gamma activity (Diete-Spiff *et al.*, 1962; Andrew, 1966; Pascoe, 1965). This is illustrated in Fig. 10, where the level of spontaneous activity in a gamma efferent is observed to be well correlated with the level of anesthesia. This feature affords the experimenter with an opportunity to obtain different levels of fusimotor activity with the use of a vaporizer to control the level of halothane anesthesia.

Diete-Spiff and Pascoe (1959) observed excitatory effects on gamma motoneurones by ether and urethane, but inhibitory effects by chloralose, thiopental, hexobarbitone and acetylpromazine. Most of these effects must be due to activation or depression of the various reticular nuclei. Under light barbiturate anesthesia a steady spontaneous discharge of fusimotor neurones has been observed by a number of investigators (Proske and Lewis, 1972; Lewis, 1973; Gilman, 1976; Gildenberg and Murthy, 1977). A majority of these spontaneously active gamma efferents (under barbiturate anesthesia) seems to be the static fusimotor type (Lewis, 1973; Gladden and McWilliam, 1977b). Gildenberg and Murthy (1977) were able to observe a population of slowly discharging gamma efferents that were more depressed by barbiturate anesthesia than others with faster mean rates.

7. Fusimotor Effects Observed in the Human

Fusimotor effects in conscious and normal human volunteers and in patients with motor abnormalities have recently begun to be demonstrated in greater detail by the technique of microelectrode recordings in peripheral nerve fascicles of activity originating from muscle spindle endings. The technique was introduced by Hagbarth and Vallbo (1967, 1968) and was subsequently used extensively in investigations on normal subjects and on patients with CNS lesions conducted in Hagbarth's and in Struppler's laboratories (Vallbo *et al.*, 1978). The results from their observations will be reviewed here. Earlier investigations on fusimotor function in the human have used more indirect techniques. These have involved studies of tendon reflexes (knee and ankle jerks) and H-reflexes for phasic responses and the studies of stretch and vibration reflexes for tonic effects. In addition, a number of studies have attempted to evaluate the effects of a "gamma block" on the motor performance by injecting local anesthetics to block preferentially the conduction in gamma efferents. Such techniques and others have been described in a number of papers presented at recent symposia (Desmedt, 1973, 1977).

In comparison to the data from animal experiments, the results from human experiments are obviously of great importance due to the variety of voluntary movements that the human is capable of executing and the variety of supraspinal excitations that can be achieved to modulate the spinal motor apparatus. In spite of the restraints and constraints imposed on the repertoire of movements that may be performed by the human subjects during a microelectrode recording from peripheral nerve fascicles, a number of interesting features of fusimotor excitations to the human muscle spindles have been observed (Burke, 1978). The differences in observed effects have contributed to conflicting points of view. The following pages will be devoted to an analysis of such issues and to determine the answers.

7.1. RESTING FUSIMOTOR TONE AND THE SENSITIVITY OF HUMAN MUSCLE SPINDLES

As mentioned earlier in Section 4 of this review, spontaneous fusimotor activity is a commonly observed feature of many animal preparations. Hagbarth (1974) points out that though there may be a resting fusimotor activity in the conscious man, it will be an insignificant amount as observed from a lack of effect on muscle spindle discharge on application of a lidocaine block of the muscle nerve (Wallin *et al.*, 1973). In passive, relaxed human muscles, the muscle spindle endings possess a low rate of spontaneous activity (less than 20 imp $\sec^{-1}$) and display poor position sensitivity (Vallbo, 1974a). Under these conditions, a peripheral fusimotor block with lidocaine (Burke *et al.*, 1976b) produces very little effect on the resting background discharge rate of the muscle spindles (Fig. 11). Burke and Eklund (1977) arrived at a similar conclusion from observations of muscle spindle discharge in

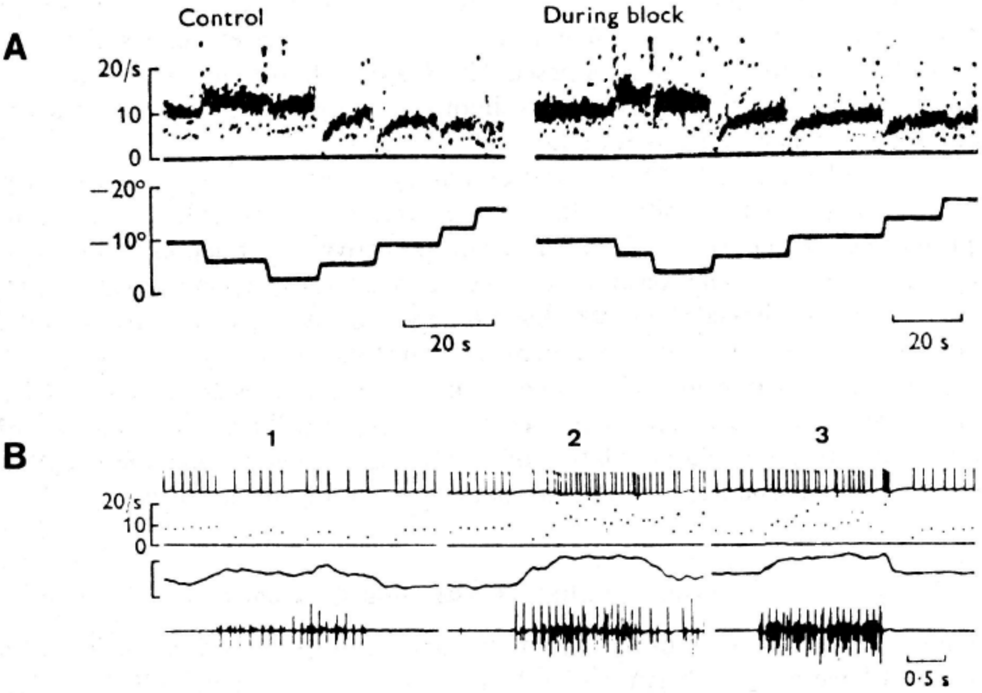

FIG. 11. The effect of deprivation of fusimotor control through a "gamma block" (achieved by injecting lidocaine to produce peripheral nerve block) on human muscle spindle afferent responses (A) to passive stretch and shortening and (B) to isometric voluntary contractions. A: Peroneus longus spindle—complete nerve block (both alpha and gamma axons). B: Tibialis anterior spindle—(1) partial nerve block (alpha axons preserved) (2) during partial recovery, (3) after complete recovery. Note that loss of gamma control has not affected sensitivity of the spindle afferent to passive muscle stretch in A and that the resting discharge rates in B (1) and B (2) are identical (reproduced with permission from Burke *et al.*, 1976b).

standing subjects. About 75–80% of the spindle afferents studied by them exhibited either no activity or very low and irregular resting discharge.

Such an interpretation is difficult to accept since even under conditions of strong fusimotor activation during voluntary movements, human spindle afferents hardly attain firing rates of above 50 imp sec^{-1}. In addition, the spontaneous discharge rates in fusimotor neurones themselves are likely to be under 100 imp sec^{-1} (an observation based upon animal experiments—Ellaway, 1972; Gildenberg and Murthy, 1977). The experiments of Lewis and Proske (1972) suggest that fusimotor stimulation at rates below 100 imp sec^{-1} does not significantly alter the spontaneous rates of impulses in spindle afferents. Thus lack of reduction in spindle firing rates after a peripheral procaine block is not a sufficient reason for concluding that resting fusimotor tone is weak, particularly when the control rates (before such a block) of spindle afferent discharges are under 20 imp sec^{-1}. The fusimotor effect under these conditions is more likely to be seen as a reduction in the latency of spindle response to mechanical stimuli (Lewis and Proske, 1972).

