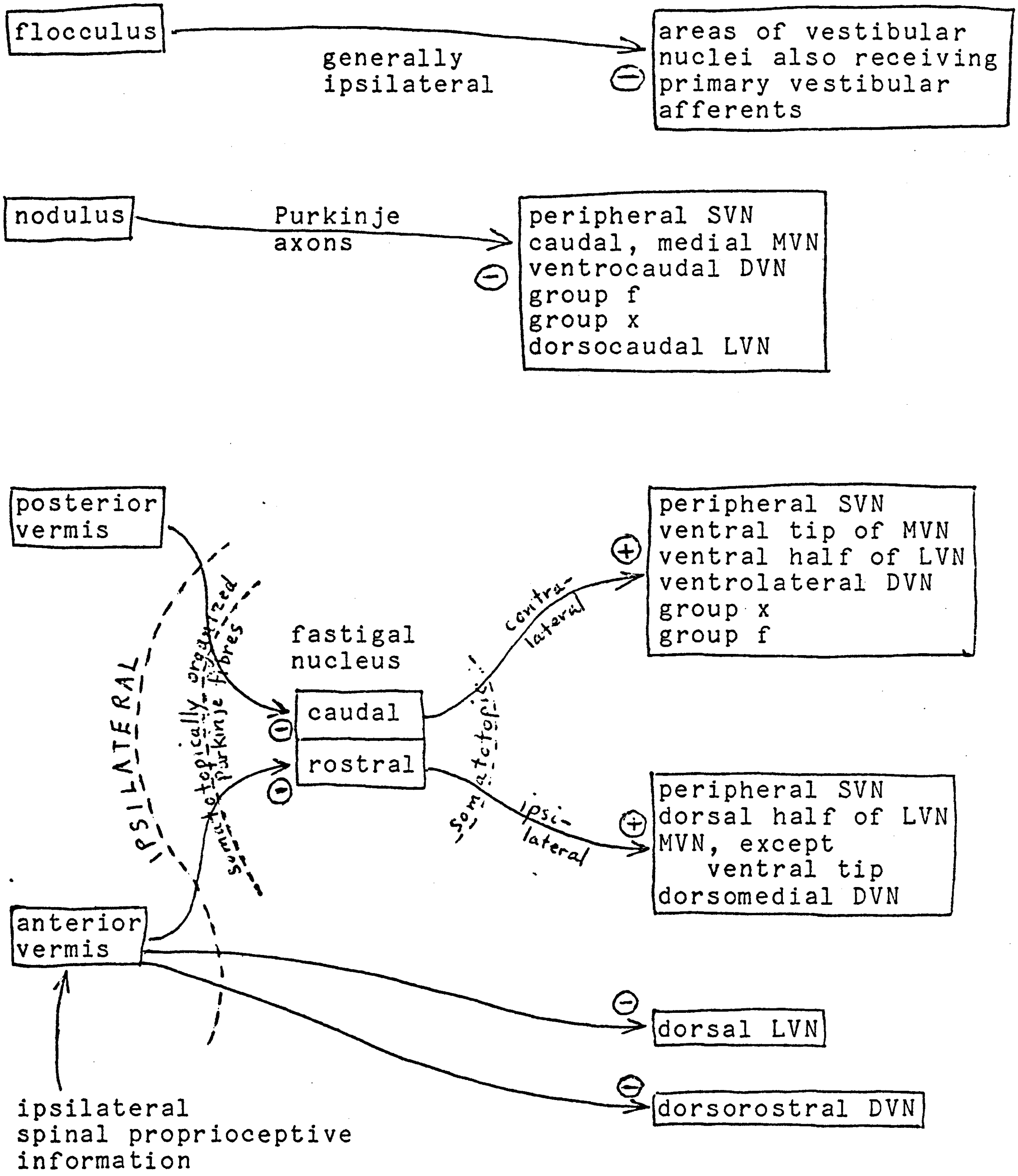


Figure B.3. Cerebellar outflow to the vestibular nuclei.

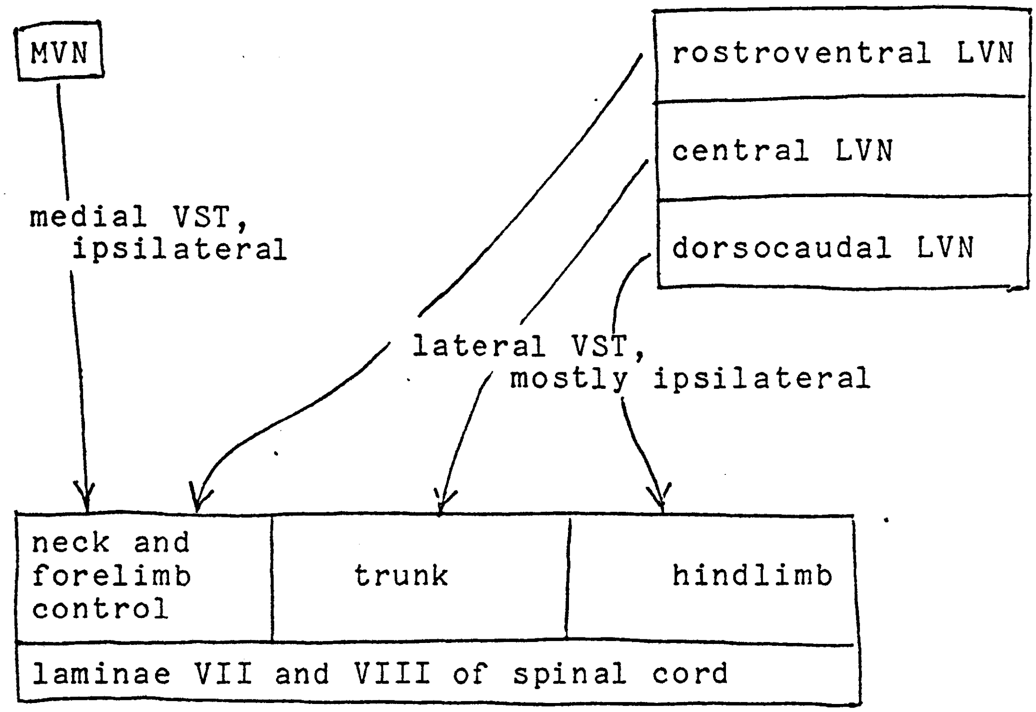


Figure B.4. Vestibulospinal tract projections.

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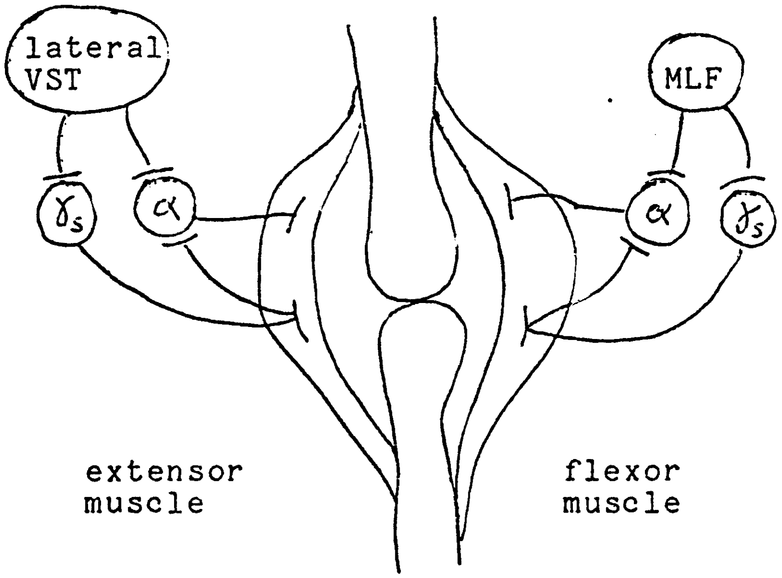

Figure B.5. Simplified representation of VST and MLF innervation pattern. All synapses shown are excitatory. (Grillner, 1969) influences on spinal motor systems. While all of the four major nuclei, except the DVN, contribute to oculomotor function via the ascending medial longitudinal fasciculus (MLF), the SVN contributes the most to this function. The SVN also relays information from the oculomotor nuclei to other vestibular nuclei and the pontomedullary reticular formation.

Each of the major nuclei can be further subdivided into functionally differentiated regions according to whether or not these regions receive primary vestibular afferents, the nature of their connections with the cerebellum and reticular formation, and connections with the spinal segments controlling neck, trunk or limb muscles. Somatotopic mapping is maintained in the LVN, the cerebellar areas relaying to the vestibular nuclei, and to a lesser degree, the MVN and DVN.

The discovery of such somatotopic mapping combined with a knowledge of vestibular afferent connections and spinal connections makes possible the conception of likely strategies for maintaining equilibrium during posture and locomotion. While more rostral CNS structures such as cortex, thalamus, and basal ganglia certainly have an important influence on motor control, the nature of their interaction with more caudal brainstem structures mediating postural reactions is not known in any detail. Therefore, in this study, the more automatic processes of posture will be interpreted primarily in terms of known spinal-vestibular-cerebellar interactions. Any experimental results requiring a more volitional explanation must be interpreted from a phenomenological perspective; this is equivalent to postulating a "black box" of relatively unknown structure which sits above the central postural stabilizer (the vestibular nuclei and associates) and provides commands which interact with the postural stabilizer. Physiologically, this translates into experimentally determined interactions between corticospinal impulses and vestibular commands, for example.

