Modulation of postural reflexes by voluntary movement

1. Modulation of the active limb

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SUMMARY Experiments were performed involving isometric activation/relaxation of the agonist-antagonist muscle groups about the ankle joint. It is shown that phasic changes of foot torque in the dorsal direction are associated with a transient inhibition of the soleus H-reflex which is independent of anterior tibial contraction. During phasic changes in foot torque in the plantar direction, facilitation, as opposed to disinhibition of the soleus H-reflex, is graded by soleus contraction. These results support the hypothesis that the sensitivity of the monosynaptic reflex arc is one of the controlled variables of the motor system. The stretch reflex of a shortening muscle is generally facilitated, while that of a lengthening muscle is inhibited. These hypotheses are in keeping with our present knowledge of the linkage between skeletomotor and fusimotor neurones for the organization of voluntary movements.

The widespread influence of voluntary muscular contraction upon tendon-jerk reflexes (Jendrassik, 1883; Bowditch and Warren, 1890; Fearing, 1928) was recognized even before the monosynaptic nature of those reflexes was demonstrated (Lloyd, 1943, 1946; Magladery and McDougal, 1950; Magladery, Porter, Park, and Teasdale, 1951). These early studies were, for the most part, of the knee jerk and voluntary contractions were of remote muscles such as the arms.

The ability to record the electromyogram (EMG) of the voluntarily and the reflexively contracting muscles greatly increased the sensitivity and precision of such experimental techniques. Of special importance was the ability to record reflex EMG responses from the same muscle that was undergoing voluntary contraction. Hoffmann (1922), using electrically evoked monosynaptic reflexes (now called the Hoffmann or H-reflex), and later Paillard (1959, 1965), using both H and tendon jerk reflexes, showed clearly that tonic voluntary contraction of a muscle facilitates the spinal component of the

monosynaptic reflex arc of that muscle. At the same time they also showed that tonic voluntary contraction of the muscle that was antagonist to the muscle in which the reflex was elicited, produced inhibition of the monosynaptic reflex.

These findings were recognized as fully in keeping with established properties of the nervous system. When a single motoneurone pool is the final common path for converging excitatory inputs, it is reasonable to expect that a tonic excitatory input will facilitate the response to a temporally discrete converging volley. The well-known reciprocal patterns of spinal innervation also suggest that a descending excitation upon one motoneurone pool is likely to be accompanied by an inhibition of the antagonistic motoneurone pool which originates both centrally and from afferent nerve fibres.

The fact that the sensitivity of the spinal reflexes can be and is modulated by voluntary contraction of the reflex agonist and antagonist muscles is of great importance because of the possible role the stretch reflex may play in the control and coordination of voluntary move-

ments. Merton's (1953) servo hypothesis that voluntary movements may be initiated through this reflex arc would make monosynaptic sensitivity one of the dominant parameters of the motor system. The less speculative suggestion by Granit (1971) of an alpha-gamma linkage effecting voluntary motor control also places great emphasis on the importance of this reflex pathway for the organization of voluntary movements.

It is of interest, therefore, to ask if the sensitivity of the monosynaptic reflex arc is one of the *controlled* parameters of the nervous system. The fact that this sensitivity is *altered* by tonic contraction is not sufficient evidence for, as noted above, we expect such changes as consequences of the fact of alpha motoneurone activation. It is necessary, therefore, to examine the dynamic behaviour of the reflex sensitivity during phasic contractions of the reflex agonist or antagonist muscles.

Previous investigations have shown that a vigorous muscular contraction is preceded by a large increase in the sensitivity of the monosynaptic reflex, whether tested by electrical stimuli (Gottlieb, Agarwal, and Stark, 1970; Kots, 1969a, b; Pierrot-Deseilligny, Lacert, and Cathala, 1971), stretch (Gurfinkel and Pal'tsev, 1965) muscle unloading (Angel, Garland, and Alston, 1970) or vestibular stimuli (Nashner, 1970). This increase begins approximately 50 msec before the appearance of the EMG of voluntary muscle contraction by which time it reaches its maximal level (Gurfinkel and Pal'tsev, 1965; Kots, 1969a; Pierrot-Deseilligny *et al.*, 1971). The sensitivity subsequently declines to levels which are dependent on the level of sustained muscle contractions (Gottlieb *et al.*, 1970; Gottlieb and Agarwal, 1971).

