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Monosynaptic reflexes in falling man

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SUMMARY We have examined peripheral proprioceptive input during fall in man. The first 80 ms of unexpected free fall, both in a parachute harness and while seated, has been studied using the monosynaptic Hoffman (H) and Achilles tendon (T) reflexes. Facilitation of the H reflex begins about 30 to 40 ms after release, representing the onset of motor neurone facilitation before the electromyographic activity which begins about 80 ms after release. Earlier facilitation of the T reflex may represent spindle excitation due to change in muscle shape as suggested by Matthews and Whiteside (1960), but the T reflex inhibition described by these authors after 50 ms of seated fall is probably a purely mechanical phenomenon.

In 1971 Melvill Jones and Watt described the EMG activity of gastrocnemius in response to an unexpected fall in man. They found that muscle activity began with a latency of about 74 ms independent of height, using falls from up to 200 mm. We have amplified and extended their observations (Greenwood and Hopkins, 1974, 1976 a, b), and found that muscle activity began with a latency of about 81 ms in soleus during falls from up to 1200 mm. We also found that, during falls lasting longer than about 200 ms, the initial burst of muscle activity was followed by a second peak of activity timed to occur before the moment of landing whether the duration of the fall depended on the height or the acceleration of the fall. We showed that the vestibular apparatus probably plays a large part in the genesis of the initial peak, and contributes towards the timing of the second peak.

Matthews and Whiteside (1960) studied changes in the tendon (T) and Hoffman (H) reflexes in subjects seated in a drop chair. This consisted of a chair guided by vertical tubes between floor and ceiling, released by an electromagnet, and decelerated by pneumatic rams. They found that both these monosynaptic reflexes were depressed between about 50 and 100 ms after release. They suggested that change in muscle shape, induced by release, caused a reduction of proprioceptive inputs and consequent decrease in monosynaptic reflexes.

H reflex activity reflects the excitability of alpha motor neurones at a spinal level, bypassing muscle spindles (Paillard, 1955). Since muscle activity in soleus begins about 80 ms after release from a hanging position, we thought it unlikely that H reflex activity was inhibited between 50 and 100 ms after release, even during seated falls. However, it seemed reasonable that the T reflex was depressed due to spindle deformation upon release. We have, therefore, examined the T and H reflexes during fall from a hanging and seated position. We have not found any indication that either of these monosynaptic reflexes are depressed during this period; indeed they appear to be facilitated. Reasons for this and the apparent variance of our results with those of Matthews and Whiteside are discussed.

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Methods

The apparatus used to suspend subjects, to time release and landing, and to record EMG activity and joint angle during the drop have been previously described (Greenwood and Hopkins, 1976 a, b). In brief, subjects were suspended in a parachute harness through a system of pulleys from a metal plate attached to an electromagnet. When the current in the magnet was switched off an unheralded fall occurred. In other experiments the subject was suspended in a chair with a platform attached to support the feet.

The H reflex was elicited by an 8 mm silver/silver chloride surface electrode placed over the popliteal nerve as the cathode, and a metal plate strapped to the thigh as the anode. Similar electrodes were used to record the evoked muscle responses. These were placed approximately 20 mm apart over the lower part of the soleus muscle. Monopolar rectangular current pulses of 0.5 ms in duration were delivered *via* a Devices stimulator type 3072 at intervals of more than ten seconds. In some experiments, stimuli eliciting maximal H responses were used. In other experiments, the stimulus amplitude while the subject was suspended was adjusted to elicit a response about 25% of the amplitude of the maximal H response obtained while suspended. Thus both facilitation and inhibition of the motor neurone pool during fall could be examined. The amplitude of the M wave (the direct motor response) served as a control for constancy of the stimulus amplitude before and during fall; experiments in which the M component varied in amplitude were not used in the analysis of the results. Timing of events was controlled by a Devices Digitimer 3290.

Tendon reflexes were elicited by means of a spring-loaded hammer held away from the Achilles tendon by a solenoid. The apparatus was supported on a frame strapped to the leg (Fig. 1). When the current to the solenoid was switched off by a relay operated by the Digitimer, a tendon tap was delivered with a delay of about 10 ms. The moment of delivery of the tendon tap was indicated electrically by contacts located on the hammer and tendon.

In some experiments, auditory and visual cues of release were excluded as described in a previous paper (Greenwood and Hopkins, 1976b). Subjects were aged 30–40 years. The numbers of subjects in each group of experiments are given in the appropriate section below. The Ethical Committee of St. Bartholomew's Hospital approved these experiments and subjects gave their informed consent.