B.2 Afferent inflow to the vestibular nuclei

Precht (1974b)

Each type of afferent inflow to the vestibular nuclei usually terminates in a preferred region of each nucleus, and some types of afferents terminate predominantly in specific nuclei. The main groups of afferent fibres are: primary vestibular, cerebello-vestibular, spino-vestibular, reticulo-vestibular, and commissural fibres. Much of the afferent inflow arrives indirectly, via the cerebellum and reticular formation.

B.3 Primary vestibular afferents

Primary sensory information reaches the vestibular nuclei through the vestibular portion of the vestibulo-cochlear nerve. Low frequency stimuli, linear acceleration, and gravity primarily excite the otolith receptors; higher frequency angular acceleration stimuli excite the semicircular canal receptors. Otolith input can be further subdivided into utricular and saccular afferents. The utricle and saccule are believed to be primarily responsible for sensing gravity and linear acceleration.

Most primary afferent fibres bifurcate just before entering the vestibular nuclear complex; these bifurcations, in turn, sprout numerous collaterals. Ascending branches terminate in the SVN and ventrorostral LVN. It may be functionally significant that the rostral LVN is the "forelimb" area, relative to the efferent outflow from the LVN; the preferential termination of primary fibres in this region may indicate more direct control of the forelimbs by the vestibular system. Some primary fibres reach the dorsolateral reticular formation. Descending branches of the bifurcation terminate in the ventromedial DVN and rostrolateral MVN. No primary afferents have been shown to innervate contralateral vestibular nuclei. Areas of primary afferent terminations are not sharply delineated, but rather, are indicated by distinct gradients of afferent terminal densities.

The primary vestibular afferents can be subdivided into canal, utricular and saccular fibres. Canal afferents terminate in the SVN and rostral MVN. Utricular fibres project to the caudolateral MVN, medial DVN, and a smaller number to the ventral LVN. A relatively small number of saccular fibres reach the rostral DVN and ventral LVN. Electrophysiological recordings indicate that LVN neurons, in general, respond primarily to otolith stimulation rather than to canal stimulation. While these patterns of termination represent predominant tendencies, some higher order neurons receive input from several receptor organs, for example, saccule and canal. Both somata and dendrites of many rostral LVN neurons are contacted by terminal boutons of utricular afferents, in addition to terminals of cerebello-vestibular fibres.

B.4 Response patterns of central vestibular neurons to primary vestibular afferent input

Precht (1974)
Fernandez and Goldberg (1971, 1976a,b,c)
Goldberg and Fernandez (1971, 1980)
Fujita et al. (1968)
Schor (1974)

Both primary and many secondary vestibular sensory neurons discharge spontaneously at relatively high rates. Primaries have resting discharges of 20 per second, and second order neurons fire at rates of 2 to 30 per second. A few secondaries fire at rates up to 90 per second. While the origin of resting discharge in primary neurons is unknown, the resting discharge of the secondary vestibular neurons seems to be due to the reflex effect of convergent input from the primaries, since resting discharge ceases temporarily after section of the vestibulo-cochlear nerve. It recovers to some degree, possibly because of reflex excitation originating from other sources.

Central vestibular neurons that respond to vestibular afferent input demonstrate either a "tonic" or "kinetic" response. Of the three pairs of canals, the horizontal canals have been studied the most. For step angular accelerations in the plane of the horizontal canals, the tonic neurons respond with a gradually changing rate of firing which eventually reaches a new steady, maintained level. The threshold for a statistically significant change in impulse frequency in primary tonic neurons is 0.65 deg/sec^2, which agrees with sensation and nystagmus thresholds. Kinetic neurons do not discharge spontaneously, and have a higher threshold of about 5 deg/sec^2. Once the threshold has been reached, however, kinetic neurons are more sensitive to further increases of acceleration than the tonic neurons, which may be of functional importance for large angular accelerations.

In addition to the tonic-phasic dichotomy, vestibular neurons responding to horizontal canal stimulation may also be categorized according to whether the firing rate increases or decreases to a given direction of angular acceleration. All primary neurons in the nerve branch of the horizontal canal respond with increased discharge to utriculopetal cupula motion, and decreased discharge to utriculofugal motion. (Utriculopetal endolymph flow occurs on the right side for clockwise acceleration the horizontal plane.) These neurons are referred to as type I units and are the most common. It should be evident that because of the spontaneous discharge, such a bidirectional response is possible. Secondary neurons demonstrate several other types of responses as indicated in the following table:

	utriculopetal	utriculofugal
type I	+	-
type II	-	+
type III	-	-
type IV	+	+

The sign indicates the direction of change in the firing rate.

Primary neurons in the nerve branch from the vertical canals have higher thresholds than the afferents from the horizontal canals. In these neurons, utriculofugal cupula motion produces increased discharge and utriculopetal motion produces decreased discharge. Some secondary sensory neurons show the inverse of this pattern in response to angular motion in the vertical plane.

In response to sustained acceleration, the firing rate of a tonic neuron decreases somewhat after reaching a maximum. It is unclear whether this is due to a low frequency oscillation in the peripheral neuron response, or whether it is due to central neural habituation. The firing rate of primary neurons of the cat show some oscillation in response to an impulse in deceleration resulting from the sudden stopping of a rotating platform. In addition, higher order mechanisms may account for much of the sensory adaptation resulting during maintained accelerations.

Otolith afferents also discharge spontaneously. Most secondary vestibular neurons which respond to otolith stimulation show increased discharge during ipsilateral tilt and decreased discharge during contralateral tilt. Higher order neurons exist which show increased or decreased firing rates to both directions of tilt, analogous to the types of units responding to horizontal canal stimulation. These types of tilt neurons are often classified as follows:

	ipsilateral	contralateral tilt
type α	+	-
type β	-	+
type γ	+	+
(type δ not found)	-	-

where sign indicates direction of change of firing rate. Most of these neurons are sensitive to tilt about only one axis and are mutually orthogonal.

LVN neurons in the cat which respond to otolith stimulation have characteristic response patterns which differ in the hindlimb and forelimb regions of the nucleus. Primary vestibular afferent terminals are restricted predominantly to the forelimb region, which projects to cervico-thoracic segments. These neurons show type α responses. The hindlimb neurons, which project to lumbosacral segments, show mostly type γ responses. This has significance in terms of the observed postural reactions and will be discussed later. Most of the neurons show graded responses to varying degrees of tilt. In addition, a few LVN neurons respond transiently to tilt. This could either be caused by convergence of higher order information from the canals, or by transient neural response to changes in input from the otoliths.

Goldberg and Fernandez (1980, in the squirrel monkey) located neurons interposed between the abducens nucleus and the SVN which exert excitatory influence upon primary vestibular afferents. When these neurons of the vestibular efferent system are stimulated, the excitatory influence acts to decrease the response gain of irregularly discharging primary neurons to natural vestibular stimulation. It was proposed that such a mechanism might function to extend the dynamic range of the afferents during intended head movements, during which the accelerations are often very large.

B.5 Commissural connections

The SVN is the source of most of the commissural fibres to the contralateral vestibular nuclei. The majority of these fibres terminate in the contralateral SVN, but all of the vestibular nuclei receive some projections. The DVN also sends a significant number of fibres to the contralateral DVN, MVN, and LVN. Most of these fibres terminate in the ventral aspects of the contralateral nuclei. No primary vestibular afferents have been detected which relay to the contralateral nuclei.

Recordings of field potentials in the contralateral vestibular nuclei induced by pulse stimulation of the vestibular nerve indicate that both inhibitory and excitatory influence crosses to the other side with latencies of several milliseconds. Most of the type II neurons are influenced primarily by the contralateral labyrinth via commissural fibres. Mild stimulation of the vestibular nerve results in inhibition of contralateral type I neurons; type II neurons probably act as inhibitory interneurons upon homolateral type I neurons, mediating the stimuli from the opposite side. Kinetic type I neurons have been shown to receive monosynaptic excitation during ipsilateral vestibular nerve stimulation and disynaptic inhibition during contralateral stimulation. The general pattern for crossed inhibition for canal-type neurons is as follows: horizontal canal stimulation inhibits contralateral horizontal canal units; posterior canal stimulation inhibits contralateral anterior canal units; and, anterior canal stimulation inhibits contralateral posterior canal units. This scheme, as well as the bidirectionality allowed by spontaneous firing, enhances the range of firing rates in response to a given range of stimuli. In each case, input from the ipsilateral side is augmented by reinforcing input from the opposite side. Note that because of their position, the two horizontal canals detect rotation in a sense opposite from each other, whereas both posterior canals and both anterior canals form pairs which detect motion similarly. Each posterior canal is coplanar with the contralateral anterior canal, which explains the utility of the particular arrangement of crossed inhibition described above.

B.6 Direct spinal afferents

Rubin et al. (1977)
Ezure et al. (1978)

Direct spinal afferents to the vestibular nuclei are relatively sparse compared to the massive input from the cerebellum. Some of the direct input originates in the spinal hindlimb area, which lies below the caudal end of the column of Clarke. (Most dorsal spinocerebellar tract (DSCT) fibres arise from the column of Clarke itself.) This direct spinal projection is entirely ipsilateral, and terminates on ventrocaudal DVN, ventrolateral MVN, groups x and z, with a smaller number projecting to dorsocaudal LVN. These areas do not receive primary vestibular afferents.

The direct spinal input is primarily excitatory, but indirect spinal input via the inferior olive and cerebellum may be excitatory or inhibitory. Both the hindlimb and forelimb areas of the LVN receive indirect excitatory and inhibitory spinal input via the inferior olive and cerebellum. Most of this input arises from the ipsilateral limb, but EPSP's have been detected in responses to peripheral stimulation of the contralateral limb.