7.2. ON THE ABILITY TO VOLUNTARILY ENHANCE THE FUSIMOTOR DRIVE

There has been considerable differences of opinion on the ability of conscious human subjects to voluntarily activate selectively the fusimotor efferents to a particular muscle without simultaneously activating the alpha motoneurones to the same muscles. In acute animal experiments fusimotor gamma efferents have often been found to possess a lower threshold to both central (supraspinal) and peripheral (reflex) activation when compared to alpha motoneurones to the same muscle. Burg *et al.* (1973) recorded from forearm muscle spindle afferents in the median nerve and found them to be activated by an acoustic stimulus or during a contraction of a remote muscle in the lower extremities. In addition,

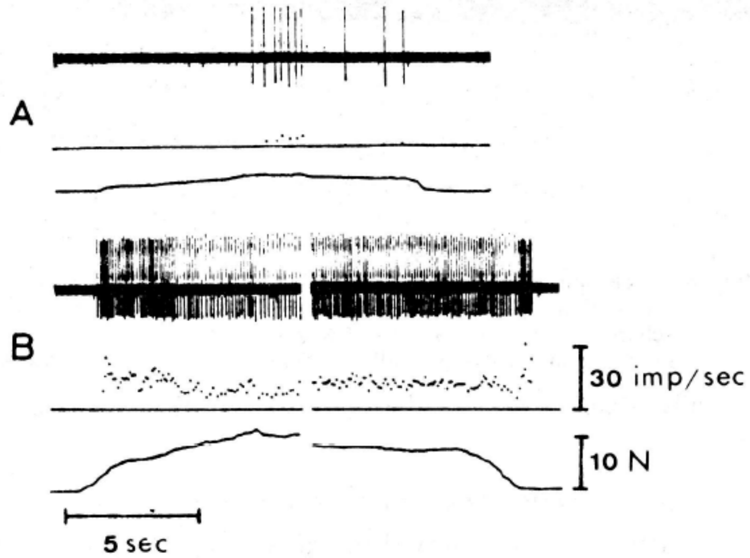

FIG. 12. Human muscle afferent responses to voluntary contractions of different intensities (A and B). In each case, the traces indicate spike discharge, instantaneous rates and force of contraction (reproduced with permission from Vallbo, 1970).

the spindle discharge was also found to increase when the attention of the subjects was diverted by asking them to perform silent computations. While Burg *et al.* (1973, 1974, 1976) reported that fusimotor drive may thus be preferentially increased, experiments performed in other laboratories have always been able to detect a simultaneous increase in alpha motoneurone activity to the same muscles, though on many occasions this could be detected only with sensitive transducers (Hagbarth *et al.*, 1975c; Vallbo *et al.*, 1978).

7.3. ALPHA-GAMMA COACTIVATION IN VOLUNTARY MOVEMENTS

Coactivation of skeletomotor and fusimotor systems is a standard feature of voluntary contractions in human subjects (Vallbo *et al.*, 1978). The fusimotor effects were consistently found to lag behind the skeletomotor drive (Vallbo, 1971) with the acceleration of spindle discharges invariably occurring after the start of the electromyographic activity in the parent muscle.

7.3.1. *Isometric contractions*

For many spindle endings, fusimotor drive was not observed to occur until 10–50 msec after the onset of extrafusal muscle activity in an isometric voluntary contraction (Vallbo, 1971). Such a feature indicates a strong alpha-gamma linkage. In voluntary isometric contractions this feature may be observed in the form of a proportional increase of fusimotor drive with the intensity of contraction, particularly if the resting discharge of the spindle has been initially low (Fig. 12).

The fusimotor modulation during an isometric voluntary contraction does not increase the spindle discharge rate to the extent passive stretch or lengthening of the muscle does (Fig. 13) and the spindle discharge does not follow variations in muscle tension as effectively as a Golgi tendon organ does (Fig. 14). The main feature of alpha–gamma linkage during isometric voluntary contractions seems to be most effective in achieving a close relationship between muscle spindle firing rates and the torque of contraction (Vallbo, 1974b) at least for the finger flexor muscles of the forearm. The fusimotor effects observed in such instances of alpha–gamma coactivation have mainly been due to static fusimotor drive (Vallbo, 1971; 1974b). In addition, dynamic fusimotor drive can also be concomitantly present to provide the muscle spindles with the sensitivity to follow minute disturbances in maintained contractions (Vallbo, 1974b). The fusimotor drive occurs mainly to the spindles in the same portion of the muscle which receives the skeletomotor drive (Vallbo, 1970) thus exhibiting a close territorial coupling in the periphery and supporting the suggestion that each muscle

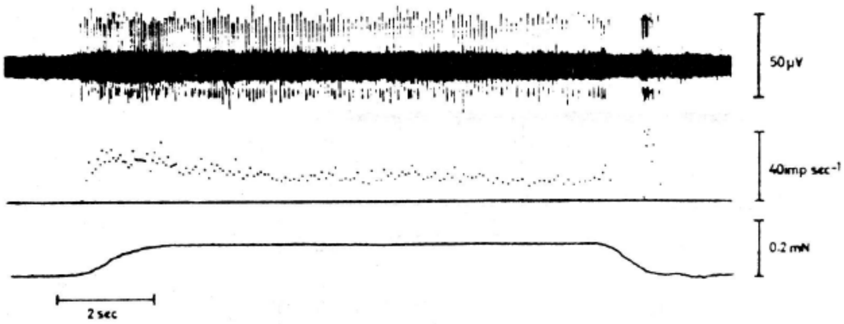

FIG. 13. Human muscle spindle response during voluntary contraction against a fixed resistance. Note the burst of discharge on passive lengthening at the end of the contraction. Top to bottom: spike discharge, instantaneous frequency and the torque due to contraction (reproduced with permission from A. B. Vallbo, 1970: *Acta physiol. scand.* **78,** 315–333).

spindle is functionally related to a particular set of motor units (Binder *et al.*, 1976; Binder and Stuart, 1978).

7.3.2. *Fusimotor drive during changes in muscle length and loading*

Alpha–gamma coactivation is observed in alternating, fast voluntary movements, during the contraction phases, with the muscle spindles mainly exhibiting passive responses during the stretching phases (Hagbarth *et al.*, 1975a). The effect of a slowly changing load when the subject is instructed to maintain a constant joint position seems to result in a modulation of the spindle discharge in parallel with the extrafusal muscle contraction (Burke *et al.*, 1978a), the excitation arising from static fusimotor efferents.

In movements due to active shortening of the muscle, the speed of movement has a significant effect on the discharge rate of the muscle spindles (Burke *et al.*, 1978b). The spindle discharge under these conditions is essentially determined by the loading of the muscle in addition to the speed of movement. In shortening contractions, the muscle spindles accelerate their rates of discharge after the onset of the electromyographic activity in the muscle but before a significant amount of tension is produced. Burke *et al.* (1978b) also studied lengthening contractions and found the fusimotor drive to be enhanced, with the sensitivity of the spindle afferents being greater under these conditions when compared to passive stretch.

Thus the emerging general principle of alpha–gamma coactivation in voluntary movements in the human seems to be that of maintenance of the dynamic sensitivity of the muscle spindle afferents to detect irregularities and perturbation in movement (Vallbo, 1974b; Burke *et al.*, 1978b; Vallbo *et al.*, 1978). It has also been determined that during such an alpha–gamma coactivation the threshold force when fusimotor effects are displayed by various spindle afferents in a muscle differs, exhibiting a type of recruitment of spindle afferents (Burke *et al.*, 1978c). Such effects are observed as differences in the latency of onset of spindle acceleration relative to the start of the electromyographic activity in the muscle.

7.4. EFFECTS ON PHASIC REFLEXES

Reflexes may be elicited in the human originating from the primary endings of the muscle spindles activated phasically by a mechanical tap applied to the tendon (the tendon reflex)

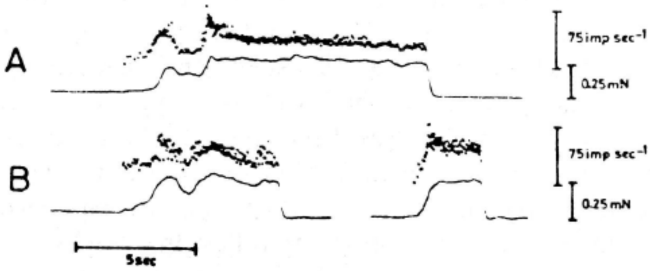

FIG. 14. Response of a Golgi tendon organ in the human illustrates a pronounced correlation with the muscle force during a voluntary movement (reproduced with permission from A. B. Vallbo, 1970: *Acta physiol. scand.* **78,** 315–333).

or by direct electrical stimulation of the afferent nerve fibers (H-reflex). While a temporal dispersion of afferent action potentials occur in the former from the process of intramuscular transmission of the mechanical vibration, the monosynaptic H-reflex is elicited by a synchronous volley in the Ia afferents. Thus, the character of motoneuronal activation will be different in these two cases—a temporal summation of afferent impulses in the case of the tendon reflex and a spatial summation in the case of the H-reflex (Gassel and Diamantopoulos, 1964a–c, 1966). In many studies, a comparison of the amplitudes of the tendon and H-reflexes have been performed with the hope of determining whether selective fusimotor effects are present. While the effects on alpha motoneurones will affect both these reflexes, the gamma effects have been considered to be dominant in cases where a selective change in the amplitude of the tendon reflex is observed (Buller and Dornhorst, 1957; Weaver *et al.*, 1963).