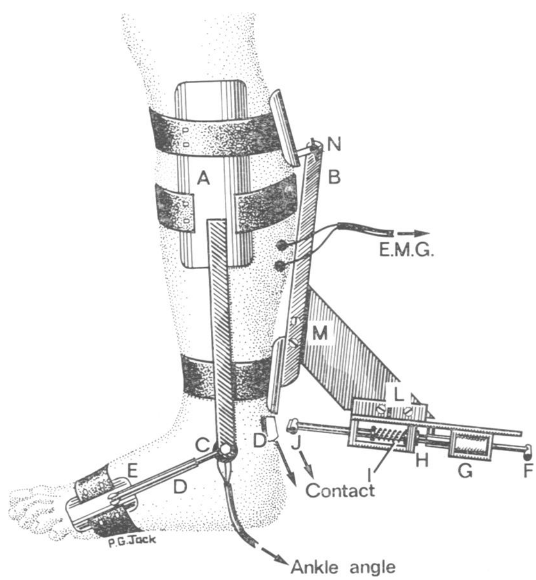

Fig. 1 *Apparatus used to measure ankle angle and to deliver a tap to the Achilles tendon. Potentiometer C, which measures the angle at the ankle, is supported lateral to the lateral malleolus by metal plates A and E strapped to the leg and foot. Piston D prevents stress of the potentiometer due to abduction and adduction of the foot. The tendon tap is delivered by spring-loaded hammer J which makes electrical contact over the Achilles tendon at D. After energising the solenoid G, the hammer is pulled back by handle F, compressing spring I against end-stop H. The apparatus is supported on the leg by means of frame B which is adjustable in three planes at L, M, and N.*

Results

As described previously (Greenwood and Hopkins, 1976a), EMG activity in soleus began about 80 ms after the onset of free fall when the subject was suspended in a parachute harness. During seated falls, EMG activity in soleus also began about 80 ms after release.

We found that during falls in the harness with the feet hanging freely, *dorsiflexion* of the foot of up to 20° occurred at the same time as, or before, the onset of EMG activity. Conversely, during seated falls, *plantarflexion* of up to 20° occurred, again before the onset of EMG activity (Table and Fig. 2). As electromechanical coupling time is of the order of 30 ms (Melvill Jones and Watt, 1971), it appears that movement at the ankle joint during either type of fall must be due to factors other than active contraction of muscle.

Table *Timing of soleus EMG activity and movement of the foot during unexpected free falls in harness and while seated*

Type of fall	*Direction of movement*	*Onset of EMG (ms)*	*Onset of movement (ms)*
In harness	Dorsiflexion	81.6 ± 1.0	78.3 ± 5.3 (range 60–100)
Seated	Plantarflexion	83.2 ± 3.1	48.6 ± 8.3 (range 40–70)

THE H REFLEX

Harnessed falls

The subjects had no difficulty in relaxing in the harness. As long as there was no distraction of the subject and the interstimulus interval exceeded 10 seconds, the H response was of nearly constant amplitude with repeated identical control stimuli while hanging. A stimulus was given either immediately upon release, or at 10, 20, 30 ,40, 50, and 60 ms after release. Three falls were performed at each stimulus interval in each subject. With five subjects the stimulus was submaximal, the intensity being adjusted to elicit a con-

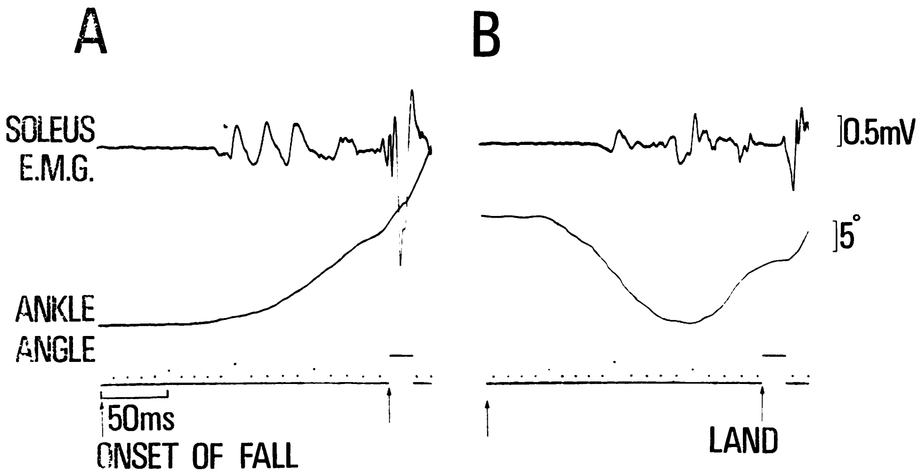

Fig. 2 *Soleus EMG and ankle angle during falls in a harness (A) and while seated (B). Calibration: EMG 0.5 mV; ankle angle 5°, dorsiflexion up, plantarflexion down.*