In order for vestibular sensory input to be useful for postural control, a head-body transformation must occur at some level of processing. This implies that neck afferent information must eventually converge with vestibular information either directly in the vestibular nuclei, or indirectly, by route of the cerebellum or reticular formation.

Ezure et al. (1978) showed that the neck afferents participate in the vestibulocollic reflex. Following section of dorsal roots C1 to C4, the response gain and phase of individual motor units was unchanged, but the gain as measured by the EMG response was diminished. The DC component of individual motor unit firing rates was reduced, which suggests that the deafferentation may result in fewer motoneurones participating in the reflex. Spindle afferents continued to show modulation in phase with alpha activity, indicating a pattern of alpha-gamma coactivation. Dorsal root stimulation indicated that the largest EPSP's observed in the motoneurones were mediated via polysynaptic pathways; the identity of these pathways was not determined, but the medial vestibulospinal tract was considered unlikely.

B.7 Cerebellar function in relation to the vestibular nuclei

Pompeiano (1974)
Precht (1974b)

With respect to the vestibular nuclei, cerebellar function can be divided into three convenient categories: vestibular input to the vestibulo-cerebellum, output of the vestibulo-cerebellum to the vestibular nuclei, and the spino-cerebello-vestibular pathway for indirect information from the spinal cord to the vestibular nuclei.

B.7.1 General cerebellar physiology

Bell and Dow (1967)

Before reviewing the input and output tracts of the cerebellum, a few points concerning cerebellar physiology are relevant. The cerebellar cortex is highly organized somatotopically. Any processing which the cortex performs tends to be very localized, as opposed to diffuse spread of activity. Most of the input to the cerebellum is ipsilateral, via two basic types of fibres: climbing and mossy fibres. Climbing fibres originate solely from the inferior olive and terminate on Purkinje cells with strongly excitatory synapses. All other input arrives by mossy fibres, which directly excite granule cells and can ultimately either inhibit or excite Purkinje cells due to inhibitory stellate and basket cells which may be interposed between the granule and Purkinje cells.

Purkinje cell axons, which are the only efferent connections from the cerebellar cortex, synapse primarily on the cells of the deep cerebellar nuclei, and are inhibitory. The deep nuclei also receive excitatory input from collaterals of climbing and mossy fibres. Nuclear neurons fire at very high rates, providing a generally tonic efferent outflow upon which a rate modulation is superimposed.

B.7.2 Input to the vestibulo-cerebellum

Marini et al. (1975)

Either primary or secondary vestibular afferents are not numerous compared to other cerebellar input. Primary vestibular afferents have been shown to terminate in the flocculus, nodulus, caudal uvula, ventral paraflocculus, and a small ventral edge of the dentate nucleus. Many of the secondary vestibular afferents originate in group x and ventrocaudal MVN. Areas of termination in the cerebellum are similar to the primary vestibular afferents, excluding the dentate nucleus and also including significant projections from the fastigial nucleus. All of these inputs are in the form of ipsilateral mossy fibres. Climbing fibres to the vestibulo-cerebellum from the inferior olive probably consist of indirect input from the vestibular nuclei, but the nature of such connections has not been determined.

Note that the areas of origin of most of the so-called secondary vestibular afferents do not receive primary vestibular afferents. Because of this, the secondary vestibular afferents to the cerebellum probably comprise links in a spinocerebellar pathway rather than a true secondary vestibular afferent pathway. Convergence of vestibular and somatic information probably occurs to a significant degree in the vestibulo-cerebellum; as one known example, group x receives spinal afferents and projects to the vestibulo-cerebellum.

The inferior olive is probably an important way station for convergence of spinal afferents and descending motor commands upon the cerebellum. Lesions of the olive result in poor postural symmetry and, during locomotion, result in unsteadiness and an asymmetric hindlimb gait. This suggests that the vestibulo-cerebellum may function to integrate proprioceptive information and motor commands with vestibular information in order to correct posture.

The nodulus, in particular, receives both primary and secondary otolith input. The presence of equal ratios of α and β-type units and some γ units indicates strong bilateral representation from the vestibular nuclei. By integration with oculomotor and neck afferents, nodular output may serve to regulate head and trunk position.

B.7.3 Output of the vestibulo-cerebellum

Ito et al. (1968)

Most studies to date confirm the inhibitory influence of the vestibulo-cerebellar cortex on the vestibular nuclei. This is consistent with the general principle that Purkinje cells exert inhibition, and suggests that, in some aspects, the vestibular nuclei are functionally similar to the deep cerebellar nuclei; in both cases the Purkinje cells act to modulate tonic activity of the nuclei. Purkinje cells from the vestibulo-cerebellum respond to horizontal canal stimulation with patterns similar to the various four types (I to IV) of cells found in the vestibular nuclei.

All of the vestibular nuclei receive input from the vestibulo-cerebellum, although the projection to the LVN is scanty. A general principle of organization applies here: the flocculus projects to those regions also receiving primary vestibular afferents, and the nodulus and uvula project to roughly similar regions to which the contralateral fastigial nucleus also projects. (See section B.7.5 describing fastigio-vestibular projections.) These nodular and uvular projections terminate in peripheral SVN, caudal and medial MVN, ventrocaudal DVN, group f, group x. A few fibres also project to dorsocaudal LVN.

The vestibulo-cerebellum seems to be primarily involved with oculomotor function, although it may have significance for postural regulation. Lesions in the cortex of this region result in enhancement of vestibular-induced nystagmus, the appearance of spontaneous nystagmus, and lack of habituation. Lesions of the nodulus impair otolith influence on the oculomotor system.

B.7.4 Direct projections of the spinal cerebellum to the vestibular nuclei

Ito et al. (1968)
Ito et al. (1970b)

The anterior vermis of the cerebellum, which receives mostly spinal proprioceptive information, projects to the dorsorostral DVN and dorsocaudal LVN. The spinal input to the vermis is generally ipsilateral, and the outflow from the vermis to the vestibular nuclei via the inferior cerebellar peduncle is also ipsilateral. Note that the dorsocaudal LVN to which the anterior vermis projects covers parts of both the forelimb and hindlimb regions of this nucleus.

A direct inhibitory path via Purkinje cells from anterior vermis to the dorsal LVN has been confirmed electrophysiologically, although some investigators claim to have also detected excitatory efferents to LVN neurons by stimulating anterior vermis. The conduction velocity over this pathway is 15 to 20 m/sec. Difficulties of stimulation experiments of cerebellar cortex become evident here, since a number of possibilities complicate the interpretation; the presence of basket and stellate cells in the cortex which inhibit Purkinje cells, the presence of Golgi cells which normally provide recurrent inhibition of parallel fibres, and possible antidromic activation of spinocerebellar afferents which have collaterals to the fastigial nuclei. In general, cerebellar cortex stimulation experiments are difficult to interpret.

B.7.5 Fastigial nuclei

Ito et al. (1970a)

An indirect pathway exists from the Purkinje cells in the vermal cortex to the vestibular nuclei via the fastigial nucleus. This route includes inhibitory synapses in the fastigial nucleus and excitatory synapses in the vestibular nuclei. A very specific somatotopic mapping exists for this system, also. Vermal regions of lobules I to III, corresponding to the hindlimb area, project onto the rostral pole of the fastigial nucleus. The vermis of lobules IV and V, which is the forelimb region, also projects to the rostral pole of the fastigial nucleus, but more medially than the hindlimb projection. Vermis of lobules IX (hindlinb region of posterior vermis) projects to the caudal pole of the fastigial nucleus just medially to the hindlimb area.

Most of the fastigio-vestibular fibres arising from the rostral half of the fastigial nucleus project ipsilaterally and those of the caudal half project contralaterally. The crossed fastigio-vestibular fibres terminate in the SVN, ventral tip of MVN, ventral half of LVN, ventrolateral DVN, group f, and group x. Uncrossed fibres terminate in most of the MVN except for the most ventral tip, dorsal half of LVN, and dorsomedial DVN. This pattern of innervation indicates that crossed and uncrossed fibres project to different regions with the exception of the SVN. Excitatory fastigio-reticular connections are also numerous.

Recordings from fastigial neurons in decerebrate cats during lateral tilt indicate that most units increase their firing rate during ipsilateral tilt and decrease during contralateral tilt (type α). A smaller number of β and γ units are also found. Curarization does not alter the responses, indicating proprioceptive feedback is not the cause of the observed response patterns. Many of the units seem to be velocity sensitive, as indicated by their response to a step tilt; the firing rate increases transiently, then decays to a rate which is slightly greater than the resting rate. No anatomical evidence of macular or ampullar input to the fastigial nuclei has yet been found.

The fastigial nuclei also receive input from many other sources, mostly in the form of collaterals from climbing and mossy fibres projecting to the cortex. These sources include spinal proprioceptive afferents and precerebellar reticular nuclei. The existence of fastigio-reticular positive feedback loops may help to explain the high rate of continuous firing of most fastigial units.

Electrical stimulation of the fastigial nucleus causes consistent patterns of excitation and inhibition in SVN neurons which can be independently classified as type I or type II by horizontal canal stimulation. Type I neurons are disynaptically inhibited by stimulation of the contralateral fastigial nucleus and monosynaptically excited by the ipsilateral fastigial nucleus. Type II neurons are excited monosynaptically by the contralateral fastigial nucleus, and probably function as inhibitory interneurones acting on type I cells.

B.8 Reticular formation afferents to the vestibular nuclei

Clendenin, et al. (1974)

The organization of input from the reticular formation is not known in much detail. Most of the input to the vestibular nuclei is derived from collaterals of axons projecting elsewhere. Some of the tracts which sprout collaterals to the vestibular nuclei are the RST, MLF and VST. The reticular formation is the most probable link between the vestibular nuclei and more rostral parts of the brain, as well as acting as an additional relay for spinal afferents.