7.4.1. *The controversy regarding fusimotor contributions during reinforcement maneuvers*

Interest has centred on studies of fusimotor contributions to a reflex reinforcement similar to that resulting from a Jendrassik maneuver (Jendrassik, 1883). This maneuver consists of locking the two hands in a firm grip and pulling each other in opposition. Such a maneuver essentially increases the excitability of spinal motoneurones by flooding them with a barrage of afferent information in addition to direct supraspinal influences. Sommer (1940) advanced the theory that the reflex reinforcement observed in a Jendrassik maneuver would result from increased contribution from the muscle spindles. It has been commonly observed that the amplitude of the tendon jerk increased during a reinforcement maneuver. Earlier studies have compared the tendon jerks with H-reflexes during a Jendrassik's maneuver and concluded that facilitation of the H-reflex was less prominent (Sommer, 1950; Paillard, 1955; Buller and Dornhorst, 1957). Thus, the effects of a reinforcement maneuver were believed to be predominantly on the fusimotor neurones. Clare and Landau (1964; and Landau and Clare, 1964) obtained greater facilitation of H-reflexes which continued after the gamma fusimotor fibers were blocked peripherally in the muscle nerve by injection of procaine. They then suggested that very little, if any, of the reflex reinforcement resulted through the fusimotor efferents. The central action directly converging upon alpha motoneurones was thought to be the dominant effect. Dietrichson (1971a) has used considerably more elaborate instrumentation (Dietrichson and Sorbye, 1971) than that of earlier investigators to show that the tendon reflex was affected at all levels of reinforcement while H-reflex was not affected. Bishop *et al.* (1968) employed different strengths of the reinforcement maneuvers and found that as the strength of the maneuvers increased the tendon reflexes increased more than H-reflexes with the latter being slightly inhibited with stronger maneuvers. Recently Bussel *et al.* (1978) used similar comparisons of H-reflexes with tendon reflexes during Jendrassik maneuvers after an ischaemic block (produced by a pressure cuff) of the large afferent fibers from the muscle spindle. These authors also observed that the ischemic block had no effect on the potentiation of H-reflexes resulting from a Jendrassik maneuver.

The controversy regarding fusimotor contributions to the phenomenon of reinforcement has continued to the present day even with microelectrode recordings from human peripheral nerves. Results from Struppler's laboratory have suggested that muscle spindles in

FIG. 15. Response of a human muscle spindle in the lower extremity during a Jendrassik maneuver (reproduced with permission from Burg *et al.*, 1974).

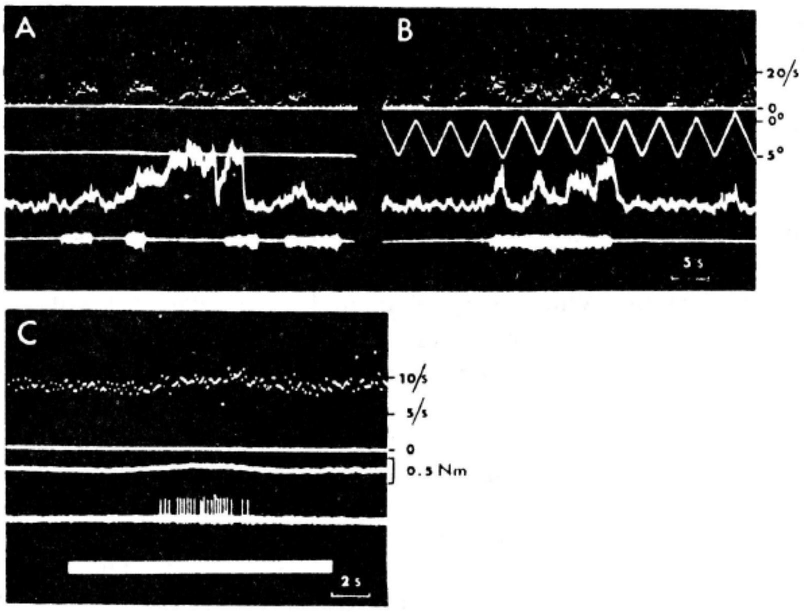

FIG. 16. Coactivation of alpha and gamma motoneurones is observed in the human during reinforcement maneuvers. A and B are from a peroneus group IA fiber. Traces are from above, frequency, joint position, integrated EMG of the peroneus, and EMG of the finger flexor muscles (reinforcement marker). In A, spindle activation coincides with the onset of the maneuver but outlasts each maneuver and correlates more closely with the unintentional contraction that developed in the peroneal muscles. In B the unintentional contraction that developed during the reinforcement increases spindle frequency and changes the pattern of response to the stretching movements so that the spindle also discharges during muscle shortening. In C, the discharge of a tibialis anterior group II fiber increased slightly during a Jendrassik maneuver (indicated by the solid bar) but this was correlated with a slight increase in torque (second trace) and the appearance of EMG potentials from a single motor unit in tibialis anterior muscle (third trace) (reproduced with permission from Hagbarth *et al.*, 1975c).

a particular muscle may become active on voluntarily contracting a remote muscle (Fig. 15) as well as during a Jendrassik's maneuver and that such effects may precede and outlast the electromyographic activity of the contracting muscles (Burg *et al.*, 1973, 1974, 1976). Such reinforcement effects were suggested to involve dynamic fusimotor neurones (Burg *et al.*, 1974; Szumski *et al.*, 1974). Similar conclusion was arrived at from observations on averaged surface electrode recordings of ulnar nerve responses to tendon taps of the first dorsal interosseus muscle with and without a reinforcing maneuver (Murthy *et al.*, 1978b, c). Hagbarth *et al.* (1975c) using microelectrode recordings were unable to find a selective fusimotor activation in Jendrassik maneuvers. Using sensitive transducers for measuring muscle tension, Hagbarth *et al.* (1975c) always found a coactivation of the alpha motoneurones of the same muscle whenever a fusimotor effect in increasing muscle spindle discharge rates was observed on a Jendrassik maneuver being performed by their subjects (Fig. 16). In addition, these investigators did not find evidence for any selective activation of dynamic fusimotor fibers under these conditions, though appropriate tests were employed to detect changes in the dynamic sensitivity of the spindle afferents studied.

Although the significance of fusimotor contributions to such reflex reinforcement has thus been questioned, there is no doubt increased fusimotor activity does occur during a Jendrassik maneuver. The arguments in favor or against the claims of fusimotor effects being dominant over direct effects on alpha motoneurones have mainly depended upon comparisons of the H-reflex with the tendon reflex. A number of reasons can be advanced to show that such a comparison has its limitations.

(1) It was briefly mentioned earlier that the nature of the synaptic activation of the alpha motoneurones responding in an electrically elicited H-reflex features spatial summation whereas a case of temporal summation is present in a mechanically elicited tendon reflex even though both may use the monosynaptic pathways (Gassel and Diamatopoulos, 1966).

(2) Gottlieb and Agarwal (1973) showed that during a voluntary movement of the ankle joint, the tendon jerk was facilitated by a Jendrassik maneuver to a considerably greater

extent than the facilitation observed in the size of the H-reflex. In addition, while the H-reflex facilitation lasted only about 400 msec, the facilitation of the tendon reflexes continued for another 500 msec.

(3) In eliciting an H-reflex, the electrical stimulus would have excited most of the afferent fibres contributing to the monosynaptic reflex. Under these conditions any increase or decrease of the size of this reflex response has to be predominantly a central effect and not peripheral. The changes observed in the size of the H-reflex during a Jendrassik maneuver are thus truly direct effects on the alpha motoneurones. It is not then justified to study the effects of a procaine block of the gamma fusimotor fibers (Clare and Landau, 1964) or of an ischemic block of the Ia afferent fibers (Bussel *et al.*, 1978) when these are being electrically stimulated. Instead of attempting to evaluate fusimotor influences from observation of H-reflex sizes, it would be more appropriate to study the effects of the fusimotor block on the tendon reflexes and compare these with the H-reflexes which remain unchanged during the peripheral block of Ia input. Bussel *et al.* (1978) used stimuli of strength less than that necessary for eliciting maximum H- and tendon reflexes and obtained nearly equal sizes of these reflexes in controls. The results also indicate that the size of the H-reflex is not a suitable index of fusimotor contributions where the muscle length is constant. However, during a slow or steady stretch of the muscle, the H-reflex is considerably potentiated when a Jendrassik maneuver is simultaneously performed (Mark *et al.*, 1968).

There are also other difficulties in comparing the results from different studies. Reflexes have been studied in subjects in different postures (sitting or lying down—prone or supine). It is known that the sizes of the lower limb reflexes are affected by postural changes of upper extremities (Delwaide *et al.*, 1977). Different types of maneuvers have been used, varying considerably from the conventional Jendrassik maneuver. Different strengths of the reinforcement maneuvers have been used. In addition, the reflexes have been measured either as neural response or electromyogram response or muscle contraction. In any event, there is no question that reinforcement maneuvers cause facilitation of the start of a voluntary movement (Gottlieb *et al.*, 1970; Gurfinkel *et al.*, 1971; Gottlieb and Agarwal, 1973).