trol H response while hanging which was about 25% of the maximal H response while hanging. In experiments with five other subjects, the stimulus elicited the maximal H response while hanging. In both, the stimulus was kept at the same intensity for the subsequent fall. It should be noted that, in effect, each experiment was one of a pair. The M response obtained with a chosen stimulus while suspended was compared carefully with the subsequent M response evolved by the same stimulus during the fall. If there was any difference that experiment was discarded.

Experiments using a stimulus which elicited a submaximal H response while hanging showed that there was little change in the H response during fall for stimuli given up to 30 ms after release. After this there was considerable facilitation (Fig. 3). This facilitation occurred before there was any detectable movement at the ankle joint. In one subject, exclusion of auditory and visual cues of release did not alter the timing or the amplitude of the facilitation.

Experiments using a stimulus which elicited a maximal H response while hanging showed that the H response resulting from stimuli delivered before about 30 ms of fall were much the same as control H responses while hanging. Using a stimulus which elicited a maximal H response while hanging, H responses elicited after about 30 ms of fall showed considerable variation. In some subjects there was facilitation, in others inhibition (Fig. 4). The average response for five subjects, using a stimulus which evoked a maximal H response while hanging, showed no significant change in the H response while falling.

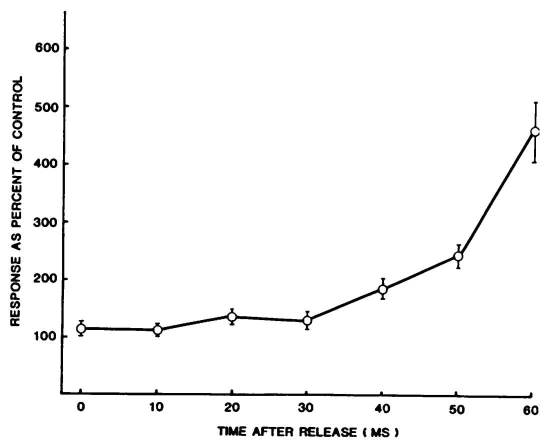

Fig. 3 *H reflex delivered between 0 and 60 ms after onset of harnessed falls. Control H response while hanging is 25% of maximal H response while hanging. Abscissa: time after release (ms). Ordinate: test response while falling as a percentage of control value. Each value is the mean of three falls in each of five subjects; vertical bars indicate one SE.*

Seated falls

Three subjects were studied during falls while seated with the feet supported on a foot rest. In these experiments the stimulus was always submaximal so that the control H response while hanging was 25% of the maximal H response. A stimulus was delivered immediately upon release or at 10, 20, 30, 40, 50, 60, and 70 ms after release. The results were similar to those found during harnessed fall: H reflexes resulting from stimuli delivered after about 40 ms of fall showed considerable facilitation (Fig. 5). There was never significant inhibition of the H reflex. In some

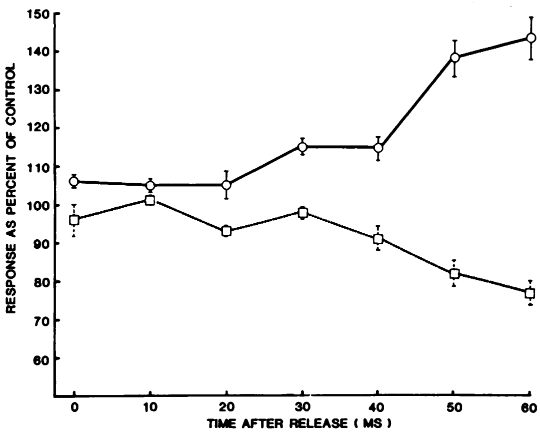

Fig. 4 *H reflex delivered between 0 and 60 ms after onset of harnessed falls in two subjects. Control H response while hanging is 100% of maximal H response while hanging. Abscissa: time after release (ms). Ordinate: test response while falling as a percentage of control value. Each value is the mean of three falls; vertical bars indicate one SE.*

experiments significant facilitation occurred before any movement of the ankle joint.