B.9 Efferents from vestibular nuclei to reticular formation

Peterson and Abzug (1975)

All of the four major vestibular nuclei project to the pontomedullary reticular formation, and each nucleus has a different pattern of termination. Of these projections, only the LVN and SVN project to reticular nuclei (the lateral reticular nucleus and the nucleus reticularis tegmenti pontis) which have projections to the cerebellum. Therefore, these two reticular nuclei provide links in a cerebello- vestibulo- reticulo- cerebellar loop.

B.10 Influence of brainstem and cerebellum on spinal mechanisms

The descending motor tracts from the brainstem include the reticulospinal tract (RST) and the vestibulospinal tract (VST). The latter can be subdivided into two tracts, the lateral VST (lVST) and the medial VST (mVST), which is part os the descending MLF. These pathways transmit the results of cerebellar and vestibular processing to α and γ motoneurones primarily through interneurones in the spinal cord.

B.11 Lateral vestibulospinal tract (lVST)

Grillner et al. (1970)
Grillner (1969)
Hongo et al. (1975)
Kato and Tanji (1971)
Nyberg-Hansen (1975)
Peterson and Coulter (1977)
Peterson et al. (1978)
Pompeiano (1975)
Wilson and Yoshida (1969)

The lVST originates in the LVN and descends ipsilaterally. This tract is somatotopically organized; most fibres originating in the rostroventral LVN terminate at the cervical level (neck and forelimb segments), fibres from the central areas project to thoracic segments (trunk) and fibres from the dorsocaudal LVN project to lumbosacral segments (hindlimb). The conduction velocity of these fibres is very fast, up to 100 m/sec. Most of the fibres at all levels terminate in laminae VII and VIII of Rexed on the border of the medial motoneurone cell group. Very few fibres reach laminae IX where most of the α motoneurone cell bodies are located. However, electrophysiological experiments indicate monosynaptic contacts exist, which implies that dendritic trees of α motoneurones probably extend into lamina VIII. Polysynaptic effects are mediated through interneurones in laminae VII and VIII. Electrical stimulation of the VST monosynaptically excites knee and ankle extensor α, but rarely hip and toe extensor α. Disynaptic IPSP's have been recorded in flexor α and some hip extensor α. Some of the cells in lamina VIII send axons across the midline, which may explain the bilateral effects upon stimulation of the VST.

The LVN, which receives primarily otolith input, functions to regulate tonic labyrinthine reflexes in the neck and body. Most of the control it exerts is through VST axons which directly or indirectly contact motoneurones of axial and proximal limb musculature. Monosynaptic EPSP's can be recorded from spinal neurons with latencies as short as 3 msec, with amplitudes of 1 to 4 mV. These monosynaptic responses are shortly followed by polysynaptic potentials. As a rule, this monosynaptic excitation impinges on extensor α, and disynaptic IPSP's can simultaneously be recorded in the antagonist flexor α. This inhibition is probably mediated via Ia interneurones.

Unilateral lesions of the LVN in rats cause asymmetric posture with outward splaying of the limbs ipsilateral to the lesion, prolonged fits of rolling after tilting the body, staggering gait and tremor. The rats lie flattened against the ground, unable to lift head or body. In monkeys, lesions of the caudal LVN result in more severe postural disturbances than lesions of any other areas in the vestibular nuclei. Symptoms include head tilt and falling toward the side of the lesion. SVN lesions result in similar symptoms, except that no difficulty elevating the body occurs, suggesting that descending influence of a tonic nature is not affected as much. In all of these cases, some compensation occurs after a period of recovery. The mechanisms for regaining the necessary tonic activity are not known in detail, but it appears that the remaining areas of the vestibular nuclei somehow compensate for the lost tonic activity.

B.12 Medial vestibulospinal tract (mVST)

Grillner et al. (1971)

The mVST is less prominent than the lateral tract. The fibres originate in the MVN and descend primarily ipsilaterally with the MLF, along with fibres of the RST and interstitiospinal tract. The fact that the fibres of these tracts are so closely associated in much of the spinal cord has led to some confusion of terminology in the literature. The confusion can be partly avoided by noting that the mVST and the descending MLF are not synonomous. Stimulation of the MLF at levels above the mid-thoracic segments will result in stimulation of all of these tracts. No fibres of the mVST have been traced below mid-thoracic segments. Thus, its primary function is probably control of neck and forelimb. The fact that the forelimb areas of the LVN (but not the hindlimb area) and the MVN receive primary vestibular afferents suggests that the neck and forelimb are under more direct control of the vestibular senses than the hindlimbs. Conduction velocities of mVST fibres average 63 m/sec.

Neurons in the MVN exert monosynaptic inhibition on neck α and monosynaptic excitation on forelimb flexor α.

Electrical stimulation of the labyrinths also produces disynaptic IPSP's in neck α, probably through a relay in the MVN. See figure B.5 on page 200.

B.13 Caudal vestibulospinal tract

Peterson and Coulter (1977)
Peterson et al. (1978)

A new projection from the vestibular nuclei to the spinal cord has been discovered, named the caudal vestibulospinal tract. It projects from the caudal poles of the MVN and DVN and from the cell group f to the cervical and lumbar spinal cord. This tract is anatomically unlike the lVST and mVST since it projects bilaterally in both the ventral and dorsolateral funiculi. Conduction velocities are much slower (12 m/sec) than for the lVST and mVST. The mode of action on spinal motoneurones has yet to be determined.

B.14 Reticulospinal tract (RST)

Grillner et al. (1971)

About half of the neurons in the pontomedullary reticular formation contribute fibres to the RST, especially neurons of the nucleus reticularis pontis caudalis and nucleus reticularis gigantocellularis. This tract descends with the mVST in the MLF, but continues beyond the thoracic segments as far as the lumbosacral enlargement. Most of these fibres synapse on layers VII and VIII of Rexed. Conduction velocities range from 90 to 130 m/sec, which, like the fibres op the VST, is very fast. Electrical stimulation of the caudal pontine reticular formation evokes monosynaptic EPSP's in flexor α and some hip and toe extensor α, and polysynaptic IPSP's in extensor α and a few flexor α.

The lVST and the tracts of the MLF constitute an antagonist pair, as a rule. Stimulation of the latter causes flexor activation, and stimulation of the former causes extensor activation, with some exceptions as mentioned previously. The effects of RST activity on the lower limbs have been deduced from MLF stimulation. Although the MLF includes other tracts in addition to the RST, these other tracts do not extend below mid-thoracic segments. See figure B.5 on page 200, for a schematic of the antagonist principle of VST and MLF activation.

B.15 Control of the γ motor system

Grillner (1969)

The brainstem and cerebellum exert control of γ motoneurones which is largely independent of α control. α and γ coactivation is frequently the rule in most intentional movements. However, what has been demonstrated is that γ activation is not dependent upon α excitation, and that separate activation can occur. Monosynaptic connections from α to γ have not been found, but weak polysynaptic excitation may occur. Following selective blocking of the extrafusal endplates, γ motoneurones can still be fired by cerebellar stimulation, resulting in intrafusal spindle contractions. Normally, cerebellar stimulation will activate both α and γ. γ are probably controlled by the vestibular nuclei by mechanisms analogous to control of α units.

Lesions of the cerebellum, especially the anterior lobe, cause depression of γ activity. This depression is eventually compensated to some extent. Flexor γ tend to recover more than extensor γ, which may contribute an exaggerated flexor bias ipsilateral to the lesion. Beside abnormal posture, symptoms include hypotonia, pendular tendon reflexes and tremor. Following cerebellar lesions, the excitatory patterns of γ and the phasic α activity in response to external disturbances of limb position remains basically unchanged, although the general level of tonic γ activity is lower and the level of tonic α activity is higher. It has been postulated that one function of the cerebellum is to act as a switch, channeling excitation originating elsewhere into either α or γ activity. However, such conclusions seem highly speculative, given the degree of complexity of the strong excitatory and inhibitory effects of various neurons in the cerebellum.

The previous generalizations concerning supraspinal γ control apply to the static γ motoneurones, γ_s , since γ_s and γ_d (dynamic γ motoneurones) seem to be controlled quite differently. In the decerebrate cat, both γ_s and γ_d fire spontaneously, but after spinalization, the γ_s rate decreases, but γ_d remain unchanged. This implies that γ_s are affected by supraspinal tonic influences, whereas γ_d are activated by tonic dorsal root inflow. γ_d receive input from flexor reflex afferents, and in segmental flexor reflexes, α and γ_d are coactivated. However, this does not exclude the possibility of supraspinal γ_d control in certain circumstances.

The functional significance of the γ_s and γ_d motoneurones is that they allow adjustment of the muscle spindle velocity versus position sensitivity, as well as control of the resting discharge rate of the spindle receptors. A much simplified summary of the result of γ activation is that γ_d firing increases primary afferent (Ia) response to velocity; γ_s firing increases the resting discharge of Ia and II afferents and may decrease the velocity sensitivity of the Ia afferents.

In order to further understand the significance of the γ system, it is necessary to review the functional properties of the various somatic efferents. Ia and II afferents are present throughout the body of a muscle and are sensitive to intrafusal muscle spindle length and higher derivatives, which depend on both overall muscle length and impinging γ activity. The Ia afferents are more sensitive to velocity and can be selectively activated by vibration; the II afferents are much less affected by vibration and are primarily sensitive to position. Ia afferents respond to the onset of stretch with a transient increase and a temporary cessation of firing upon release. Muscle spindles respond to local pressure with sustained firing.