7.4.2. *Temporal considerations of fusimotor effects*

An analysis of the available data suggests that the enhancement of H-reflexes during reinforcement maneuvers is dominantly a central effect whereas the potentiation of the tendon reflexes in the same maneuver is predominantly a fusimotor effect. Hagbarth *et al.* (1975c), on the basis of observations in microelectrode recording, suggest that the fusimotor effect is never dominant as long as the muscle remains relaxed. Their conclusion is based on the observation of no change in the size of integrated multiunit neurograms in response to a tendon percussion when a Jendrassik maneuver was performed. The reflex contraction of the muscle, on the other hand, was considerably potentiated. In such cases there is a possibility that fusimotor effects are present in the form of a reduction in the latency of the afferent response to the tendon percussion rather than as a change in the size of the integrated neurogram (Homma *et al.*, 1962; Clarke, 1967; Murthy *et al.*, 1978c). There is considerable indirect evidence to support the idea that increased fusimotor drive can result in reducing the latency of the tendon reflex, presumably by sensitizing the Ia afferent endings to the phasic stimulus (Clarke, 1966, 1967). It is also interesting to note here that observation of movements deprived of fusimotor control through a procaine block of the peripheral nerve have all shown that the speed of the movements is affected rather than their amplitude (Smith *et al.*, 1972; Herman *et al.*, 1973; Abbs, 1973). Such temporal effects during a "gamma-block" can often manifest in an overshoot of and oscillations in intended movements (Shambes, 1969; Smith *et al.*, 1972).

The reason why such fusimotor effects, when present, appear not to significantly alter the firing rate of muscle spindle afferent impulses may be that the basal rates of discharge displayed by these receptors are low. These are often under 10–20 imp $\sec^{-1}$. Even with their high dynamic sensitivity their discharge rates hardly rise above 50–60 imp $\sec^{-1}$ (Fig. 11; also refer Vallbo, 1974a, b). Their inter-spike intervals then considerably overlap the latencies for the monosynaptic reflex. The resulting extrafusal activity will then diminish the excitatory effects on the spindle endings. The importance of consideration of resting discharge rates in spindle afferents in evaluating reinforcement of H-reflexes is emphasized by the results of Mark *et al.* (1968) who observed a potentiation of the reflex, by a Jendrassik maneuver when the muscle was simultaneously stretched. Thus quantitative studies of temporal fusimotor effects on the discharge of impulses by muscle spindle endings need to be performed.

7.5. OBSERVATIONS DURING TONIC REFLEXES

The participation of fusimotor excited muscle spindles in tonic reflexes induced by either a maintained stretch (Tonic Stretch Reflex, TSR) or by a high frequency mechanical vibration applied to the muscle (Tonic Vibration Reflex, TVR) have been discussed extensively in earlier reviews (Marsden *et al.*, 1969; Herman, 1970; Matthews, 1972) and in a recent symposium on the stretch reflex (Homma, 1976). Such segmental reflexes have been suggested to be exceptions to the rule of alpha–gamma coactivation (Burke *et al.*, 1976b).

7.5.1. *The stretch reflex and the problem of load compensation*

The stretch reflex is not observed in normal relaxed subjects but may be activated by voluntary contraction, reinforcement or other factors that alter supraspinal influences (Landau *et al.*, 1966; Andrews *et al.*, 1973). The tonic stretch reflex thus produced should involve a maintained fusimotor action (Lance and McLeod, 1975).

The stretch reflex in man may involve a long-loop via the motor cortex (Marsden *et al.*, 1972, 1976a, b, 1977) in contrast to the phasic tendon reflexes which depend only on segmental circuitry. Studies of such trans-cortical reflexes have been performed to obtain support for the servo control theory of movements (Merton, 1953) which emphasizes the significance of the fusimotor control. Adaptive gain control of the stretch reflex as observed in response to changes in load during voluntary movements is a unique feature of the physiological control system (Marsden *et al.*, 1972).

The stretch reflex latencies for both distal and proximal muscles were studied by Marsden *et al.* (1976b) who noted that the proximal muscles exhibited a spinal component of the reflex in addition to the transcortical component whereas the muscles which are prime-movers of the digits display only the longer latency transcortical reflex. Since anesthesia of the digit abolishes the servo action in these distal muscles (Marsden *et al.*, 1977), it is possible that fusimotor drive is affected due to removal of cutaneous excitations (Matthews, 1972). Thus, although muscle receptors may provide the major input for load compensation, the cutaneous afferents may reinforce them by their reflex effects on gamma motoneurones. In the case of a gradually changing load, however, the coactivation of alpha and gamma motoneurones may be observed (Burke *et al.*, 1978a).

7.5.2. *Effects during vibration reflexes*

Low amplitude vibration of a muscle excites the spindle endings with the effects predominantly on the Ia afferents (Brown *et al.*, 1967; Burke *et al.*, 1976a). Although the sensitivity of the primary spindle endings may be high during vibration of the muscle combined with stretch, during passive shortening the secondary endings may be more sensitive (Burke *et al.*, 1976b). A concomitant fusimotor activity while the vibration is applied increases the static sensitivity of the Ia afferents (Brown *et al.*, 1969b). The response of primary endings "saturates" under these conditions, irrespective of whether the static or the dynamic fusimotor activity occurs concomitantly with the vibration applied to the muscle. However, concomitant fusimotor effects have been shown in animal experiments to increase the reflex responsiveness of the alpha motoneurones to vibration of the muscles they innervate (Anastasijevic *et al.*, 1971). Such concomitant fusimotor activation of spinal motoneurone pool probably occurs in disturbances to postural equilibrium observed in human subjects on applying vibratory stimuli to the muscles (Eklund, 1972).

The pathways for the maintenance of muscle tone and that for the production of phasic reflexes need not be interdependent (DeGail *et al.*, 1966). During a tonic vibration reflex in a muscle, the tendon jerks are depressed but reinforcement maneuvers or active voluntary contraction of the muscle can cause an augmentation of this phasic reflex (DeGail *et al.*, 1966; Lance *et al.*, 1966; Marsden *et al.*, 1969). However, in microelectrode recordings of human muscle afferents, it has been found that responsiveness to tendon taps of the primary afferents themselves is decreased during muscle vibration (Burke *et al.*, 1976a). This fact may also be contributory to the observed reduction in size of the tendon reflexes. Agarwal and Gottlieb (1976) determined that the tendon reflexes may actually be potentiated at higher rates of vibration. Burke *et al.* (1976b) showed that fusimotor action increases the vibration response of spindle endings during a concomitant voluntary contraction showing coactivation of alpha and gamma motoneurones.

7.6. FUSIMOTOR EFFECTS IN DISEASE STATES

Motor abnormalities may be observed to affect the phasic and tonic reflexes as well as the muscle tone and voluntary movements. Study of tendon reflexes may reveal dynamic fusimotor effects, while observations during the tonic stretch and vibration reflexes may be pertinent to static fusimotor effects. However, recent microelectrode recordings from patients are more informative and definitive.

7.6.1. *Spasticity*

In the case of spinal shock, the fusimotor neurones are initially depressed. As the spasticity develops, the dynamic fusimotor neurones may become hyperactive (Jansen, 1962) in a manner similar to that observed in the spinal cat (Alnaes *et al.*, 1965). This is believed to be the reason for the observed preservation of tendon reflexes in patients exhibiting flaccid and hypotonic muscles (Lance and McLeod, 1975). Dietrichson (1971b) studied the phasic reflexes and also the muscle silent period (Dietrichson, 1971c) resulting from isometric and isotonic contraction in spastic patients. It was observed that the ratio of tendon jerks to H-reflexes was significantly higher in spastic patients than in normal subjects and that this ratio is reduced by 30% when the gamma efferents were blocked by the application of a local anesthetic to the peripheral nerve (Dietrichson, 1971b). On the basis of the observation of an increased silent period in the electromyogram of the spastic patients, Dietrichson (1971c) concluded that dynamic fusimotor activity was dominant. Szumski *et al.* (1974) expressed a similar view based upon microelectrode recordings of spindle afferents during clonus exhibited by patients who were spastic from cerebral vascular lesions or due to multiple sclerosis. Using similar microelectrode techniques, however, Hagbarth *et al.* (1975b) were unable to confirm the suggestion of an increased dynamic fusimotor action on the spindle endings recorded during clonus of patients with spasticity due to cerebral vascular accidents or spinal injury or due to multiple sclerosis. Hagbarth *et al.* (1975a) also compared the observations made during clonus in spastics with spindle activity recorded in normal subjects executing similar fast voluntary alternating movements and suggested spindles under clonus were essentially being unloaded during the contraction phases of these fast contractions. These investigators consider the clonic contractions to be primarily a feature of hyperactive or disinhibited segmental reflexes. Thus, the controversy (Buller, 1957; Landau and Clare, 1964; Herman, 1970) regarding fusimotor contributions to spasticity still continues.

In order to determine differences in the involvement of alpha and gamma motoneurones, the ratios of tendon jerk to H-reflex and the ratios of H-reflex to M-response have been studied in patients during spinal shock and during the display of spasticity (Weaver *et al.*, 1963; Ashby *et al.*, 1974).