These investigations have also shown that contraction of the reflex antagonist muscle produces an inhibition of the monosynaptic reflex that begins with the onset of the voluntary EMG, becomes stronger as the contraction progresses and finally diminishes to levels dependent on the level of sustained contraction as the phasic portion of the contraction is completed.

We have more recently shown that these phenomena are not dependent on mechanisms peculiar to the organization of only the fastest and most vigorous contractions but are observed

under conditions of much slower, deliberate contraction as well (Gottlieb and Agarwal, 1972).

Such experiments as these show that there is no observable temporal correlation between the EMG of voluntary phasic muscle contraction and the observed modulation of the monosynaptic reflex arc. As such, they may be taken as evidence for making a functional distinction between mechanisms for the recruitment of alpha motoneurons in a voluntary contraction, and those associated with the accompanying modulation of reflex sensitivity which takes place. The experiments described in this paper are intended to support the necessity for these distinctions and to describe further the patterns of reflex modulation that occur during voluntary muscle contraction.

This paper will be concerned only with voluntary contractions of the reflex agonist and antagonist muscles. A companion paper will discuss interactions with contractions of more remote muscles (Gottlieb and Agarwal, 1973).

Those elements of the peripheral motor system with which we shall be concerned are diagrammed in Fig. 1. They consist of the alpha and gamma motoneurone pools, the muscle, the mechanical load moved by the muscle, and the sensory spindle of the muscle with its primary afferent nerve fibres. The diagram may seem unusual in that the Ia afferent fibres do not connect

FIG. 1. A simplified block diagram of the peripheral motor system. Three classes of controlling signals from higher centres are shown: N_1 signals generate efferent outflow from the alpha motoneurone pools, N_2 signals regulate the sensitivity of the monosynaptic reflex arc, and N_3 signals determine fusimotor activity which influences spindle performance.

directly with the alpha motoneurone pool but rather pass their information first through a junction where it is modulated by the signal N_2 which originates in supraspinal centres. This diagram is not intended to deny the monosynaptic connection between Ia afferent and alpha efferent nerves. It is intended, rather, to make entirely explicit the superordinate influence which higher centres exert over the sensitivity of this reflex arc. The mechanism of this control may be pre-synaptic (Eccles, 1964, 1967; Decandia, Provini, and Tabořikova, 1967) or postsynaptic—that is, dendritic—(Rall, Burke, Smith, Nelam, and Frank, 1967; Kuno and Llinás, 1970) but cannot be determined by the experiments described here. The effects of this influence and their time-course during voluntary efforts are the subject of our inquiry.

EXPERIMENTAL PROCEDURE

These experiments tested the sensitivity of the Ia afferent—alpha motoneurone monosynaptic arc over the full time-course of a (repeated) voluntary effort. Seven adult male subjects were used in the study.

Electrical testing stimuli (20–60 V, 1.5 msec monophasic pulse from a Grass S-8 stimulator with SIU5 isolation unit) were delivered to the tibial nerve in the popliteal fossa. The stimulating electrodes were positioned and strapped in place and the stimulus intensity adjusted so that an H-reflex was elicited in the triceps surae muscles. Differential cutaneous electrodes (1 cm discs) placed low on the midline of the soleus muscle recorded the EMG reflex volley (H-wave). The peak-to-peak amplitude of the H-wave, amplified by a Tektronix 2A61 unit with 60–600 Hz bandwidth, was used as the measure of reflex response. All experiments were done at stimulus intensities below those at which most soleus alpha motor axons would have been excited (Magladery and McDougal, 1950; Magladery *et al.*, 1951; Paillard, 1959).

The electrodes used to measure the H-wave also recorded the EMG of voluntary soleus contraction. A similar pair placed over the anterior tibial muscle and amplified by a second Tektronix 2A61 unit were used to measure voluntary contraction of that muscle.

Before recording the EMG of voluntary contraction, the signals were full-wave rectified and filtered by a third order low-pass filter with 100 Hz cut-off (Agarwal and Gottlieb, 1969). This procedure provides an excellent measure of the EMG envelope.