γ_d and γ_s activation has a number of specific effects on the responses of Ia afferents to stretch which are summarized below:

(1) With no γ bias, resting discharge occurs and the afferent response has a high dynamic sensitivity to unloading and some sensitivity to stretch.

(2) With γ_d drive, dynamic sensitivity to stretch increases, but dynamic sensitivity to shortening decreases.

(3) With γ_s drive, the resting discharge rate increases, and output is linearly related to length, with little dynamic sensitivity to either stretch or unloading.

(4) With both γ_s and γ_d drive, output has a high dynamic sensitivity to lengthening, but not to shortening.

Other afferents are important in motor performance and reflex regulation, but are not directly modulated by efferent control like the spindle receptors. Group Ib afferents, or Golgi tendon organ afferents, are located in tendons, in series with muscle fibres. Thus, stretch of the tendon organs acts as a measure of muscle tension, and the group Ib afferents increase their firing rates during increased tension. Ib afferents are relatively insensitive to passive muscle stretch.

In addition to muscle receptors, cutaneous and joint receptors also are important in spinal reflexes. Passive joint sense is impaired after selectively blocking the joint receptors, but position sense during active movement is not impaired. Cutaneous receptors are responsible for the flexion reflex, which excites fast flexor α units ipsilateral to the stimulus. The cutaneous receptors in the soles of the feet may be especially important in providing afferent information for postural control. Differential sensations of pressure from posterior to anterior and medial to lateral areas of the soles of the feet may provide substantial cues for body center of gravity determination.

B.16 Functional characteristics of stretch reflex

Dufresne et al. (1978)
Ghez and Shinoda (1978)
Herman et al. (1973b)
Jack and Roberts (1978)
Stein and Bawa (1976)

In order to assess the capability of segmental reflexes to provide corrective movements, a number of characteristics are crucial: afferent discharge pattern, neural time delays, tonic versus phasic motoneurone discharge, and inherent muscle stiffness (viscoelastic properties). The purpose here is not to examine the details of particular reflexes, but to establish general qualities of the segmental reflexes which will indicate the manner in which supraspinal control is likely to be exerted.

The mechanical properties of muscle may significantly contribute to "reflex" regulation of static posture during small disturbances. Studies of EMG and torque reponses of ankle muscles to small-amplitude sinusoidal displacements indicate that most of the torque can be accounted for by mechanical properties, since phase lag is independent of neural reflex activity. Peak torque was developed much more quickly than could be accounted for by reflex compensation. In addition, the frequency spectrum of the torque response to a tendon tap contains higher frequency components which are not present in the frequency response obtained from sinusoids. This suggests that nonlinear mechanical factors such as "stiction" act immediately to hinder small movements, but that as the stiction is overcome, the more linear qualities of the muscle become dominant.

For large postural disturbances, the segmental stretch reflex is insufficient to correct the position. Longer latency responses initiated by higher CNS structures provide most of the corrective action. The vestibular system initiates powerful descending control of posture during instability, but proprioception can also account for corrective action, depending upon the circumstances. Proprioceptively initiated corrections may occur either before or after vestibular corrections.

With the aid of a servo-controlled platform which could effectively alter the gain of ankle feedback from +1 (normal) to -1, Nashner was able to demonstrate the adaptability of the long latency response due to propriception. The subjects stood on the platform as a step rotation of the platform occurred. When ankle feedback was removed (gain=0), changes in ankle torque occurred 200 to 300 msec later, due to vestibular feedback. When ankle feedback gain was normal, about half of the subjects demonstrated a torque response latency of only 120 msec, which was referred to as the functional stretch reflex (FSR). The remaining subjects developed torque only after the longer "vestibular" latency. However, when ankle feedback gain was suddenly changed to -1, the subjects who responded with the FSR were destabilized.

After several more trials at a gain of -1, the FSR responses disappeared. This was interpreted as evidence for a mechanism which presets the state of segmental reflexes based on learning and an expectation of types of disturbances to be encountered. If the prediction is incorrect, then the reflex preconditioning must readapt to the new situation.

B.17 α - γ interaction during reflexes and movement

Allum (1975)
Allum and Budingen (1976)
Bizzi et al. (1978)
Burke and Eklund (1977)
Evarts et al. (1970)
Henneman (1974e,f)
Houk (1974)
Houk and Henneman (1974)
Kots (1976)
Marsden et al. (1977)
Morin and Pierrot-Deseilligny (1977)

Monosynaptic facilitation of α motoneurones by spindle afferents has long been known, but the significance of such feedback is still debated. The gain of this reflex is not high enough to develop significant force. Allum has shown that in subjects instructed to resist movement, deflection of the arm is countered by viscoelastic properties for the first 100 msec, followed by a long latency increase in force which acts to fully restore position. The reflex increase at 100 msec is probably due to the segmental reflex. The role of spindle feedback may be to activate suprasegmental centers and, also, to facilitate the corresponding α units as preparation for the descending impulses to follow. This theory is supported by the fact that many γ units have very large receptive fields, which would seem unsuitable for precise reflex control via segmental reflexes, but would be conducive to a potentiation effect upon α units by means of generalized spindle feedback.

Time delays and muscle properties combine to cause a sluggish response to corrective impulses during large disturbances. This can be compensated to an extent by velocity feedback, which is provided by the Ia afferents. However, according to experimental results, this does not stabilize or damp the response as is commonly proposed, since the relative gain at the resonant frequency is higher with velocity feedback. It was suggested that the damped oscillatory response to brief stretches is, in fact, due to such feedback and may be a source of normal tremor.

Both during voluntary and more automatic postural corrections and movements, α and γ motoneurones are coactivated. A γ bias which increases during muscle contraction allows the spindles to remain in their most sensitive region of operation. Ia afferents are ten times more sensitive to small stretches than to larger stretches, but with proper γ activation, the sensitive region can be maintained during active movements. This allows the movement to be servo-assisted, so that unexpected external disturbances can be corrected.

Most supraspinal centers which control posture and movement often exert differential control of γ_d and γ_s. Sometimes, only the γ_s are affected. The advantages of this can be appreciated by recognizing the differing requirements during various kind of activity. For example, during controlled movement, γ_s are activated and γ_d are usually suppressed. γ_d activation results in increased velocity sensitivity and is useful to regulate maintained positions, but during movement, segmental reflex excitability of the flexor reflex is not desirable and would tend to destabilize.

The administration of DOPA has been very useful in determining the patterns of activation of the γ system during movement. DOPA is an important precursor of norepinephrine, which is a neurotransmitter at many synapses in brain regions controlling locomotion, but is not found in spinal cord neurons. In the spinal cat, γ_d are reflexly excited by dorsal root afferents, but γ_s are relatively inactive. Following DOPA administration, norepinephrine is released and causes flexor γ_s activation and total suppression of flexor γ_d discharge, but excites extensor γ_s and γ_d. During locomotion, rapid flexion rather than regulatory properties of the flexors is important. The extension phase, however, must provide both movement and regulation of position. Short latency reflex effects from group II and III (cutaneous and joint) afferents are depressed, but long latency reflexes are not affected. This suggests that group II afferents may be more important for signaling muscle length rather than for facilitating spinal reflexes.

B.18 Effects of LVN and VST activity on motor activity initiated elsewhere

Gernandt (1974)
Pompeiano (1975)

The LVN exerts facilitatory influence on the myotatic reflexes of extension, which is essential for postural tone. This facilitation does not have a continuous effect on the segmental reflexes, but seems to act as a trigger, even though the impulses transmitted by the VST axons may be continuous. For example, the myotatic reflex in gastrocnemius increases in strength when preceded by VST impulses by up to 25 msec. Local reflex activity inhibits the effect of VST impulses following the reflex activity up to 15 msec, indicating that the VST impulses must act as triggers of local reflex activity, after which the segmental activity completely dominates.

During high frequency stimulation of the vestibular nerve, both flexor and extensor segmental reflexes are augmented, but a potent inhibition follows the cessation of the stimulation, which lasts for several minutes. This potent inhibitory after-effect is thought to be due to maintained firing of reticulospinal neurons. Unilateral ampullary nerve stimulation results in limb extension ipsilaterally and limb flexion and curvature of the trunk contralaterally.

VST activity also affects intersegmental reflexes. When immediately precede by stimulation of the VST, stimulation of the brachial plexus results in a much reduced lumbosacral ventral root response, which is an intersegmental proprioceptive coordination reflex. However, when the plexus is stimulated before the VST, lumbosacral ventral root response is enhanced considerably, if the interval between plexus and VST stimulation is less than 40 msec.

Another example of a somewhat complex intersegmental interaction is the inhibition of labrynthine reflexes during maintained off-center head positions. Movements of the head are normally accompanied by a transient hindlimb extensor discharge. After elimination of neck afferents, this reaction is replaced by continuous facilitation during maintained off-center head positions and inhibition of hindlimb reflexes. This suggests that the neck afferents may be responsible for inhibiting lumbosacral extensor α.

VST impulses also interact with corticospinal impulses in a manner which is very dependent on temporal sequencing. If a volley of VST impulses preceeds an evoked corticospinal impulse by 10 to 15 msec, the corticospinal response in the corresponding motor nerve is abolished. If the VST volley preceeds the corticospinal impulse by 30 msec, the motor nerve response is enhanced.

Descending tracts from the vestibular nuclei also have a degree of control over the ascending spinal afferent pathways. Stimulation of areas in the vestibular nuclei causes presynaptic afferent depolarization of Ia and Ib terminals, which results in presynaptic inhibition. The monosynaptic stretch reflex is still enhanced, though, because the depolarization of α outweighs the reduction of the afferent feedback. Similarly, stimulation of the caudal fastigial nucleus results in facilitation of contralateral γ and presynaptic afferent depolarization.