Spasticity has also been studied in animals with various lesions of the central nervous system (Denny-Brown, 1966; Van der Meulen *et al.*, 1966). In monkeys made spastic by pyramidal lesions, the sensitivity of extensor muscle spindles is observed to be greater than that of flexor spindles (Gilman and Van der Meulen, 1966).

7.6.2. *Rigidity in Parkinsonism*

Application of procaine to peripheral nerves to relieve rigidity in Parkinsonism (Walshe, 1924) is effective through a block of conduction in gamma efferent fibers (Rushworth, 1961). Hagbarth *et al.* (1975b) in microelectrode recordings of muscle spindle activity in Parkinsonian patients showed that the spindle afferent discharge increased simultaneously in proportion to the rigidity. Further, such alpha–gamma coactivation was also observed in the tremor exhibited by Parkinsonian patients. The gamma efferents dominant in Parkinsonism appear to be the static fusimotor neurones (Hassler, 1973). Similar conclusions were arrived at by Dietrichson (1971b) on the basis of effects observed on the phasic reflexes studied in Parkinsonian patients as compared to normal subjects.

Neuronal loss in the substantia nigra observed in Parkinsonian disease (Hassler, 1938, 1966, 1973) may lead to a selective depression of dynamic fusimotor neurones and activation of static fusimotor neurones since it has been shown from animal experiments that stimulation of the caudal part of the substantia nigra elicits dynamic fusimotor effects and the rostral part of the nigral cells inhibit dynamic fusimotor effects (Hassler and Wagner, 1975; also refer to Section 5.4). Thus, there is some support for the existence of a hyperactive static fusimotor system in Parkinsonian rigidity and tremor states. Burke *et al.* (1977) feel that the amount of fusimotor influence on spindle discharge seen in Parkinsonian patients is no different from that observed in normal subjects who cannot relax or when they perform a weak voluntary contraction. They express the view that there is no selective hyperactivity of the fusimotor system in Parkinsonism. In other words, Parkinsonian rigidity also displays α–γ coactivation.

Other experimentally induced states of rigidity or tremor also exhibit similar hyperactivity of the gamma efferents with a coactivation of the alpha and gamma motoneurones being observed. These have been described earlier under the effects of drugs (Steg, 1966; Jami, 1973, 1974; Lamarre and Weiss, 1973; Martins, 1975).

8. Fusimotor Contributions to Motor Behavior

In attempting to ascribe a role for the fusimotor neurones in the control of voluntary movements, the basic question has been whether movements ought to be considered as servo-controlled through the fusimotor pathways (Merton, 1953) or as servo-assisted, with some kind of a coactivation of alpha and gamma motoneurones (Matthews, 1972; Stein, 1974).

Further questions of relevance to the role of the fusimotor gamma and beta efferents in motor behavior are:

(1) What is the functional importance of differences in alpha and gamma activation in various movements?

(2) What are the criteria for preferring coactivation of alpha and gamma motoneurones?

(3) Are the same types of alpha and gamma units coactivated in various movements?

(4) Under what conditions is a pure gamma excitation preferred?

(5) Under what conditions does a pure alpha or beta excitation occur?

8.1. GAMMA-INITIATED VERSUS GAMMA-ASSISTED MOVEMENTS

The earliest theory of fusimotor control in voluntary movement to be advanced came from Merton (1953) suggesting that the gamma efferent pathway represented an indirect route for supraspinal influences to reach the alpha motoneurones through an excitation of the muscle spindle afferents. The monosynaptic pathway from the primary muscle spindle ending by itself being a powerful excitatory pathway to the homonymous motoneurones, such an indirect gamma-induced contraction would constitute a servo-initiated or servo-controlled movement by analogy with engineering control systems. This "follow-up length servo" hypothesis has been one of the most stimulating in muscle spindle research. Pro and contra results and viewpoints of relevance have been discussed by Matthews (1972), and other recent reviews (Taylor, 1972; Houk, 1972; Stein, 1974) have analyzed the consequences of pure gamma control versus alpha–gamma coactivation using engineering control systems theory.

The subject of alpha–gamma coactivation (Granit, 1970) initially called "alpha–gamma linkage" by Granit (1955a), on the other hand, has been more acceptable since it was originally observed in decerebrate preparations by Eldred *et al.* (1953). A number of instances of coactivation of alpha and gamma motoneurones in anesthetized as well as in awake and conscious animals has been observed both in movements resulting from electrical stimulation and in spontaneously occurring rhythmic movements (Section 8.2) of respiratory muscles or in locomotion and in masticatory movements of the jaw muscles. Most convincing demonstration of alpha–gamma coactivation has also been observed during voluntary movements in the normal human and in patients (Section 7).

8.2. ALPHA–GAMMA COACTIVATION IN RHYTHMIC NATURAL MOVEMENTS

Even before the development of the elegant microneurographic techniques for study of human muscle afferents, studies had been initiated to determine fusimotor behavior during the naturally occurring rhythmic movements of respiration (refer Euler, 1970; Sears, 1973), mastication (Taylor and Davey, 1968) and locomotion (Severin *et al.*, 1967). While respiratory movements can be conveniently studied in anesthetized or decerebrate preparations, studies of other rhythmic movements, i.e. mastication and locomotion had to wait until the development of new experimental techniques using chronic or semi-chronic recording methods (Taylor and Cody, 1974; Cody *et al.*, 1975; Goodwin and Luschei, 1975; Matsunami and Kubota, 1972; Prochazka *et al.*, 1976, 1977; Loeb *et al.*, 1977; Loeb and Duysens, 1978). It must be noted that chronic microelectrode recording techniques were developed at roughly the same time for studying the voluntary movements in primates (Evarts, 1968). The results of all these investigations have considerably advanced our understanding of fusimotor control during normal movements in the intact animal. A number of recent reviews have been devoted to the study of locomotion (Grillner, 1975; Shik and Orlovsky, 1976; Orlovsky and Shik, 1976; Wetzel and Stuart, 1976). The respiratory movements have earlier been reviewed (Euler, 1970; Sears, 1973).

8.2.1. *Respiratory movements*

While fusimotor effects in many of the natural movements had to be interpreted from observations on muscle spindle afferent discharges, it has been possible to record directly from gamma efferents to intercostal muscles (Sears, 1964; Eklund *et al.*, 1964; Corda *et al.*, 1966). Fusimotor drive to respiratory muscles has been found to be of two types—tonically discharging units and units which discharged rhythmically with the respiratory frequency (Corda *et al.*, 1966). Of the two, the "rhythmic" gamma motoneurones seemed to be coactivated with the alpha motoneurones and were silenced by a high-spinal section. The "tonic" gamma motoneurones, on the other hand, remained active in the spinal preparation and were more responsive to proprioceptive reflex activation and to other stimuli.

8.2.2. *Masticatory movements*

Unlike limb movements, jaw movements display more unique features. While the jaw closing muscles can develop a great amount of tension, the jaw opening muscles exhibit much weaker activity (Anderson, 1956; Lamarre and Lund, 1975). The former also are richer in muscle spindles. Thus jaw movements display a great disparity in coupling between the agonist–antagonist muscles when compared to the flexors and extensors acting around various joints in the extremities.

Access to the first order afferent neurones from jaw muscle spindles is easily obtained through microelectrodes inserted into the mesencephalic tract (Taylor and Davey, 1968; Cody *et al.*, 1972). An analysis of the discharge of muscle spindle afferents in the jaw closing muscles of both the cat (Cody *et al.*, 1975) and the monkey (Goodwin and Luschei, 1975) reveals that coactivation of alpha and gamma motoneurones is present. However, the fusimotor drive may not be significant to initiate or control the jaw movements (Cody *et al.*, 1975).

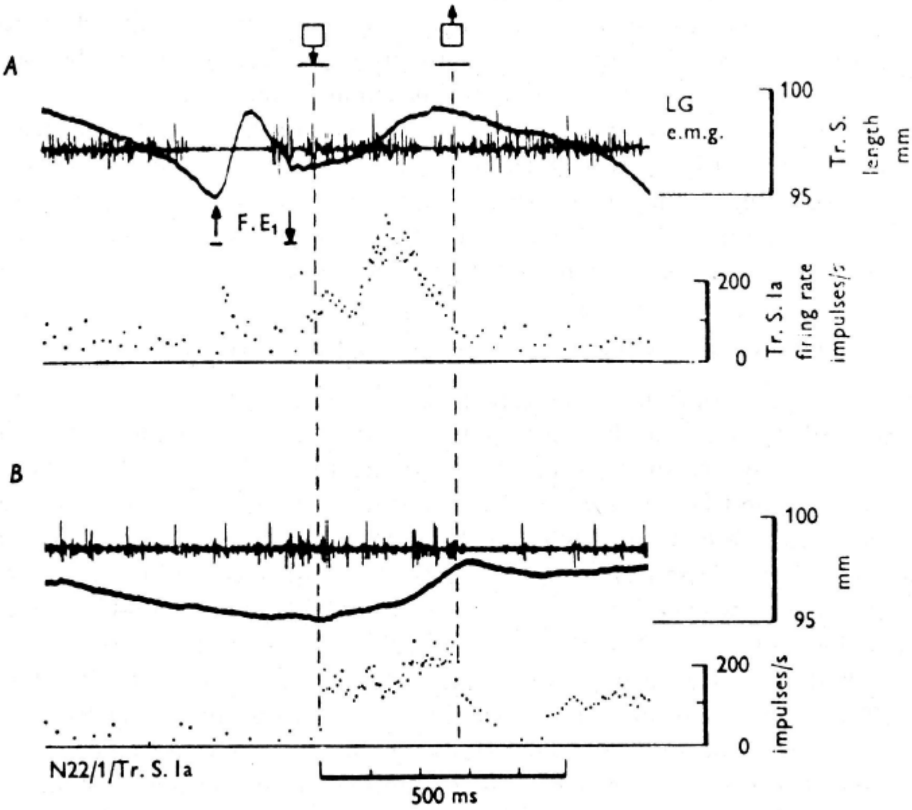

FIG. 17. Behavior of an ankle extensor spindle primary ending in the cat during application of a light thrust to the animal's back (arrows). A: Thrust applied just after onset of E_2 phase of a step. B: Thrust applied during a slow extension (reproduced with permission from Prochazka *et al.*, 1977).