THE T REFLEX

Harnessed falls

The T reflex could not be elicited during suspension in the harness because the foot hung in a plantar flexed position, and the Achilles tendon was relaxed. In this series of experiments, slight tension was applied to the Achilles tendon by a line tied between the foot and knee, but the foot remained slightly plantarflexed. Tendon reflexes were then easily elicited during suspension. With the foot in this position, during fall, plantarflexion rather than dorsiflexion took place at the ankle 80 to 100 ms after release. These experiments were uncomfortable for the subject because the foot fouled the mechanical hammer on landing. Thus only twelve falls in two subjects were performed, the stimulus being delivered at either 10, 30, 60, or 70 ms after the onset of fall. The T reflex was found to be facilitated on all occasions (Fig. 6). The increase in amplitude ranged from 50 to 400 per cent.

Seated falls

Tendon reflexes were easily obtained while seated with the feet supported at a right angle on a foot rest. A tendon tap was delivered at either 10, 20, 30, 40, 50, 60, 70, or 80 ms after release. As with the harnessed falls, there was facilitation at 30 and 40 ms after release. However, after the onset of plantarflexion at about 50 ms after release, there was marked inhibition of the tendon jerk, and after 60 ms it was virtually

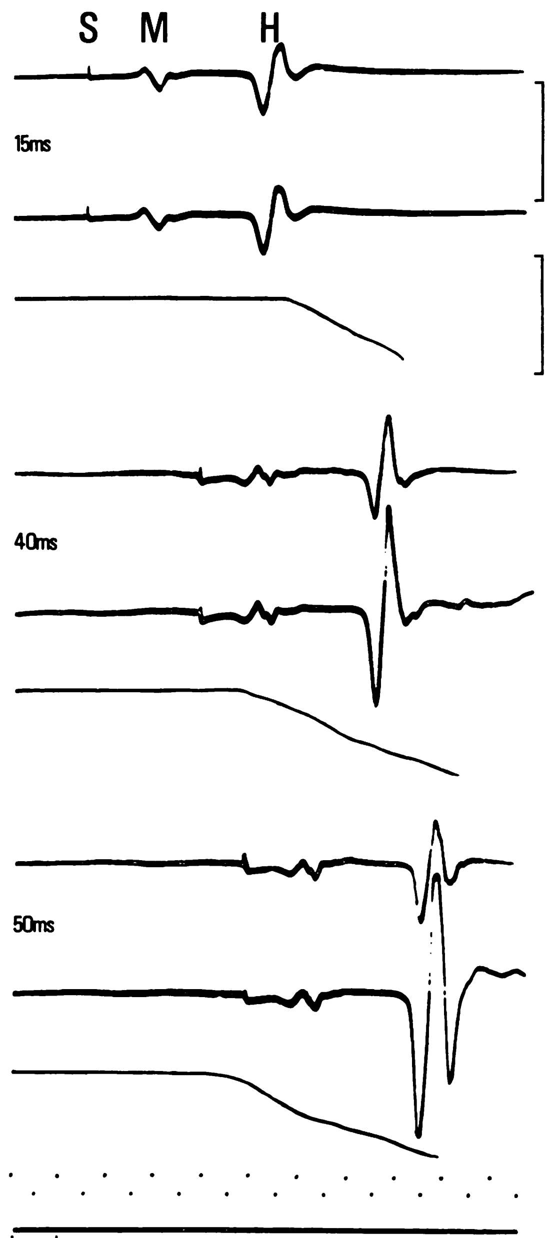

Fig. 5 *H reflex delivered 15, 40, and 50 ms after onset of seated falls. Control H response while hanging is 25% of maximal H response while hanging. For each set of three traces, upper trace is the control response, middle trace the test response while falling, and lower trace ankle angle while falling. Note that there is no change in the M response in each pair of traces. Calibration: action potential 0.5 mV; ankle angle 10°, plantarflexion down; time scale 10ms. S—stimulus; M—direct motor response; H—monosynaptic H reflex response.*

absent (Fig. 6). Since plantarflexion of the foot occurs at about the same time as the tendon reflex becomes unobtainable, we thought that the absence of the tendon reflex might be due to shortening of the Achilles tendon. A further experiment was, therefore, performed in which the foot was strapped firmly to the foot rest so that no recorded movement took place at the ankle during fall. The T reflex was then obtained with ease between 40 and 80 ms after release (Fig. 6). Plantarflexion of only two degrees due to inadequate strapping was associated with a partial or complete suppression of the T reflex.