The experiments were performed by asking the

FIG. 2. Diagram of the experimental apparatus. Stimuli were triggered by the computer which recorded foot torque and EMGs on digital magnetic tape. The computer-controlled target was a spot on the face of the dual beam Tektronix 502A CRT. The subject could control the position of a second spot on the face of the 502A by varying the force he exerted on the rigid foot plate. Not shown is a fifth analogue data line by which the computer could also record the stimulus itself.

subject to track a computer-controlled target which jumped between two positions on the face of the cathode ray tube (CRT), by varying the force exerted on the rigid aluminium foot plate (Agarwal and Gottlieb, 1969). This plate was clamped and the foot strapped to it so that the efforts were essentially isometric. At random times during these tracking efforts, an H-reflex was elicited by the computer and recorded on magnetic tape. A diagram of the apparatus is shown in Fig. 2.

In order to distinguish clearly these experiments from those reported previously (Gottlieb *et al.* 1970; Gottlieb and Agarwal, 1972) it is useful to define a term 'track' to describe the voluntary efforts. As used here, a track is a dynamic change in voluntary, isometric foot torque (torque being the actual measured variable produced by muscular tension) made by the subject in following the target. A plantar track is a change in torque in the plantar direction and a dorsal track is a change in the dorsal direction. No constraint is placed by the term on the absolute level of foot torque.

In these and previous experiments, the subject made alternate plantar and dorsal tracks at seven to 10 second intervals in following the target. In these experiments, however, the tracks involved the alternate contraction and relaxation of a single muscle

or group. Thus, the subject would alternately contract and relax the anterior tibial muscle to generate alternating dorsal and plantar tracks, as shown in Fig. 3, or he would alternately contract and relax the soleus muscle to generate alternating plantar and dorsal tracks. As Fig. 3 shows, only a single EMG would be active during such efforts but both were always recorded.

One further factor to be noted is that, in order to measure the facilitation or inhibition produced by

FIG. 3. The time-course of a voluntary dorsiflexion followed by a plantar-going relaxation. Only the anterior tibial muscle is electromyographically active. Bottom trace shows foot-torque (starting from zero torque at the left), middle trace shows anterior tibial EMG (increasing upward), and top trace shows soleus EMG (increasing downward). Time scale 0.2 sec/unit, EMG 1 V/unit, torque 0.2 kg-m/unit.

the dynamic phase of the track, computations of relative facilitation were made with the following equation:

$$\Delta H = (H_p - H_s)/H_s$$

Here, H_p is the amplitude of the H-wave elicited during the phasic track. H_s is the amplitude of an H-wave, elicited at the same level of sustained, static foot torque.

DATA REDUCTION

Three types of analogue signals were digitized by the computer and recorded on digital magnetic tape. These were the foot torque, recorded at 250 samples per second (SPS), the rectified and filtered EMGs from the soleus and anterior tibial muscles, recorded

at 500 SPS and the unfiltered soleus EMG at 1000 SPS.

The foot torque was measured by strain gauges attached to the arms of the foot plate shown in Fig. 2 and connected in a bridge circuit. This signal was used to compute numerically the first two time derivatives of the torque.

One source of variability we wished to remove from the data was the reaction time of the subject—the interval from the jump of the target on the CRT to the voluntary foot response.

The recorded data were aligned with respect to the start of each track so that this normal, variable reaction time could be eliminated. The start of the track was identified by the computer from the first derivative of the foot torque (Gottlieb *et al.*, 1970). This method gives times for the start of the movements which lag the appearance of the EMG of voluntary contraction by about 50 msec. The EMG could not be used as an indicator of the start of contraction because, in half of the tracks, there was no contraction of an agonist muscle, only relaxation of the nominal antagonist. The sensitivity of the algorithm is quite good as can be seen in Figs 4 and 5 where the tracks have been aligned to start at the 200 msec point. Each figure is the average of 20 individual tracks, generated by taking the ensemble averages of the prealigned data.

In Fig. 4B it will be noted that the dorsal track appears to be preceded by a 'false start' in the plantar direction. This is an artefact produced by those reflex muscular contractions (plantar twitches) which were elicited before the voluntary initiation of the track.

We have already noted that the EMG of voluntary contraction was rectified and filtered before being measured by the computer. The information contained in such a signal is assumed to be a measure of the level of activity of the motoneurone pool innervating the muscle.