B.19 Flexor reflex interaction with the vestibular system

Anderson, Berthoz, et al. (1977)
Anderson, Soechting, et al. (1977a)
Anderson, Soechting, et al. (1977b)
Bruggencate and Lundberg (1974)
Coulter et al. (1974)
Hinoki and Ushio (1975)
Tokita et al. (1972)

The flexor reflex afferent (FRA or spinoreticular) pathway can be influenced by LVN stimulation. The effect is generally excitatory, providing a positive feedback loop to the vestibular nuclei, with inhibitory control exerted by the anterior vermis. The FRA pathway can be subdivided into two components: the bilateral ventral flexor reflex tract (bvFRT) and the ipsilateral forelimb tract (iFT). bvFRT neurons are activated by diffuse flexion of all four limbs, and can be directly modulated by descending VST activity by monosynaptic excitation. The bvFRT crosses at the segmental level and proceeds to a relay in the lateral reticular nucleus, from which efferents arise to the anterior vermis. All of these characteristics are analogous to those of the ventral spinocerebellar tract (VSCT), which terminates directly in the cerebellum. The iFT transmits similar afferent information from the forelimbs to the ipsilateral reticular nucleus, from which fibres project to the anterior vermis.

Stimulation of the LVN facilitates crossed reflexes, which are characterized by ipsilateral extension and contralateral flexion in response to noxious stimuli contralateral to the LVN stimulation. In addition, reflex conditioning of the contralateral FRA tract facilitates EPSP's ipsilateral to VST stimulation. The FRA tract, which receives input from muscle, joint and skin receptors, probably provide a major source of tonic excitability to maintain movements evoked by higher CNS centers.

Proprioceptive impulses from the lumbar and thoracic muscles to the vestibular system can become strong enough in cases of whiplash injuries and scoliosis, such that symptoms appear which are usually associated with vestibular disturbances. Such symptoms include vertigo, spontaneous nystagmus, and nausea. In these cases, righting ability may also be impaired. Procainization of the painful loci often decreases all of these symptoms and restores righting ability. These results indicate the importance of spinal input to the brainstem vestibular centers.

B.20 Sources of decerebrate rigidity

Modianos and Pfaff (1976)
Schaefer (1974)
Soechting et al. (1977)

Decerebrate rigidity has been studied extensively as a means of determining the contribution of cerebellar and brainstem mechanisms to this extreme tonic state. In the decerebrate cat, a number of sources still remain which provide an interplay of excitatory and inhibitory influences on the motor system. Total deafferentation abolishes this rigidity, demonstrating the importance of sensory feedback as a tonic source. However, post-brachial section of the cord restores rigidity to the forelimbs. This results from the release of the forelimb spinal segments from inhibitory influences arising in the lumbosacral area. If, instead of a post-brachial section, either the complete cerebellum, the anterior vermis, or the fastigial nucleus has been destroyed, a similar disinhibition results. This latter finding is difficult to interpret, since a complex interplay of inhibitory and excitatory influences occur within the cerebellum itself.

Labyrinthine input is also a source of rigidity in the decerebrate preparation. Unilateral section of the vestibulo-cochlear (eighth) nerve causes flaccidity in the ipsilateral limbs, but if the opposite nerve is also sectioned, rigidity returns, indicating that crossed inhibitory influences are important. As discussed previously, the return of spontaneous discharge in secondary vestibular neurons after eighth nerve lesions is not understood. Crossed inhibition arises from both the contralateral vestibular nuclei via commissural fibres and at the segmental level through inhibitory interneurones to the contralateral limb. Although decerebrate rigidity is not abolished by bilateral eighth nerve section, rigidity and opisthotonus are abolished in the decerebellate decerebrate cat. These effects are not significantly altered by interruption of the γ loop. Therefore, the α motoneurones are affected directly by labyrinthine influences. Apparently, the cerebellum is necessary to restore tonic activity to descending pathways after bilateral eighth nerve section.

B.21 Eighth nerve section in intact animals

Precht (1974a)
Putkonen et al. (1977)

Section of the eighth nerve in otherwise intact animals (including humans, dogs, cats, guinea pigs) results in a transient severe disturbance of equilibrium, including weakness of extensor tone of the ipsilateral limbs, spontaneous head turning toward the side of the lesion, nystagmus, tremor, and staggering gait. After several days to several weeks, depending upon the species, most of the symptoms diminish markedly, indicating neural compensation. A number of sources may be responsible for such compensation. Tactile, proprioceptive, and visual feedback assume much greater importance for maintaining balance.

Electrophysiological recordings of units in the affected vestibular nuclei indicate that spontaneous discharge, which is drastically reduced immediately following the lesion, recovers to a significant degree. During the initial post-operative stage, type II neurons ipsilateral to the lesion are not affected, since they receive their input from the contralateral vestibular nuclei. Type I responses to horizontal canal stimulation cannot be found ipsilateral to the lesion. Type I neurons are normally the most common type. In addition to the removal of the primary source of excitatory input, many type I neurons are inhibited by type II neurons, which further decreases the general level of spontaneous discharge in vestibular nuclei ipsilateral to the lesion. Eventually though, type I neurons regain a spontaneous discharge. Whether this is due to a truly spontaneous mechanism, or whether other afferent channels sprout collaterals to provide excitation is not known. The latter possibility seems unlikely, since lesions of the reticular formation do not prevent the resting discharge from returning.

B.22 Fastigial lesions and atonia

Unilateral destruction of the fastigial nucleus, similar to the effect of LVN lesions, abolishes extensor tone ipsilaterally, but increases tone contralaterally. Only the rostral pole of the fastigial nucleus needs to be lesioned in order to observe this effect. After a symmetric lesion of the contralateral fastigial nucleus, rigidity returns due to the removal of crossed inhibitory influences at the vestibular nuclei and the spinal cord.

A syndrome called crossed fastigial atonia occurs following lesion of the caudal fastigial nucleus. The symptoms are analogous to rostral fastigial lesions, except that the contralateral extensors are atonic and the ipsilateral extensors are facilitated due to release from crossed inhibition. Following fastigial lesions in general, crossed inhibitory influences are sufficient to suppress tonic activity in the disfacilitated side. The fastigial nuclei in the normal person probably function to balance and adjust interlimb inhibitory influences.

Corticobulbar Purkinje axons, in their course to the inferior cerebellar peduncle, pass just rostrolaterally to the fastigial nuclei. If this bundle, which arises from the anterior vermis, is interrupted, ipsilateral extensor tonus increases, due to release of tonic inhibition. Contralateral tonus decreases due to an increase of crossed inhibition.

B.23 Brainstem and cerebellar function during locomotion

Grillner (1975)
Hayes and Clarke (1978)
Kornhuber (1974b)
Shik and Orlovsky (1976)
Soechting et al. (1978)
Stein (1974)
Thach (1978)

To understand the issue of equilibrium control during movements, it is instructive to examine the role of descending pathways during locomotion. From studies of the spinal cat it is apparent that the basic pattern for locomotion is contained in the spinal cord itself. Supraspinal control provides the trigger to initiate movement, and once it has been started, the supraspinal controllers provide additional tonic and phasic excitation to maintain the movement and make fine adjustments in force. They do not modify the basic pattern of motion, including the timing and interlimb coordination. The descending motor pathways include the corticospinal, rubrospinal, reticuluspinal (RST) and vestibulospinal (VST) tracts.

The VST, for example, seems to exert descending control of each limb only during the extension phase. This fact is consistent with results of electrical stimulation of the VST in spinal reflexes, which depend upon the timing relative to on-going reflex activity and descending corticospinal activity. Speed of locomotion is controlled by the power developed by the limbs during the stance phase of each limb, and it is reasonable that equilibrium should be also be controlled by fine adjustment of this power during the stance phase. The bipedal locomotion of humans can be viewed as a continuously unstable process, during which a tendency to fall in one direction is countered by corrective forces developed by the extended leg such that the flexed leg will fall at an optimal pivot point. Large errors must also be accompanied by active participation of the flexed leg and the arms.

The RST, which is in many respects, the complement of the VST, exerts facilitatory influence on flexion during the flexion phase. Electrical stimulation of this tract during extension has no effect. Therefore, continuous activity in both the RST and VST might theoretically be sufficient to exert phasic control since the descending control commands are read, in a sense, only during the appropriate phase. Actually, phasic activity does occur in the RST and VST during locomotion, but such phasic activity requires an intact cerebellum.

The cerebellum is also necessary to permit termination of a movement without oscillation. This is achieved by a precisely timed contraction of antagonist muscle at the end of a movement. As a movement is initiated, the antagonists are suppressed before the agonists contract. Such coordination, together with the observed phasic activity of the RST and VST, suggests that both ascending proprioceptive cues and corticospinal impulses may be used by the cerebellum to control a switch which selectively activates the VST and RST during the appropriate phases of movement. During the initiation of locomotion, the corticospinal, rubrospinal, and reticulospinal tracts are all activated to facilitate flexion of the starting limb, while VST activity is suppressed.

APPENDIX C

EMG PROCESSOR SCHEMATIC AND SPECIFICATIONS

For a schematic of one channel of the EMG processor, see figure C.1 on page 250. All of the operational amplifiers are type μ741.

Because full wave rectification is a nonlinear process, the band-pass stage preceding the rectifier and the averaging filter following the rectifier are analyzed separately.