Discussion

We found that, during falls in the harness, the H reflex was facilitated if delivered after about 30 to 40 ms of fall. This facilitation occurs well before any movement at the ankle, which hangs passively plantarflexed by gravity until dorsiflexion begins at about 80

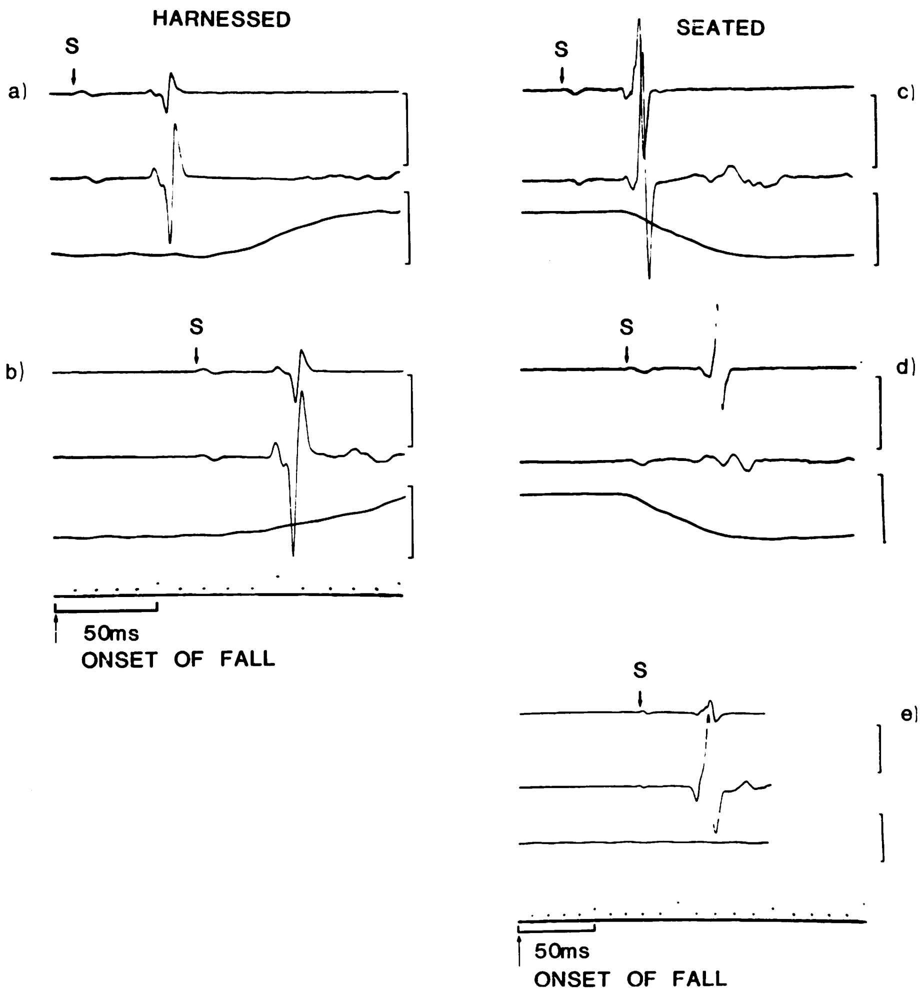

Fig. 6 *T reflex during falls in a harness and while seated. In each set of three traces the upper trace is the control response while hanging, middle trace the test response, and lower trace the ankle angle while falling. Note that the T response is facilitated in the experiments in the harness at 15 and 70 ms (series a and b). In seated falls the T response elicited about 70 ms after the onset of fall (series d) is inhibited unless the foot is firmly strapped down. If the foot is strapped down facilitation occurs (series e). Calibration: EMG 0.5 mV; ankle angle 10°, dorsiflexion up, plantarflexion down. S—tendon tap stimulus.*

ms. Facilitation of the H reflex represents a progressive increase in the excitability of soleus alpha-motor neurones which results in EMG activity about 80 ms after release (Greenwood and Hopkins, 1974). This course of events is similar to the H reflex facilitation before voluntary movement which begins about 60 ms before the onset of voluntary EMG activity (Kots, 1969). We have shown elsewhere (Greenwood and Hopkins, 1976a) that muscle activity in soleus after release depends largely upon labyrinthine function, but we were not able to exclude the possibility that peripheral receptors play some part in its genesis. The latency of onset of increase in alpha motor neurone excitability in the present monosynaptic reflex studies is such that the increase in excitability cannot be attributed reliably to descending pathways from the otolith. Soleus alpha motor neurone facilitation must begin about 40–50 ms after release, allowing about 13 ms afferent conduction time in the H reflex arc (Magladery *et al.*, 1951). As the latency of a cortical evoked response after stimulation in the popliteal fossa is about 25 ms (Giblin, 1964), and conduction to the lumbar cord after stimulation in the internal capsule may be calculated from published data to be about 15 ms (Pagni *et al.*, 1964), 40–50 ms is sufficient to allow a long loop reflex through the cortex, originating in receptors in the lower limbs.

