

CROSSED SEGMENTAL INHIBITION IN MUSCLES

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INTRODUCTION

Muscle spindles are critically involved in the reflex regulation of the dynamic and static actions of muscles; the sensitivity of the actions is under strong efferent control^{2,8}. In the usually studied mammal, the cat, the receptor elements in the muscle spindles convey by two types of fibers (Groups I and II) muscle displacement and velocity information to the central nervous system. The functions of amphibian muscle spindles, usually studied in the frog, appear to be similar to mammalian although the spindles lack a separate system of efferent control and lack the secondary endings of mammalian spindles.

Frog skeletal muscle is also similar to mammalian in having twitch fibers, but in an important respect differs in that slow (tonic) muscle fibers are present⁶. In contrast with the cat, the hindlimbs of the frog are not as critically involved in postural adjustments. The animal normally sits on the ventral surface of the caudal end of its body with its hindlimbs folded. However, postural adjustments must be maintained during jumping, landing and swimming. The existence of the crossed extension reflex in the frog as in mammals suggests crossed segmental inhibition between homonymous muscles of the hindlimbs^{4,12}, but rather than reciprocal innervation of crossed extensor and flexor muscles as in the mammal, at least jumping (take-off) and swimming behavior in the frog must be determined by a different kind of central organization. Hindlimb movements in the frog are typically synchronized in extension and flexion.

In the present study the properties of frog muscle spindles have been used to establish the quantitative relationships between the gastrocnemius muscles of the two limbs for various stretch velocities and preloadings and to describe the interactions of the limb muscles. The somewhat unique organization of the gastrocnemius muscles in the frog suggests a special functional role.

MATERIALS AND METHODS

Decapitate adult frogs (*Rana pipiens*) were prepared for the study of reflex tension in hindlimb gastrocnemius muscle groups. With a minimum of manipulation

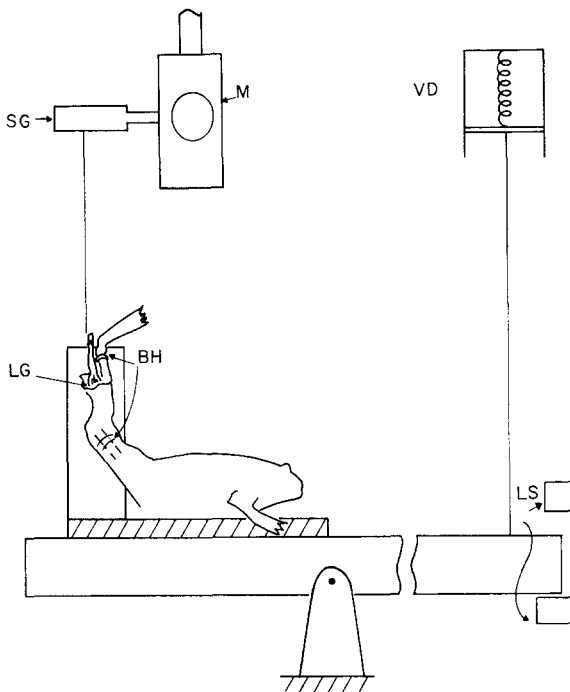


Fig. 1. Modified Sherringtonian fall table. The right end of the fall table is pulled upward by the spring in the viscous damper (VD) when the table is released. The viscous damper sets the velocity of fall table at a constant value depending on the size of the adjustable oil flow aperture. The travel of the table is limited by the limit stops (LS). The frog is pulled downward by the action of the fall table stretching the muscle, in this case the left gastrocnemius (LG). The leg is pinned at two points by bone hooks (BH) as shown. The tension is measured by a strain gauge (SG) mounted in a manipulator (M). The right gastrocnemius is stretched in the same manner.

the gastrocnemius muscles were freed throughout their middle portion from their bone attachments. Cords were placed around the freed Achilles tendons. On each limb a clamp was placed around the femur and another around the ankle (Fig. 1). These were drawn tight to the mounting apparatus. Each Achilles tendon was attached to a strain gauge (range 0–100 g).