The gain, low pass, and high pass stages are characterized by linear transfer functions, which are listed in Table C.1 on page 251. The overall magnitude function for the band-passing preceding rectification is plotted in figure C.2 on page 252.

Following rectification, a third order averaging filter conditions the signal prior to output for sampling by the computer at 500 Hz. The overall transfer function of the averager is also listed in table C.1. The step response of the averager is plotted in figure C.3 on page 252. Butterworth filter step responses are also shown for comparison.

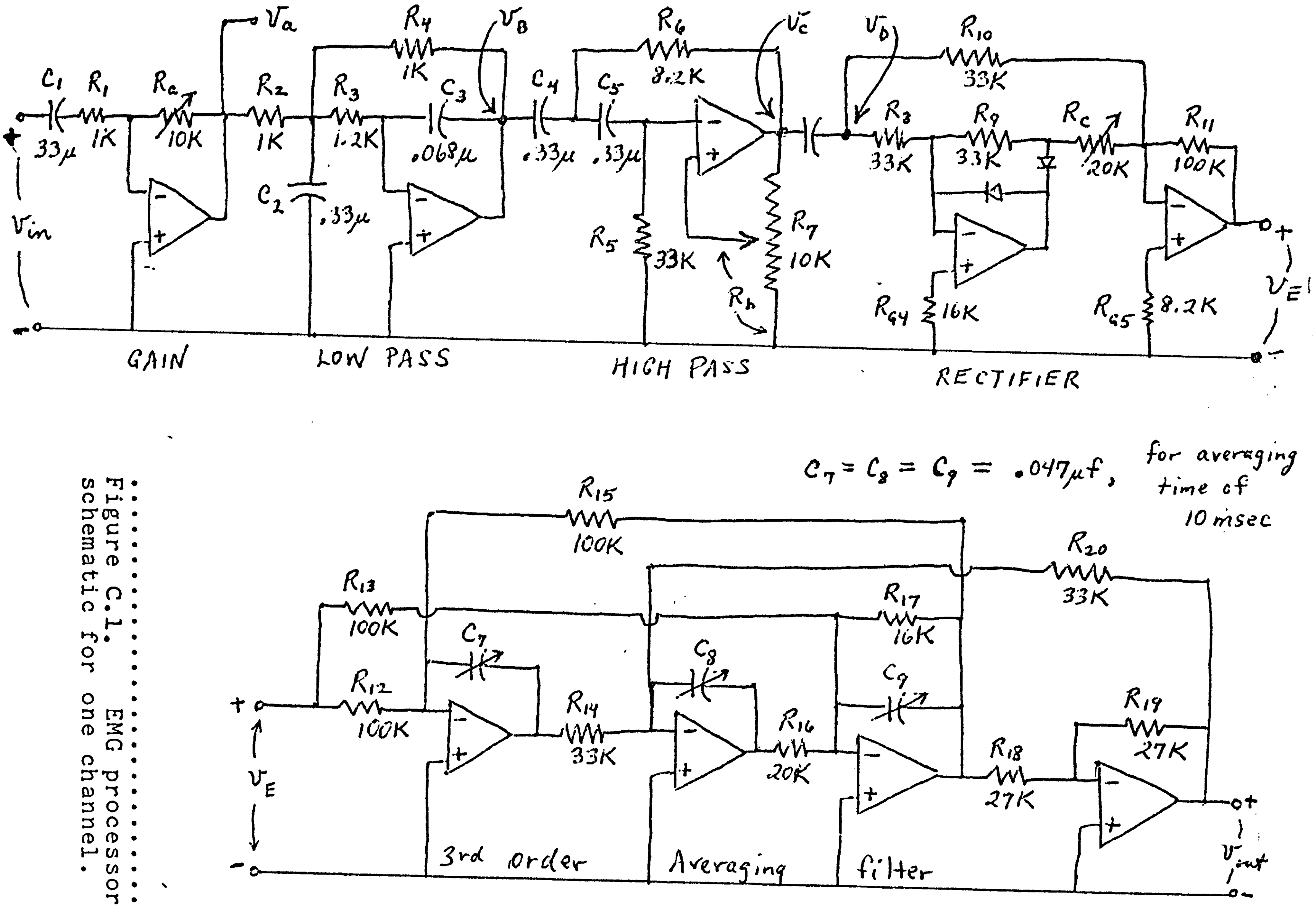

Figure C.1. EMG processor schematic for one channel.

Table C.1 Transfer functions for individual stages of the EMG processor.

……

Input gain stage

$$H_G(s) = \frac{\frac{R_a}{R_1} s}{s + 1/R_1C_1} = \frac{Gs}{s+30} \qquad 0 < G < 10$$

……

Low pass

$$H_{LP}(s) = \frac{-1/R_2R_3C_2C_3}{s^2 + \frac{s}{C_2}\left(\frac{1}{R_2}+\frac{1}{R_3}+\frac{1}{R_4}\right) + 1/R_3R_4C_2C_3} = \frac{-3.8(10^7)}{s^2 + 8.6(10^3)s + 3.8(10^7)}$$

……

High pass

$$H_{HP}(s) = \frac{s^2}{Ks^2 + \left(k\left[\frac{1}{R_6C_4} + \frac{1}{R_5C_5} + \frac{1}{R_5C_4}\right] - \frac{1}{R_6C_4}\right)s + \frac{k}{R_6R_5C_5C_4}}$$

$$= \frac{s^2}{0.85s^2 + 100s + 29(10^3)} \qquad \text{for } k = \frac{R_b}{R_7} = 0.85$$

……

High pass filtering due to C

$$H_{C6}(s) = \frac{s}{s + 1/R_8C_6} = \frac{s}{s + 1/R_{10}C_6} = \frac{s}{s+92}$$

……

Averaging filter

$$\text{for} \quad C_7 = C_8 = C_9 = C$$

$$H_{AV} = \frac{R_{12}R_{14}R_{15}R_{16}R_{17}R_{19}R_{20}C^2s^2 + R_{13}R_{15}R_{17}R_{19}R_{20}}{\left[\begin{gathered}R_{12}R_{13}R_{14}R_{15}R_{16}R_{18}R_{20}C^2s^2(R_{17}Cs+1) \\ + R_{12}R_{13}R_{14}R_{15}R_{17}R_{19}Cs \\ + R_{12}R_{13}R_{17}R_{18}R_{20}\end{gathered}\right]}$$

$$= \frac{2T^2s^2 + 120}{T^3s^3 + 12T^2s^2 + 60Ts + 120} \qquad \begin{array}{l}\text{averaging} \\ \text{time,} \\ T = 2(10^5)\frac{\text{sec}}{\text{farad}} \cdot C\end{array}$$