Matthews and Whiteside (1960) found that during seated falls the H reflex was inhibited between 50 and 100 ms after release. At about this time during seated falls the ankle begins to plantarflex. Passive plantarflexion of the ankle inhibits alpha motor neurone activity (Taboricova *et al.*, 1966). The results of Matthews and Whiteside would therefore appear, at first sight, not unreasonable. However, we found that as long as the stimulus while hanging was less than that which elicitated a maximal response, the H response was always facilitated if delivered after about 30 to 40 ms in both harnessed and seated falls. Passive plantarflexion dces not occur in harnessed falls, and in seated falls it appears that the progressive alpha motor neurone facilitation before EMG activity overcomes the inhibitory effects of passive plantarflexion (Taboricova *et al.*, 1966), much as, for example alpha motor neurone facilitation by voluntary effort overcomes the inhibitory effects of sinusoidal movement at the ankle (Delwaide and Hugon, 1969). We cannot explain the difference between this aspect of our results, and those of Matthews and Whiteside.

The failure to show any significant facilitation in H response on falling if the control stimulus while hanging had elicited a maximal H response may indicate that descending pathways from the otoliths do not have access to any alpha motor neurones to which peripheral afferent nerve fibres do not also have access.

Turning to the T reflex, we found that it was facilitated when stimuli were delivered only 10 ms after release. Since the H reflex, which bypasses spindles, is not facilitated at this time, this early T facilitation must be due to increase in spindle excitability or to a more effective mechanical stimulus. Unfortunately we were unable to measure the mechanical force with which the T reflex was elicited. If this had varied as a result of movement of the frame supporting the spring-loaded hammer during fall, we would have expected to have seen sometimes apparent facilitation and sometimes inhibition of the T reflex delivered at a given time after release. We did not, however, see this variation in T reflex amplitude. We would argue, therefore, that the early T reflex facilitation was physiological rather than artefactual. Since the facilitation occurs so soon after the onset of fall, it is possible that this early increase in excitability is due to changes in muscle shape as the body enters a zero gravitational state at the onset of the fall. However, afferent impulses resulting from a tendon tap at 10 ms must begin to reach the soleus alpha motor neurones at about 23 ms, a time within which supraspinal facilitation from, for example, the otolith apparatus could also occur (Delwaide and Delbecq, 1973). The H reflex is not facilitated as soon as this but this disparity could be explained by the difference in time course of the afferent stimulus.

If, as we have shown, soleus alpha motor neurones are facilitated at 50 ms after the onset of fall, how can we explain the inhibition of the ankle jerk reported by Matthews and Whiteside (1960) to occur between 50 and 100 ms? They attributed this to movements within the muscle due to the sudden change in acceleration at the onset of fall resulting in decreased spindle excitability. They did not believe that the effects of weightlessness acting on other sensory receptors such as cutaneous receptors in the buttocks were important. Muscle shape must change at the onset of fall in much the same way as the shape of a water filled balloon changes when released. We do not believe it possible to forecast the summated effect of weightlessness on spindles, some of which are stretched while others are slackened within the same muscle as the pulling effect of gravity is removed. We found that the T reflex was unobtainable during seated falls only if delivered after the onset of plantarflexion of the foot at about 50 ms after release. If movement of the foot was firmly prevented the T reflex was facilitated at all times. Strapping of the foot has to be done very firmly, and plantarflexion of only two degrees due to inadequate strapping resulted in inhibition or absence of the tendon reflex. Matthews and Whiteside infer that when the foot was strapped down in their experiments the T reflex was still absent. They apparently did not measure the position of the ankle under these conditions. It is possible that slight plantarflexion of the ankle could have occurred and resulted in absence of the T reflex during fall. Our experiments, therefore, suggest that the previously reported inhibition of the T reflex during seated falls is caused by passive plantarflexion of the foot, about 50 ms after release, resulting in slackening of the Achilles tendon rather than by change in muscle spindle activity. The tendon becomes so compliant that it absorbs much of the energy delivered by the hammer.

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