One problem which had to be faced was that the voluntary EMG signals were contaminated by the stimulus and H-wave artefacts which were usually an order of magnitude greater in amplitude. These artefacts were removed numerically by finding the value of the EMG immediately before the stimulus, the value 50 msec later and linearly interpolating a straight line between those two values to replace the measured EMG over that time interval. This is successful with only a 50 msec interpolation (effectively discarding 50 msec of recorded EMG data) because, during phasic contractions such as we are dealing with, the silent period and subsequent rebound in the EMG do not occur (Agarwal and Gottlieb, 1972). The ultimate justification for the procedure is that ensemble averages that have been so processed, such

FIG. 4. Averages of 50 tracks involving soleus contraction (a) and relaxation (b). Top trace is foot torque, second, and third traces are its numerically computed first ($\dot{FT}$) and second ($\ddot{FT}$) derivatives. Bottom trace shows full-wave rectified and filtered EMGs of the soleus (increasing downward) and anterior tibial (increasing upward) muscles. Alignment of individual tracks before averaging was done by detecting the start of FT.

as shown in Figs 4 and 5, are not distinguishable from averages of data from tracks in which no stimuli were delivered and therefore required no artefact removal (Agarwal, and Gottlieb, 1969).

Finally, the H-wave was measured by taking the maximum peak-to-peak values of the unfiltered soleus EMG signal. To enhance the accuracy of this measure, estimates of the true peaks were made by quadratic interpolation at the extrema of the sampled values. Comparisons between computed values and those measured from the face of a CRT monitor showed agreement within 3% for the two methods.

RESULTS

Figure 4 shows tracks involving alternating contraction and relaxation of the soleus muscle while Fig. 5 shows similar data for tracks involving the active participation of only the an-

terior tibial muscle. The top curve in each case shows the recorded foot torque. The second and third curves show the first two time derivatives of the foot torque computed numerically. The fourth curve is of the voluntary EMG with soleus increasing downward and anterior tibial increasing upward.

Parts a of both these figures are plantar tracks, while parts b are both dorsal tracks. These data show several differences between the relaxation tracks (4b and 5a) and the contraction tracks (4a and 5b).

Relaxation tracks are slower and more prolonged than their corresponding contraction tracks. This is evident from the curves of the time derivatives.

The most important distinction is found in the

FIG. 5. Averages of 51 tracks involving anterior tibial contraction (b) and relaxation (a).

EMGs. In a plantar track, the soleus EMG has a peak value of about 1.1 V when it is contracting (Fig. 4a) but, during a plantar track accomplished by relaxation of the anterior tibial muscle (Fig. 5a), soleus EMG never exceeds 0.1 V. Analogous observations can be made of the two dorsal tracks where the contracting anterior tibial muscle generates a peak EMG of about 4.7 V (Fig. 5b), while when the track is generated by soleus relaxation (Fig. 4b), anterior tibial EMG is less than 0.1 V.

Although we have indicated that each track should theoretically involve the contraction or relaxation of a single muscle, there is some EMG activity observed in the other muscle. The level of this activity is quite low but is nevertheless indicative of a degree of coactivation of the antagonistic muscle groups. Cross-correlations of the anterior tibial and soleus muscle EMGs show the signals to be independent. Therefore, the activity cannot be ascribed to 'cross-talk'

or pickup of one muscle's EMG by electrodes placed over its antagonist.

The data showing modulation of the H-reflex during these tracks are presented in Figs 6 and 7. As noted in the preceding section on experimental procedures, during the course of a track, an H-reflex was elicited and recorded. Also recorded were the instantaneous values of the foot torque and of the EMG of voluntary contraction just before the stimulus. If we define a time origin as the moment when the first detectable change in foot torque occurs, then we may plot the data versus time and observe what consistent changes occur throughout the time courses of the tracks.

Figure 6a shows the value of the foot torque versus this interval of Time After Initiation (TAI) of the track. The $\times$ points correspond with the plantar track of Fig. 4a and the $\circ$ points with the dorsal track of Fig. 4b. The range of TAI

FIG. 6. The results of a tracking experiment involving alternating contractions and relaxations of the soleus muscle (averaged in Fig. 4) (TAI—Time After Initiation). (a) Foot torque versus TAI. (b) Relative H-wave amplitude versus TAI of voluntary muscle contraction. (c) Voluntary EMG (rectified and filtered) in the 'agonist' muscle versus TAI. (d) H-wave amplitude versus foot torque. Δ points are static observations, $\times$ points recorded during a plantar track, $\circ$ points recorded during a dorsal track.

(0–400 msec) corresponds with the 200–600 msec range of Fig. 4.