The apparatus was designed so that the muscles could be stretched simultaneously, at constant velocity, for 2 mm, by a Sherringtonian-type fall table³. The procedure was to preload one muscle with 2 g and to preload the other with 0–10 g before applying each simultaneous stretch at different but constant velocities. Small differences in preloading were found to have an appreciable effect upon the tension developed under stretch. The important factor was the actual amount of preloading upon muscle spindles. The relationship between tension on the Achilles tendon and tension on muscle spindles undoubtedly varied among preparations. Further, it was not possible to set *exact* tensions on the muscle and it is reasoned that the preloadings varied by perhaps 20% from preparation to preparation. Once they were set it was possible to maintain the preloadings within 10%.

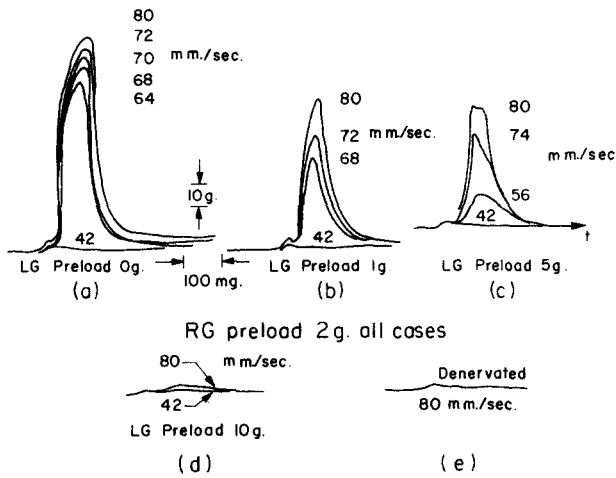


Fig. 2. Reflex twitch responses of right gastrocnemius at various stretch velocities and with different preloadings. Stretch velocities indicated for the tension curves. Velocities were measured from the slopes of fall table displacements. LG and RG are left and right gastrocnemius. In a, 0 g loading for LG, no stretch was applied to LG for it was slack.

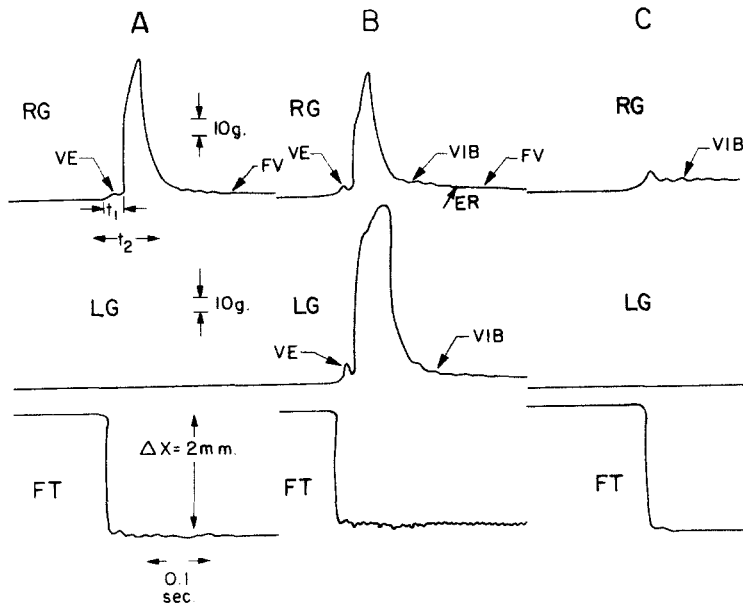


Fig. 3. Representative tension data for 3 experimental conditions. RG and LG are right and left gastrocnemius. FT is fall table displacement. Column A, RG 2 g preloaded and stretched, LG slack. Column B, RG and LG 2 g preloading. Column C, RG and LG denervated, RG 2 g preloading and stretched. Calculations from FT's show stretch velocities to be 66 mm/sec. Start of stretch indicated by passive viscoelastic response (VE). VIB: fall table vibration; ER: probable elastic resistance of muscle; FV: final value of tension.