8.2.3. *Stepping movements*

Wetzel and Stuart (1976) have reviewed in detail the fusimotor contributions to locomotion. Specific instances of increased or subdued fusimotor influences may be detected in various phases of locomotion (Prochazka *et al.*, 1977). A considerable increase in ankle extensor fusimotor drive may occur on the application of a light thrust to the animal's back (Fig. 17). The toe extensor spindles may receive very little fusimotor drive under identical conditions (Loeb and Duysens, 1978), though this feature may be related to the fact that these muscles display very weak alpha–gamma coactivation during walking. In addition, it seems that fusimotor drive may differ in intensity to different spindles in the same muscle during locomotion (Loeb and Duysens, 1978). Both types of gamma motoneurones (static and dynamic) have been thought to be coactivated with alpha motoneurones during locomotion (Perret and Buser, 1972; Perret and Berthoz, 1973). Strongest alpha–gamma coactivation is probably displayed by the ankle extensor muscles (Severin, 1970).

The observations of Sjöström and Zangger (1976) in spinal cats indicate that the alpha–gamma linked pattern is organized at the spinal level. Recently, another aspect of alpha–gamma linkage has come to be recognized as an important feature in the coupling of activity in agonist and antagonist muscles. This is the "alpha–gamma linked reciprocal inhibition" (Hongo *et al.*, 1969) in which a convergence of pathways which evoke alpha–gamma linked movements onto Ia inhibitory interneurones has been shown (Hultborn *et al.*, 1976). Such a mechanism will ensure that the gamma-assisted effects are not only limited to agonists but affect the antagonists as well through the reciprocal inhibitory pathways (Hultborn *et al.*, 1976). In human subjects such alpha–gamma linked reciprocal inhibition may be observed during a voluntary contraction (Tanaka, 1976; Morin and Pierrot-Deseilligny, 1977).

8.2.4. *Scratching movements*

Scratching movements which consist of fast alternating movements of the limbs may be elicited in a reflex (Sherrington, 1910) and display a postural component in addition to the rhythmic electromyographic activity in the muscles (Deliagina *et al.*, 1975). Feldman *et al.* (1977) studied the activity of ankle flexor and extensor muscle spindles during such scratching movements in decorticate (thalamic) and in spinal cats. Alpha–gamma coactivation was observed in such movements. Feldman *et al.* (1977) also noted that the rhythmic activity in ankle spindles started much earlier than the appearance of electromyographic activity.

8.3. EFFECT OF LOADS AND GAIN CONTROL

Validity of the arguments for pure gamma-initiated movements in a "load-compensating" reaction (Hammond *et al.*, 1956) relies upon the following:

(1) Existence of fast afferent inputs to the motor cortex which could then act on such information to modulate movements appropriately.

(2) Existence of fast cortical efferent pathways to fusimotor neurons.

(3) Adequate "loop-gain" of the feedback system in which motor output is regulated by altering the sensitivity of the stretch receptors (excitation "across the gamma loop").

Evidence is available in favor of each of the above points (refer Matthews, 1972), but counter arguments have also been advanced. Merton and his collaborators have continued to gather evidence for the power of the gamma loop in compensating for load disturbances (Marsden *et al.*, 1972, 1976a, b, 1977).

An important consideration of fusimotor contribution to motor performance is the relative value of pure gamma-bias versus an added gain control, particularly in gamma-assisted movements. An alpha–gamma coactivation may be present in either case. In the intact animal, gamma-bias may be modulated in near isometric conditions as found in hind limb muscles of a cat (Fig. 18) lying on its back and stretching out its legs (Prochazka *et al.*, 1977) or in the jaw muscles of a cat licking its lips after a meal (Cody *et al.*, 1975). Cody *et al.* (1975) point out that the spindle discharge is held constant under conditions of fluctuating fusimotor drive while the muscle underwent considerable amount of shortening. Such gamma-assisted movements in a conscious walking cat can also display features which indicate that the fusimotor drive may not necessarily be sufficient to fully compensate for the unloading of the spindles during extrafusal muscle shortening (Prochazka *et al.*, 1977). On the other hand, occasions in which gain control may be of importance have been observed in alpha–gamma linked locomotory patterns recorded in acute spinal cats (Sjöström and Zangger, 1976).

A unique situation of powerful load compensating reaction in which the fusimotor pathway appears to be effective in a servo-control mechanism has been described for the respiratory muscles (Eklund *et al.*, 1964; Euler, 1970), but such a reaction may display both inhibitory as well as excitatory responses to a suddenly applied load in the case of human (Newsom Davis and Sears, 1970).

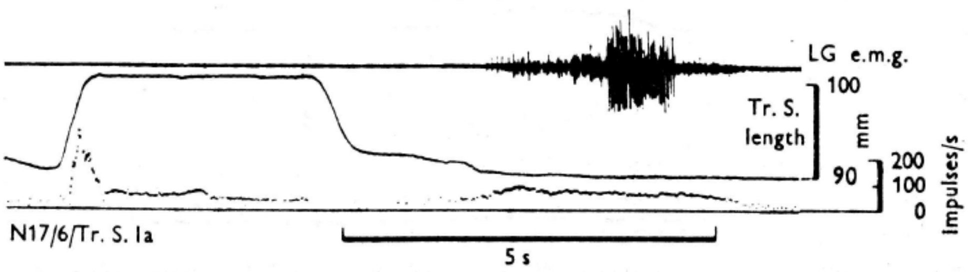

FIG. 18. Behavior of an ankle extensor Ia afferent in the cat with the animal lying on its side. In the first part of the record the responses to passive dorsiflexion of the ankle followed by passive plantar flexion are observed. In the second part the cat stretches out, illustrating alpha–gamma coactivation under isometric conditions (reproduced with permission from Prochazka *et al.*, 1977).

8.4. THE BETA FUSIMOTOR ACTION

The beta (skeletofusimotor) innervation represents a rigid form of alpha–gamma linkage and appears to be widely present in the cat hind limb muscles (see Section 2.5) as well as in the amphibian and reptilian species in which it was originally described. In addition to the slower-conducting beta fibers initially described (Laporte and Emonet-Denand, 1976), faster-conducting beta axons have also been now described (Harker *et al.*, 1977). At least on current evidence there appears to be a functional dichotomy with the slow beta axons innervating the dynamic nuclear bag intrafusal fibers and possessing an action similar to that of the dynamic gamma axons, and the fast beta axons innervating the chain intrafusal fibers and having an action similar to that of the static gamma axons (Harker *et al.*, 1977). Thus in the case of the mammal, it is to be noted that the collaterals of beta axons (both fast and slow) innervate the less fatiguable muscle fibers which are also connected to the motoneurones that receive the strongest monosynaptic excitation from Ia afferents (Burke, 1973). The beta fusimotor system in the mammal thus presents an interesting example of positive feedback mechanism that needs to be investigated in detail.

Murthy and Taylor (1978) have studied the limitations of the beta innervation in the frog hind limb muscles which were made to work under a variety of compliant loads. The most prominent peripheral effect of a beta fusimotor action is the pronounced initial burst of spindle discharge at the onset of a tetanic contraction and subsequent unloading due to extrafusal muscle shortening. However, for less compliant loads, the spindle discharge persists during the plateau of muscle contraction. With a monosynaptic connection to the motoneurone both in the amphibia (Holemans *et al.*, 1966) and in the mammal (Burke and Tsairis, 1977) this would constitute a positive feedback mechanism (Murthy and Taylor, 1971b; Houk, 1972). However, such a positive feedback may work to advantage in sharpening up the speed of muscle contraction and actually result in improvement of the stability (Houk, 1972).