Figure 6b shows the H-wave variation (ΔH as defined by the equation) versus TAI. The absolute values of these H-waves are plotted in Fig. 6d versus the values of foot torque present at the instant the H-wave occurred. Figure 6d also shows the static dependence of H-wave amplitude on maintained foot torque (Δ points) which was used to compute ΔH .

Figure 6c shows the voluntary EMG versus TAI. We show the soleus EMG only during the plantar track and the anterior tibial EMG during the dorsal track. They merely confirm, for individual data points, what may be deduced from the average responses in Fig. 4—that is, the plantar track was generated by soleus contraction and the dorsal track was generated by soleus

relaxation, rather than by anterior tibial contraction.

Figure 7 shows the same type of data for tracks involving contraction/relaxation of the anterior tibial muscle. The average responses for these data are shown in Fig. 5.

DISCUSSION

The observed changes in H-wave amplitude can be produced by phenomena occurring at at least three sites. These are the site of stimulation in the popliteal fossa, the alpha motoneurone pool in the anterior horn of the spinal cord and at the muscle itself where the EMG is recorded. If we are to be able to consider a change in H-wave amplitude as reflecting a change in the size of the efferent volley to a constant afferent

FIG. 7. As in Fig. 6, except tracking involved alternating contractions and relaxations of the anterior tibial muscle (averaged in Fig. 5).

stimulus, we must rule out the first and last of these. This can be done by examining the M-wave response to the electrical stimulus.

The M-wave is a synchronized EMG burst which is produced by direct electrical excitation of alpha fibres in the popliteal fossa (Magladery and McDougal, 1950; Magladery, Porter, Park, and Teasdale, 1951). It appears in the EMG approximately 9 msec after the stimulus as opposed to the 35 msec it takes for the H-wave to circumnavigate the reflex arc. This latency is too short to be explained by anything except direct, orthodromic conduction from the stimulus site, peripherally to the muscle.

The tibial nerve is a mixed nerve and contains a heterogeneous group of both sensory and motor fibres. At the stimulus intensities used, there was always a small M-wave present in the recorded EMG, although by proper electrode placement it could be reduced to less than 10%

of the H-wave in the relaxed muscle. Any change in the size of the effective stimulus—that is, the number of excited fibres—would be expected to be equally evident in both H and M-waves (Taborikova, Provini, and Decandia, 1966; Mark, Coquery, and Paillard, 1968). The Table

TABLE
CORRELATION ANALYSIS OF DATA IN FIGURE 7

	H-wave (MV)	M-wave (MV)	Stim. (V)	H × M	H × S
All data (51 pts)	2.75 (1.38)	0.24 (0.04)	27.5 (0.3)	-0.067	0.174
Plantar tracks (25 pts)	3.47 (0.27)	0.24 (0.01)	27.4 (0.2)	-0.016	0.064
Dorsal tracks (26 pts)	2.07 (1.66)	0.23 (0.05)	27.5 (0.4)	-0.196	0.313

Numbers in parentheses are standard deviations. H × M is the correlation coefficient between H and M waves. H × S is the correlation coefficient between the H wave and the recorded stimulus.

shows the correlation between H-wave, M-wave and recorded stimulus intensity for the data from Fig. 7. It is plain that the H-wave is uncorrelated with the M-wave and also with the small changes in the recorded stimulus (which is a measure of total system noise, since there was absolutely no variation in stimulus intensity visible on the laboratory monitor).

These data also exclude the possibility of explaining the H-wave results as a purely muscular phenomenon since, to the muscle, both H and M-waves are alike. We are forced to look to the spinal cord for an explanation and to conclude that a change in H-wave amplitude signifies a corresponding change in the motor volley, in the face of an unchanging sensory stimulus.

Turning to the data of Figs 6 and 7, we can first note that a dorsal track is associated with inhibition of the soleus H-reflex. This is accomplished whether the anterior tibial alpha motoneurone pool is active (as it is in Fig. 7) or quiescent (as it is in Fig. 6).

The very small amount of anterior tibial activity evident in the dorsal track during soleus relaxation (Fig. 4b) cannot account for the depth of the observed H-wave inhibition (to less than 0.5 mV for three responses in Fig. 6d). That phasic burst of EMG activity never exceeds 0.1 V. Tonic anterior tibial contraction producing over 1 V of EMG activity (Fig. 5b) does not inhibit the H-wave below about 3 mV (Fig. 6d, Δ points).