Each preparation was given several series of tests at the 0–10 g preloadings. Tests were separated by 5 min intervals to insure that the muscles returned to their initial state. At the completion of the series of tests the muscles were denervated and stretched with 2 g preloading in order to determine the passive contribution to stretch response.

Output of the strain gauges and fall table displacements were recorded with DC amplifiers and pen writers.

RESULTS

Constant velocity stretching of the frog gastrocnemius over a distance of 2 mm elicited a reflex twitch which was highly dependent upon the velocity of stretch. No detectable reflex response could be found for stretch velocities under 42 mm/sec (Fig. 2a). The representative data in this figure also show that the reflex tension development of the right gastrocnemius (RG) is greatly influenced by the existing preloading on the left gastrocnemius (LG) during the simultaneous stretch at different velocities. It was found that preloading LG but not stretching it, had no detectable effect on the tension development in RG.

Data from 3 experimental runs are shown in Fig. 3. These data show clearly that the reflex tension in RG was inhibited by the stretching of LG (Column B). The peak tension of RG in A was 73 g, in B it was 63 g. The reflex twitch is found to start approximately 70 msec after the onset of stretch and reach its peak in approximately 100 msec. These results were similar for different stretch velocities and for different preparations.

In Fig. 4 the peak tensions of the twitch responses for two preparations are plotted as a function of stretch velocities and preloadings of the opposite muscle. To establish base lines the muscles were denervated at the end of the experiments and peak tension curves were again obtained. It can be seen that the reaction of the muscle to stretch is essentially passive until a threshold is reached at approximately 40 mm/sec. At greater stretch velocities tension rises to higher levels and appears to approach a plateau. Increasing the preloading of the opposite muscle decreases tension development and at 10 g essentially abolishes the reflex response.

It is of interest that static preloadings of LG while only RG was tested with stretch produced no appreciable effect upon reflex tension. Further, no tonic effects on tension were observed as a result of preloadings without stretch.

During a jump and just prior to landing a frog's hindlimbs are fully extended. Upon landing, reflex extensor tension develops as muscles are stretched. The fall time from toe touch to body touch (hindlimbs in folded position) was determined in normal frogs with their eyes covered. An oscilloscope and two simple electrical circuits were used for this and the fall time was determined to be approximately 100 msec.

DISCUSSION

From the results obtained in this study it is evident that there is a cross-cord

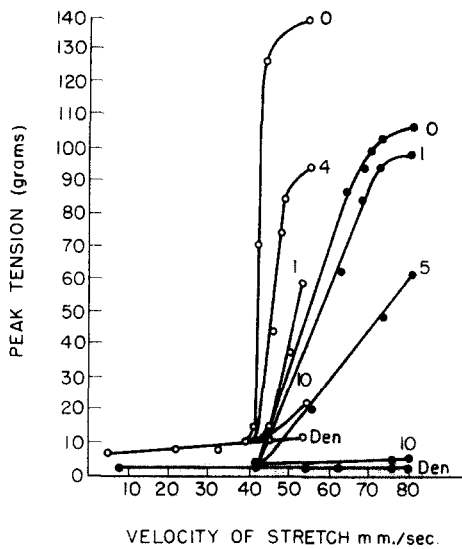


Fig. 4. Peak tensions of gastrocnemius at different preloadings as a function of various velocities of stretch. Data from 2 frogs, open and closed circles. RG always preloaded with 2 g. Numbers of curves are preloadings of LG. Den: LG and RG denervated. Length of stretch 2 mm.

inhibition of one frog gastrocnemius upon the other. This inhibition appears to be under velocity control rather than under position control since large static tensions produced no appreciable inhibition in the opposite side.

Matthews⁷ has shown that muscle spindle receptors in the cat have a discharge rate which is proportional to displacement and velocity of stretch and preloading.