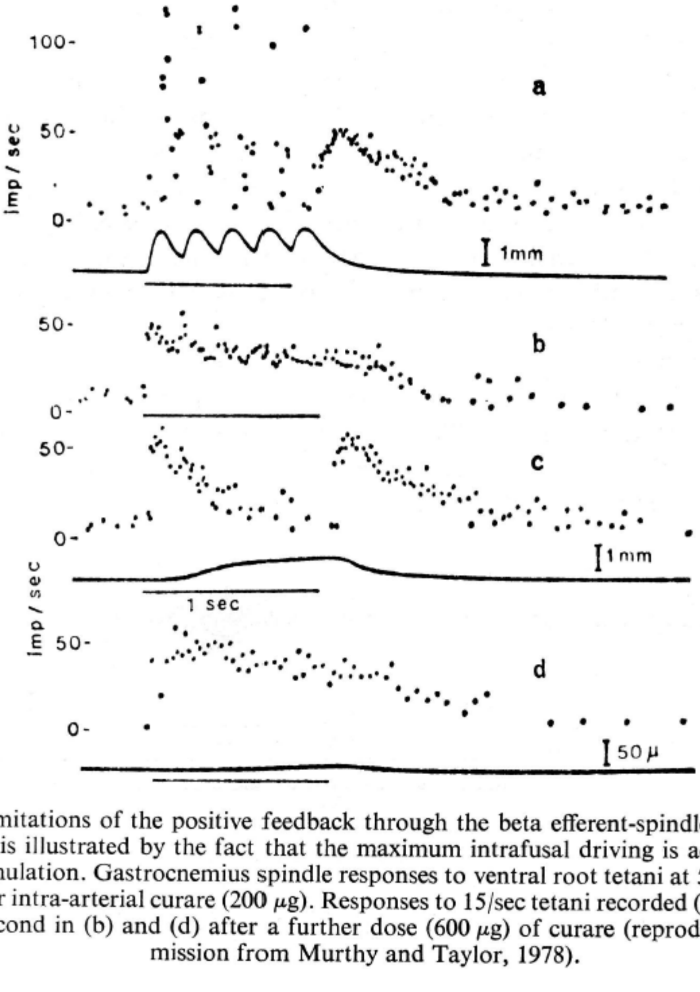

FIG. 19. Limitations of the positive feedback through the beta efferent-spindle afferent loop in the frog is illustrated by the fact that the maximum intrafusal driving is achieved at low rates of stimulation. Gastrocnemius spindle responses to ventral root tetani at 5/sec (a) before and (b) after intra-arterial curare (200 μg). Responses to 15/sec tetani recorded (c) immediately after the second in (b) and (d) after a further dose (600 μg) of curare (reproduced with permission from Murthy and Taylor, 1978).

Another feature of this positive feedback system which might be self-limiting is revealed when the amphibian muscle is paralysed with a critical dose of D-tubocurarine which leaves the intrafusal end plates unaffected (Murthy and Taylor, 1978). When the extrafusal contractions are selectively abolished by this procedure, fusimotor input is capable of driving the spindle discharge only to a maximum rate of 50 imp $\sec^{-1}$ (Fig. 19). Higher rates of spindle firing were obtained only under passive stretch or relaxation of the muscle.

8.5. ANTICIPATORY FUSIMOTION

While the power of the gamma loop in indirectly initiating movements has had a critical analysis, gamma effects have indeed been observed in the absence of alpha effects to extrafusal muscle fibers (measured as electromyographic activity). One such instance has already been described in Fig. 17 which shows an increase in spindle firing without concomitant electromyographic activity in the same muscle on application of slight pressure on the back of a conscious cat either during quite standing or during stepping (Prochazka *et al.*, 1977). The amount of fusimotor activation resulting from such a stimulus may not be entirely meant as a "load compensating reflex" but as a general reaction to a postural disturbance.

Gamma excitation can also precede the alpha activity in a muscle considerably earlier in time as observed in reflexly elicited scratching movements (Feldman *et al.*, 1977). Such a feature has been called by Granit as an "arousal" of the motor system (Granit, 1970, 1975).

The main point of disagreement between Struppler's and Hagbarth's experimental observations from human subjects appears to be whether or not the gamma excitation can occur in a noncontracting muscle. While the Munich group has observed (Burg *et al.*, 1974) such gamma excitation to occur in noncontracting muscles during reinforcement maneuvers (causing an "arousal" reaction), the Uppsala group showed (Hagbarth *et al.*, 1975c) that muscle contraction does occur in an identical situation. Hagbarth *et al.* (1975c) used sensitive tension transducers to record muscle tension. It is, however, apparent from an analysis of the muscle force and torque under the two contrasting situations that the activated alpha motoneurones may not be of the same type. In many instances during Jendrassik maneuvers, Hagbarth *et al.* (1975c) could not record an electromyogram, but they could observe the effects in the form of a change in the torque of joint movements. The possibility that activity of tonic alpha motor units may have been present under such a situation needs to be considered.

The gamma effects observed in reinforcement maneuvers have been suggested to be predominantly on dynamic fusimotor neurones (Burg *et al.*, 1974; Granit, 1975). Thus, a coactivation of dynamic fusimotor neurones may occur along with the smaller tonic alpha motoneurones during such arousal reactions in contrast to the static gamma-phasic alpha coactivation observed during voluntary movements. While the latter form of alpha–gamma coactivation is well established, the former is to be demonstrated clearly. There are, however, a number of results in support for the use of dynamic fusimotor action during an anticipatory motor excitation (Tanji and Evarts, 1976; Tanji, 1976). The response of the muscle spindle Ia afferents to a sudden stretch depends upon the level of fusimotor excitation prior to such a stretch (Brown *et al.*, 1969a) and such prior excitation through dynamic fusimotor neurones would be most effective (Rack, 1970).

In this respect, a comparison of the amphibian and mammalian fusimotor control is very useful (Figs 2 and 3 and Table 1). Both static fusimotor neurones in the mammal and the twitch motor system in the amphibia are most effective during a *decrease* in muscle length. On the other hand, the mammalian dynamic fusimotor neurones and the amphibian tonic motor neurones are most effective during an *increase* in muscle length. Also, the tonic motor system in the amphibia appears to be mostly used in postural movements, exhibiting activity (spontaneous or reflexly elicited) prior to the discharge of the twitch motor neurones (Kuffler and Vaughan Williams, 1953; Chambers and Simcock, 1960). Granit and Henatsch (1956) have pointed out the effectiveness of the gamma control of the dynamic sensitivity of the spindle endings as contributing to a powerful but indirect gamma-excited movement.

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Some of the advantages to the mammal of being endowed with separate gamma motoneurones are revealed in studies of spindle afferents during rhythmic natural movements. The experiments of Feldman *et al.* (1977) illustrate how in the decorticate or spinal cat the scratching movements display differences in fusimotor drive to the flexors and extensors, with the fusimotor radiation to the flexors being stronger. Also such fusimotor effects may occur prior to extrafusal contractions. Fluctuating fusimotor drive to the same spindles in jaw closing muscles occurs depending upon the purpose of the movement (eating or lapping) even though the magnitude of movement may be similar (Cody *et al.*, 1975).

Loeb and Duysens (1978) recorded the activity of spindle afferents in a number of hind limb muscles of the cat during normal locomotion and concluded that fusimotor drive differed in character depending upon the function of the muscles. Loeb and Duysens (1978) also found "isolated" fusimotor effects (in the absence of alpha drive) in muscles which were affected by the movements but were not directly causing the movements.

The most interesting role for gamma drive leading the alpha motoneurone activity in a muscle is revealed during an abrupt voluntary change of speed during normal locomotion (Loeb and Duysens, 1978). The ankle flexor muscle spindles which during the slower gait show a burst of discharge when the ankle flexes (alpha–gamma linkage), display a burst at the beginning of the flexion when the animal voluntarily accelerates the gait. Such a phase advance in spindle activity occurs before any significant change in electromyogram and before the faster gait appears. This observation and others discussed earlier strongly suggest that the effects of a gamma–lead in movements contribute to temporal advancement of effects on alpha motoneurones, contributing to the speeding up of movements.

8.6. EFFECTS OF A SELECTIVE LOSS OF GAMMA CONTROL

A number of investigators have attempted to study various aspects of motor behavior when the neuromuscular control system is deprived of the gamma efferent influence. Two techniques have been most popular:

(1) Injection of local anesthetics to selectively block the smaller diameter efferents in muscle nerves;

(2) Investigations during reinnervation of a previously denervated muscle.

While the gamma block was shown to be without any significant effects on the tonic stretch reflex in cats (Feldman and Orlovsky, 1972) as well as human subjects (Neilson, 1973), it is well documented that human subjects tended to exhibit "overshoot" in voluntary movements (Smith *et al.*, 1972) when deprived of gamma control. This behavior was most pronounced in fast limb movements with high initial velocities (Shambes, 1969; Smith *et al.*, 1972). In addition, the postural sway of the human subjects was also found to increase after the gamma block (Shambes, 1969).