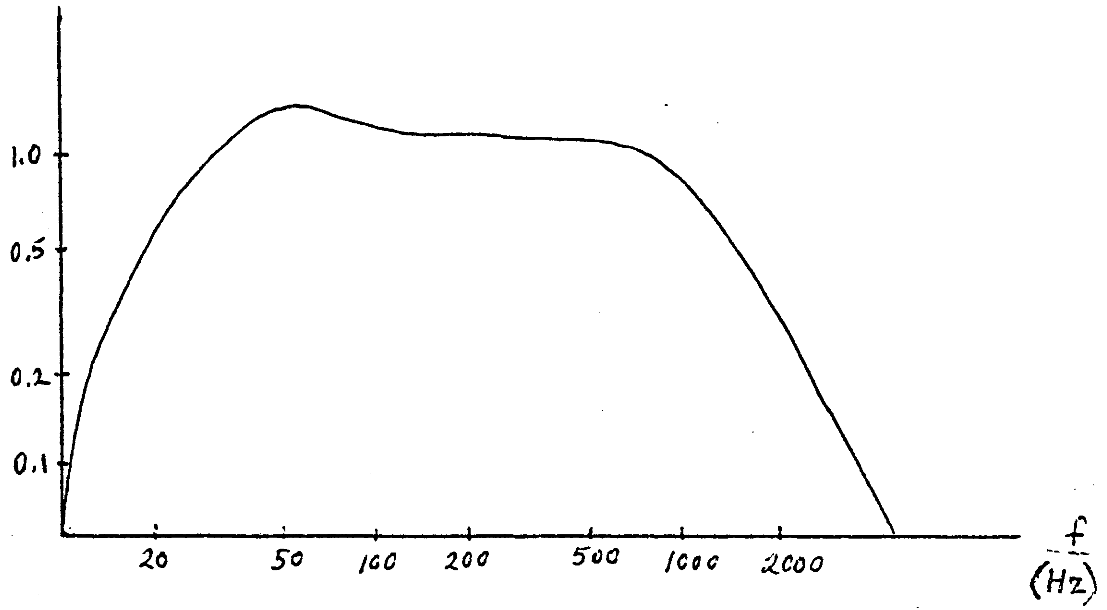

Figure C.2. Magnitude plot for bandpass stage of EMG processor

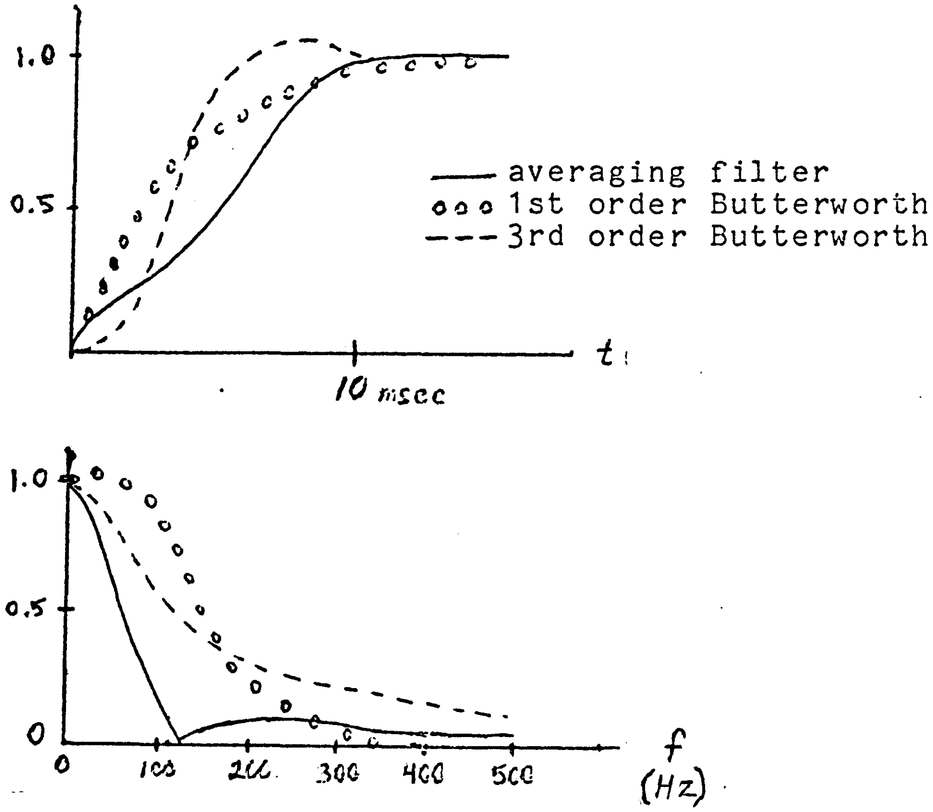

Figure C.3. Step response of third order averager compared to Butterworth filters.

APPENDIX D

STATISTICAL ANALYSIS PROCEDURE

Assuming that some measure, X_{rbc}, is obtained from the data for a given subject, block, and drop test, this measure can be modelled as a sum of components contributed by each source of variation:

$$\begin{aligned}(X_{rbc}-\overline{X}) = {} & (\overline{X}_{rb\cdot}-\overline{X}_{\cdot b\cdot}) + (\overline{X}_{\cdot b\cdot}-\overline{X}) + (\overline{X}_{\cdot\cdot c}-\overline{X}) \\ & + (\overline{X}_{\cdot bc}-\overline{X}_{\cdot b\cdot}-\overline{X}_{\cdot\cdot c}+\overline{X}) \\ & + (X_{rbc}-\overline{X}_{rb\cdot}-\overline{X}_{\cdot bc}+\overline{X}_{\cdot b\cdot})\end{aligned}$$

$(X_{rbc}-\overline{X})$ = total deviation from mean for entire experiment

$(\overline{X}_{rb\cdot}-\overline{X}_{\cdot b\cdot})$ = variation due to differences between individuals

$(\overline{X}_{\cdot b\cdot}-\overline{X})$ =variation due to differences between blocks (effect of testing sequence)

$(\overline{X}_{\cdot\cdot c}-\overline{X})$ = variation due to parameters of the fall

$(\overline{X}_{\cdot bc}-\overline{X}_{\cdot b\cdot}-\overline{X}_{\cdot\cdot c}+\overline{X})$ = block by column interaction term

$(X_{rbc}-\overline{X}_{rb\cdot}-\overline{X}_{\cdot bc}+\overline{X}_{\cdot b\cdot})$ = remainder term

Since each block uses a different group of subjects, b x r, r x c, and r x b x c interactions are meaningless for the split plot design. Thus, the corresponding terms are absent from the model.

Each component of the additive model gives rise to a variance estimate. (All cross product terms can be shown to vanish.) The formulas for these estimates are given in Table D.1 on page 256 (McNemar, 1969). The expected values of these estimates are also given.

In order to prevent spurious detection of "significant" F-test values, those F-tests which are suspected to be significant must be chosen beforehand, along with appropriate levels of significance. Any such tests performed a posteriori must attain a higher level of significance to compensate for the fact that among a large number of F-tests, several tests are more likely to exceed the significance level even though the null hypothesis may be true.

If N F-tests are performed after the data has been collected, and a level of significance, P_S, is desired, then the level of significance, P, at which each individual test must be performed must be determined as follows:

$$P_s = \text{Prob}\left\{\begin{array}{l}\text{m or more tests out of N} \\ \text{will exceed the sigificance} \\ \text{level}\end{array}\middle|\begin{array}{l}\text{null} \\ \text{hypothesis} \\ \text{is true}\end{array}\right\}$$

$$= 1 - \sum_{k=0}^{m-1} \binom{N}{k} P^k (1-P)^{N-k}$$

$$\text{for } m=1: \quad P_s = 1-(1-P)^N$$

Therefore, the criterion for P becomes:

$$1-(1-P)^N \leq P_{s,max}$$

$$\text{or, } \log(1-P) \geq \frac{1}{N}\log(1-P_{s,max})$$

where $P_{s,max}$ is the maximum significance level tolerated. For example, if N= 20 and $P_{s,max} = 0.05$,

$$\log(1-P) \geq \frac{1}{20}\log(0.95) = -0.0011$$

$$P \leq 0.0025$$

This last constraint requires choice of a standard P value of 0.001.

From the expected values of the variance estimates in Table D.1, it can be seen that the relevant F-test ratios are:

Table D.1. Variance estimates for main and interaction terms of three way split plot experimental design.

variance estimate	sum of squares / #deg. of freedom	expanded formula for computation	E[s] =expected value
$S_i^2 =$	$\dfrac{C\sum_r\sum_b\left(\overline{X}_{rb\cdot}-\overline{X}_{\cdot b\cdot}\right)^2}{B(R-1)}$	$= \dfrac{\frac{1}{C}\sum_r\sum_b S_{rb\cdot}^2-\frac{1}{RC}\sum_b S_{\cdot b\cdot}^2}{B(R-1)}$	σ_i^2
$S_b^2 =$	$\dfrac{RC\sum_b\left(\overline{X}_{\cdot b\cdot}-\overline{X}\right)^2}{B-1}$	$= \dfrac{\frac{1}{RC}\sum_b S_{\cdot b\cdot}^2-\frac{1}{RBC}S_{\cdot\cdot\cdot}^2}{B-1}$	$\sigma_i^2+\frac{RC}{B-1}\sum_b A_b^2$
$S_c^2 =$	$\dfrac{RB\sum_c\left(\overline{X}_{\cdot\cdot c}-\overline{X}\right)^2}{C-1}$	$= \dfrac{\frac{1}{RB}\sum_c S_{\cdot\cdot c}^2-\frac{1}{RBC}S_{\cdot\cdot\cdot}^2}{C-1}$	$\sigma_e^2+\sigma_{rc}^2$ $\frac{RB}{C-1}\sum_c A_c^2$
$S_{bc}^2 =$	$\dfrac{R\sum_b\sum_c\left(\overline{X}_{\cdot bc}-\overline{X}_{\cdot b\cdot}-\overline{X}_{\cdot\cdot c}+\overline{X}\right)^2}{(B-1)(C-1)}$	$= \dfrac{\frac{1}{R}\sum_b\sum_c S_{\cdot bc}^2-\frac{1}{RC}\sum_b S_{\cdot b\cdot}^2-\frac{1}{RB}\sum_c S_{\cdot\cdot c}^2+\frac{1}{RBC}S_{\cdot\cdot\cdot}^2}{(B-1)(C-1)}$	$\sigma_e^2+\sigma_{rc}^2$ $+\frac{R}{(B-1)(C-1)}\sum_b\sum_c A_{bc}^2$
$S_h^2 =$	$\dfrac{\sum_r\sum_b\sum_c\left(X_{rbc}-\overline{X}_{rb\cdot}-\overline{X}_{\cdot bc}+\overline{X}_{\cdot b\cdot}\right)^2}{B(R-1)(C-1)}$	$= \dfrac{\sum_r\sum_b\sum_c X_{rbc}^2-\frac{1}{C}\sum_r\sum_b S_{rb\cdot}^2-\frac{1}{R}\sum_b\sum_c S_{\cdot bc}^2+\frac{1}{RC}\sum_b S_{\cdot b\cdot}^2}{B(R-1)(C-1)}$	$\sigma_e^2+\sigma_{rc}^2$

Definitions: $S_{\cdot b\cdot}^2 = \left(\sum_r\sum_C X_{rbc}\right)^2$, etc.

$\sigma_i^2 =$ true individual variance

$\sigma_e^2 =$ measurement error

$\sigma_{rc}^2 =$ variance due to non-zero rxc interaction

$A_b = (\mu_{\cdot b\cdot} - \mu_{\cdot\cdot\cdot})$

$A_c = (\mu_{\cdot\cdot c} - \mu_{\cdot\cdot\cdot})$

$A_{bc} = (\mu_{\cdot bc} - \mu_{\cdot b\cdot} - \mu_{\cdot\cdot c} + \mu_{\cdot\cdot\cdot})$

$\mu =$ true mean

$\frac{S_b^2}{S_i^2}$, which tests for significant differences due to testing sequence

$\frac{S_c^2}{S_h^2}$, differences due to drop test parameters

$\frac{S_{bc}^2}{S_h^2}$, differences due to b x c interaction (testing sequence by drop test)

If results of a particular F-test indicate insignificant main block effects and insignificant block by column interaction, then columns may be averaged over all blocks and subjects, then columns may be averaged over all blocks and subjects, and F-tests performed between columns. However, since significant block (testing sequence) and block by drop test interactions are likely, column average F-tests should be interpreted with caution.

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