REFLEXES EVOKED BY RHYTHMIC STIMULATION OF MUSCLE NERVES

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As we all know, when skeletal muscles are stretched, either brief reflex responses (tendon reflexes) or prolonged, steady contractions result. The phasic stretch reflexes have been quite thoroughly studied [3, 4, 9]; but efforts to make use of the data obtained in this way to characterize static strength reflexes, which are of immeasurably greater biological importance, have run up against serious difficulties [5, 8, 13]. In the papers referred to, it was established that static reflexes evoked by rhythmic stimulation of the afferent fibers of muscle nerves can not be regarded as combinations of phasic responses. In contrast to the phasic reflexes, static stretch reflexes require for their development the presence of an initial level of motoneuron activity, as well as a relatively high stimulus frequency–conditions that favor summation of successive afferent impulses. In view of these facts, further study of static proprioceptive reflexes is needed. In particular, there is considerable interest in obtaining an answer to the question raised by N. E. Vvedenskii, regarding the effect of strength and frequency of stimulation on the course of reflex reactions.

In the present paper, we will set forth data on the way reflex excitation and inhibition of extensor muscles depend on the strength of rhythmic stimulation of the central ends of muscle nerves, and on the relation of these phenomena to excitation of particular groups of nerve fibers.

METHODS

The experiments were carried out on 40 decerebrate cats, with marked decerebrate rigidity. In both hind limbs the muscles that move the knee joint were denervated, with the exception of the quadriceps muscles. In the right limb, the nerve to the deep and medial heads (vasti cruralis et medialis) of the quadriceps femoris, or the nerve to the deep head alone, was exposed and sectioned. Immersion electrodes (Ag–AgCl, interelectrode distance 3 mm) were applied to the central end of this nerve (the words "central end" will be omitted hereafter). In some experiments an indifferent anode was used. The nerves were stimulated with electrical impulses of rectangular form (duration 0.07 msec, or sometimes 1 msec), from a stimulator with a stimulus isolation unit. Starting and stopping of the kymograph, and application of stimuli, were automatic. Stimuli were applied for two-second periods, at one-minute intervals. The stimulus intensity is indicated throughout as percent of threshold intensity.

The animal was placed in the supine position, and the femoral bones were fastened in the vertical position. Movements of the tibia (changes in the angle between the femur and the tibia), reflecting changes in the tone of the quadriceps, were recorded by means of isotonic myographs.

RESULTS

Rhythmic stimulation of the muscular branches of the femoral nerve were capable of producing both reflex contraction and deep inhibition of the tone of those heads of the ipsilateral quadriceps that were still innervated (Fig. 1). Contractions of significant magnitude developed only in response to stimulation at a rather high frequency (above 50 per second); accordingly, a stimulus frequency of 100 per second was employed. These contractions were like an enhancement of tone in character–i.e., the curves rose smoothly to a maximum, and remained at this level, in the form of a plateau, as long as stimulation continued (more than 10 minutes: Fig. 1a). Rapid, short contractions preceding the main response were observed only now and then, in response to relatively intense stimulation. But these contractions must be regarded as a response to the first afferent volley, since they disappeared or diminished when the stimulus frequency was reduced. In most cases, stimulation produced reflex contraction of the contralateral quadriceps (Fig. 1).

When impulses were applied to the nerve to the deep and medial heads of the quadriceps while the animal was in a condition of marked decerebrate rigidity, distinct reflex reactions were always observed. The maximum contraction seen upon stimulating this nerve for two seconds corresponded to extension of the knee joint of from three to 25 degrees, in the various experiments. For the smaller nerve to the deep head, the contractions were smaller (1–15 degrees) and occurred in only about half of the experiments. When both nerves were stimulated for longer periods, much stronger contractions were sometimes seen (extension of 30–50 degrees).