Applying differential block of the mandibular branch of the trigeminal nerve, Abbs (1973) was able to record changes in speech patterns of his subjects. During gamma block, the subjects exhibited clear differences in the amount of jaw opening and the speed of jaw movements. They were, however, able to compensate somewhat with lip movements which gave the subjects a sense of normal articulation.

After a peripheral denervation of the muscle nerve either by sectioning and allowing it to regenerate through a millipore filter (Thulin, 1960) or by producing degeneration by application of dry ice around the nerve and letting it regenerate (Takano, 1976b), it has been shown that the gamma efferents require a longer time to regenerate. Loss of gamma control may be present for as long as 8 weeks after the alpha fibers have regenerated (Thulin, 1960; Thulin and Blom, 1974).

In addition to these techniques to study effects of a lack of gamma influence, it has been shown that newborn kittens do not show significant gamma control in hind limb muscles for a period of up to 20 days (Skoglund, 1960a, b). This preparation may afford an opportunity to study the function of the developing gamma system. The decerebrate rigidity due to hyperactive gamma motoneurones is first demonstrable in the forelimbs of kittens at about a fortnight after birth and in the hind limbs at about 20 days after birth (Skoglund, 1960a). The development of beta fusimotor innervation may precede the gamma innervation in kittens (see Fig. 7 in Skoglund, 1960b). This feature may explain the appearance of the tonic stretch reflex in the decerebrate kitten much earlier in life than the development of decerebrate rigidity due to the gamma efferents (Skoglund, 1960a).

9. Concluding Remarks

The most significant recent finding of peripheral gamma effects is the fact that static fusimotor fibers *reduce* the sensitivity (gain) of the spindle primary endings (Fig. 20), reducing the static sensitivity by a factor of ten for low amplitudes of muscle stretch (Goodwin *et al.*, 1975; Hulliger *et al.*, 1977a, b) in addition to reducing their dynamic sensitivity for large amplitudes of muscle stretch (Matthews, 1972; Crowe and Matthews, 1964a, b). Thus, the major role of the static fusimotor neurones is likely to be one of "gain control" during voluntary movements, particularly since these have been found to be co-activated with the alpha motoneurones during muscle contraction in a variety of situations discussed in this review. The dynamic fusimotor neurones, on the other hand, *increase* the gain of the spindle primary endings to large amplitudes of muscle stretch while having no significant effects at small amplitudes of muscle stretch. Such a feature is most likely to be useful in speeding up the mechanical response at the onset of a voluntary movement.

It is also significant that of the two types of fusimotor efferents, only the static gamma efferents can elicit a 1:1 response, i.e. driving the spindle endings (Crowe and Matthews, 1964b; Appelberg *et al.*, 1966) and that the static gamma effects can completely occlude the dynamic gamma influences (Hulliger *et al.*, 1977b; Lennerstrand, 1968). If this were not so, the enhancement of dynamic sensitivity of spindle endings to minor fluctuations (noise) in voluntary movements would be quite bothersome. Thus during voluntary contractions, coactivated static fusimotor drive provides the appropriate control to reduce the dynamic sensitivity of Ia afferents.

It has become common practice to look for fusimotor effects purely on the basis of a change in the firing rate of muscle spindle afferents (see discussions in Section 7.1). This is hardly sufficient when the afferents are firing at low rates. It is a widely observed feature in the nervous system that the responsiveness to a stimulus is a function of the level of resting

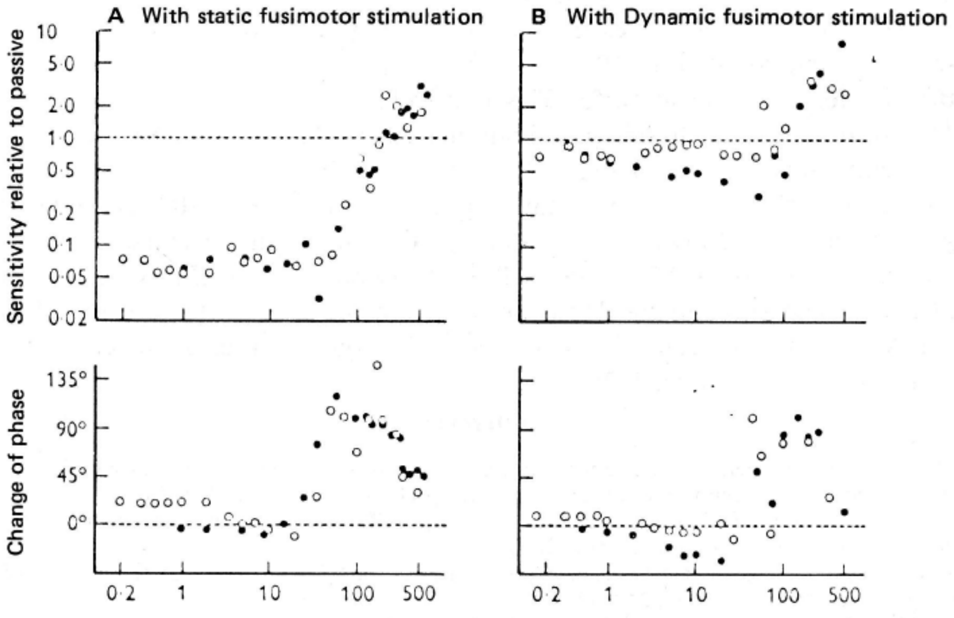

FIG. 20. Ten-fold reduction of the gain (sensitivity) of the Ia ending by stimulation of the static fusimotor fiber during small amplitude, low frequency sinusoidal stretch. The sensitivity has been normalized with respect to that in the absence of stimulation. Note the dynamic fusimotor fibre has hardly any effect for such low frequency small amplitudes of muscle stretch (reproduced with permission from Goodwin *et al.*, 1975).

or background activity. In the human, in particular, muscle spindle afferents seem to discharge at less than 20 imp sec^{-1} rates. Coupled with this, if the rates of fusimotor impulses themselves are below 10 imp sec^{-1}, the effects are observed more in a change of latency of the response of the spindle afferents to a mechanical stimulus rather than in an increase in their rates of discharge. Even if there was a change in the rate of spindle afferent discharge due to a change in fusimotor bias, such changes will be impossible to detect if they are under 50 imp sec^{-1}. This is due to the fact that at rates of less than 50 imp sec^{-1}, the inter-spike intervals are in the range of latencies for segmental reflexes. Thus fusimotor effects are likely to be countered or even masked by the extrafusal muscle contractions. Hence it is necessary to look also for temporal influences of a changing fusimotor bias.

Some features of significance relating to fusimotor control in the human are beginning to be uncovered in microelectrode recordings. One such feature illustrates that increase in spindle discharge in a muscle during voluntary contraction will be accompanied by a decrease in activity of less active synergists (Burke, 1978). Another feature of interest is that the spindle sensitivity is held maximum during a lengthening contraction (Burke *et al.*, 1978b).

Finally, the relevance of anticipatory fusimotion to agonist–antagonist coupling in motor control needs to be considered. In all movements, the muscles work against a load. This load need not be external; in most cases, the load is set by the antagonistic muscles against which the agonist muscles work. It may well be that some gamma drive would be destined for setting up a tone in the antagonist which would undergo a stretch as the agonist muscle contracts. So far, there is no evidence for the existence of this feature, but such a mechanism might provide sufficient facilitation of the antagonist alpha motoneurones to permit their synchronous activation as they are released from reciprocal inhibition.

Acknowledgments

I wish to thank Drs P. B. C. Matthews, Y. Laporte, M. C. Brown, K. E. Hagbarth, A. Struppler, A. B. Vallbo and A. Prochazka for permission to reproduce illustrations from their publications. Drs K. E. Hagbarth, G. E. Loeb and D. Burke made available some of their manuscripts prior to publication. Drs. Hagbarth and Burke also critically reviewed the sections pertaining to human data.

Acknowledgments are also due to the following:

(1) The editors of the Journal of Physiology for Figs 2A, 3, 4, 5, 7A, 11, 17, 18 and 20.
(2) Elsevier/North-Holland Press for material in Figs 7B and 9.
(3) Dr B. L. Andrew for Fig. 2B.
(4) British Medical Association for Figs 15 and 16.
(5) The editors of Acta Physiologica Scandinavica for Figs 12, 13 and 14.
(6) Academic Press for Figs 6 and 19.

I am grateful for the encouragement and support provided by the staff of the Department of Surgery in general and my colleague Philip L. Gildenberg in particular. Support for my own work has been provided by a general research grant of The University of Texas and equipment obtained through the Houston Endowment. It is a pleasure to acknowledge Ms Elena Vess and Ms Leah Alexander for typing the manuscript in record time. The review was completed in June, 1978.

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