In our experiments the tonic response for each level of preloading would be essentially the same since the displacement was the same in each case. Assuming a constant sensitivity of the stretch receptors the number of impulses impinging upon the motor neurons was then a function of preloading and stretch velocity.

The curves in Fig. 4 indicate that the effects of inhibition are not distributed uniformly over the pool of motor neurons contributing to the stretch reflex. If the inhibition was distributed uniformly the curves obtained for greater preloadings would not change in form, but would be shifted to the right.

A fractioning of the distribution of excitation and inhibition has been accepted since the time of Lloyd⁵ and has been given theoretical and experimental attention by Rall^{10,11}. Rall assumed a normal distribution of the number of monosynaptic endings on individual motor neurons and a normal distribution of threshold. An assumption of independent normal distributions of excitation and inhibition on the members of the motoneuron pool would produce curves similar to those of Fig. 4. Perhaps a rather simple organization of excitation and inhibition can give rise to the rather complex result suggested in the following discussion.

Our results suggest that the crossed segmental inhibition of the stretch reflex may be related to the frog's landing system. The development of tension begins 70 msec after the onset of stretch and reaches a maximum (peak) at 100 msec. The peak

of tension occurs almost at the instant of termination of the fall. This would 'soften' the landing greatly. The peak tension developed in the gastrocnemius is dependent on the initial loading on the gastrocnemius of the contralateral side as well as its own preloading. The relationships appear to be such that the greater tension is applied on the side that is closest to the landing surface and the least tension occurs on the side that is furthest from the surface. This would result in a correction torque which would counteract the imbalance in the frog's body. A landing system such as this is a 'predictive system' rather than a feedback control system. One might say that the necessary tension to be applied for satisfactory landing is predicted from the information obtained from muscle spindles stretched at moment of touchdown. There is time for only one correction and this correction is a function of prior muscle spindle information. This system is not entirely satisfactory in all cases. Frogs may topple when landing, on certain uneven surfaces. In addition, visual and vestibular systems must contribute substantially to landing in normal frogs.

Engberg¹ has carried out an extensive study of foot muscle reflexes in the cat. Engberg has found that extensor activity of planar muscles follows the pattern of other extensors of the hindlimb. The activity in the planar muscles begins shortly before the foot is placed on the ground. The planar muscles together with the extensor digitorum brevis constitute a system that makes the foot rigid when these muscles contract simultaneously. This system may also be regarded as a predictive system.

The simultaneous control of both intrafusal and extrafusal muscles by the motoneurons in the frog's neuromuscular system may produce an effect not found in mammals. Since branches of the same axon subserve both extrafusal and intrafusal muscle fibers the first activation of extrafusal muscle will be accompanied by an increased sensitivity of the muscle spindles. This in turn increases the afferent discharge of the muscle spindles and further excites the motoneuron pool. The system thus experiences a positive feedback situation. Under certain conditions positive feedback can cause system instability and the output can grow without bound⁹. The conditions for instability would be present only during stretch and the system would return to a quiescent state after the stretching of the muscle had ceased. Increased stretch velocity could increase the amount of positive feedback in the system and increased inhibition could decrease the amount of positive feedback.

The reflex twitch observed in our experiments may thus be a result of a temporary regenerative condition which exists during stretch.

SUMMARY

1. In decapitate frogs the response of both gastrocnemius muscles to constant velocity stretch was studied with one muscle under constant preloading and the other under a range of preloadings.

2. The reflex response was first elicited at a threshold stretch velocity of approximately 40 mm/sec and subsequently increased for higher stretch velocities.

3. The effect of increasing the preloading of one muscle was to decrease the response of the muscle with constant preload, but the velocity threshold (40 mm/sec) did not change.

4. Tests of the fall time of frogs in a landing simulation and the stretch response results suggest that the frog may utilize a predictive control system to facilitate landing.

5. Results suggest a non-uniform distribution of excitatory and inhibitory effects on the motorneurons.

ACKNOWLEDGEMENT

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