We can also exclude sensory inputs from producing this inhibition. During the dorsal track of Fig. 6, there is little likelihood of exciting Golgi tendon organs of the soleus muscle. Furthermore, if we assume that the track is not perfectly isometric (probably a reasonable assumption without having pinned the skeleton) the soleus muscle would undergo some lengthening, thereby exciting the Ia afferent fibres of the spindles. This would produce excitation, if anything.

Since we cannot correlate the observed H-wave inhibition with any observed peripheral variable, we may interpret this as an inhibition of central, descending origin, but one which is not simply reciprocal with anterior tibial excitation.

In the case of the plantar tracks, no such clear case can be made. Soleus contraction produces a facilitation of the H-reflex which is apparently

graded by the vigour of the effort. In the absence of soleus activation, when the plantar track is accomplished by relaxation of the anterior tibial muscle, the H-wave does not appear elevated above its amplitude in the relaxed limb (Fig. 7d). This may be simply a matter of disinhibition. However, noting in Fig. 5a that relaxation of the anterior tibial muscle is accomplished gradually over a 500 msec interval, the release of the soleus from inhibition is manifest within the first 100 msec (Fig. 7b, see also Gottlieb and Agarwal, 1972). We still have, therefore, modulation of the monosynaptic reflex arc which fails to show any temporal correlation with peripherally measurable variables over the course of the track.

It is important to distinguish the tracks accomplished by relaxation of the nominal antagonist muscle from previous studies of H-reflex alteration when the subject is told to suddenly relax (Paillard (1965), p. 221). Our subjects were performing a tracking task in which they learned to avoid contraction of a particular muscle, even when that would have helped in following the target. This cannot be equated with the instruction to 'relax', although a specific muscle relaxation does occur. In the above cited work, 'relaxation' is associated with a profound, transient inhibition of both H and tendon jerk reflexes. Here and elsewhere (Gottlieb and Agarwal, 1973), we have found that the effects of relaxation of specific, previously voluntarily contracted muscles have different effects. Since the instructions given to the subject can have a strong effect on the outcome of the experiment (Paillard, 1965), the observed differences in results are probably so ascribable.

CONCLUSIONS

In discussing the interpretations of these findings, we would like to free ourselves of the constraint imposed by the isometric nature of the experiments. Considering the exquisite sensitivity of the muscle spindle to changes in muscle length, it is almost certain that these tracks were not 'isometric' to the muscles' own sensors. In this light then, both types of plantar tracks, achieved by soleus contraction or by anterior tibial relaxation, were accomplished with some accompanying shortening of the soleus muscle. Similarly, both types of dorsal tracks were accompanied

by slight lengthening of the soleus muscle. Under most normal physiological conditions, the tracks would be accompanied by significantly greater changes in muscle length, depending, of course, on the opposing mechanical load.

These experiments indicate that, in a lengthening muscle, the sensitivity of the stretch reflex is reduced by descending signals which to a large measure are independent of those other descending signals which regulate the activities of the alpha motoneurone pools.

In a similar manner, in a muscle which is to shorten, if there is a pre-existing inhibition, that inhibition is withdrawn even while the alpha motoneurone pool of its antagonist is active. The degree of facilitation of the stretch reflex in this muscle is graded by the degree to which the muscle is activated but the pattern of reflex facilitation differs from that of alpha motoneurone recruitment.

In the light of recent findings on the coactivation of alpha and gamma motoneurons (Vallbo, 1971), our results only emphasize the necessity for recognizing that voluntary muscle control is organized, not merely for the control of an alpha motoneurone pool but for the control of a powerful and active negative feedback system embodied in the myotatic reflex. Voluntary movements may apparently be initiated by direct activation of the alpha motoneurone pools. However, coactivation of the fusimotor neurone pools assures a rapid afferent response concerning events in the periphery. Simultaneous control of reflex sensitivity provides that the shortening muscle will be especially sensitive to such sensory inputs. It also insures that the lengthening muscle will not oppose the movement. This is fully in keeping with the recent demonstration of the sensitivity of the stretch reflex in normal voluntary movements of the thumb (Marsden, Merton, and Morton, 1971).

That reflex modulation by voluntary muscular activity can and does occur is an old and proven fact. That this reflex modulation must be looked at as a distinguishable entity apart from and of potentially great importance to the modulation of alpha motoneurone activation is not yet a proven phenomenon but a hypothesis worthy of further investigation.

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