The intensity of the reflex responses was found to depend on the intensity of the stimulus applied to the muscle nerves. An increase in stimulus amplitude above threshold was accompanied by an increase in the height of contraction to a certain maximum level (Fig. 1b). In some experiments the stimulus intensity that produced the strongest contraction when applied to the nerve to the deep and

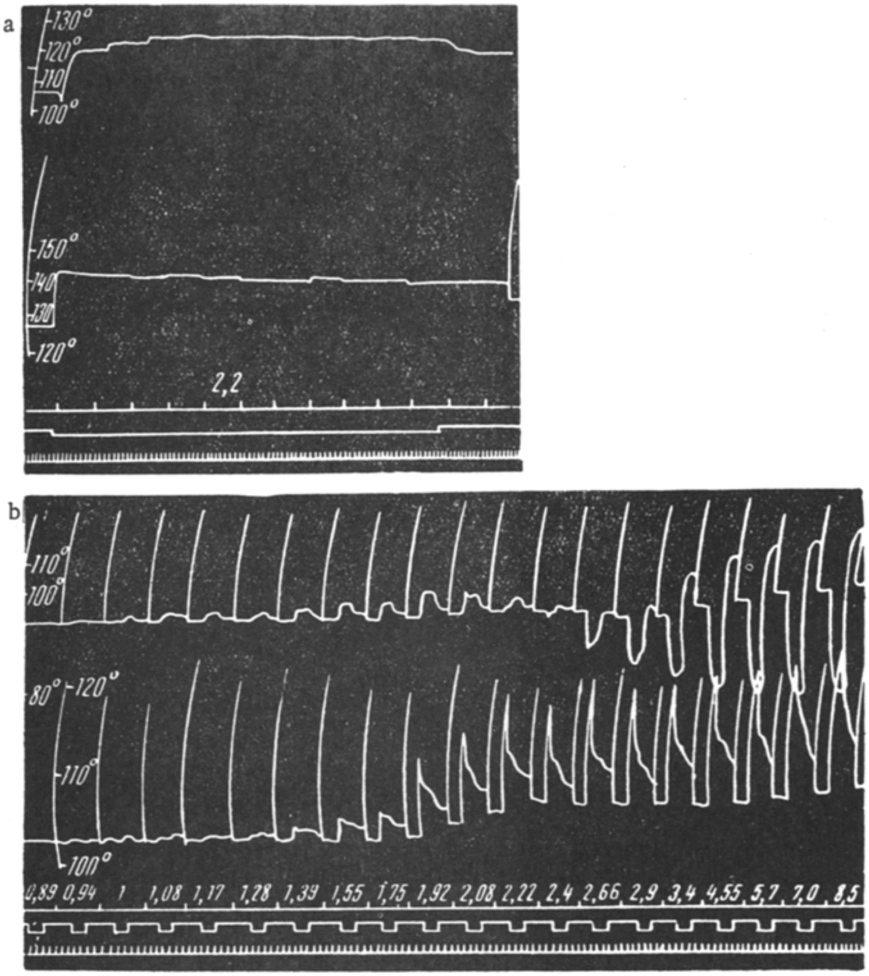

Fig. 1. Quadriceps reflexes in response to stimulation of the central ends of muscle nerves. Interpretation of records (top to bottom): movement of right (ipsilateral) tibia; movement of left tibia (upward movement corresponds to extension); mark indicating when kymograph was stopped (for one minute); stimulation of nerve to deep and medial heads of quadriceps; time marker (1 second). The vertical scale indicates the position of the limb, in degrees of angle between femur and tibia. a) prolonged stimulation (more than 10 minutes); b) stimulation for two seconds. Figures indicate intensity of stimulation: 0.89; 0.94; 1.0; 1.08; 1.17; 1.28; 1.39; 1.55; 1.75; 1.92; 2.08; 2.22; 2.4; 2.66; 2.9; 3.4; 4.55; 5.7; 7.0; 8.5 (with respect to threshold).

medial heads was between 1.4 and 2.4 times the threshold intensity (42 out of 50 determinations on 17 animals). Maximal contractions were particularly often observed at intensities of 1.8–2.2 times threshold intensity (19 determinations).

A further increase in the stimulus intensity usually resulted in lessening of the height of contraction, and then, in replacement of contraction by relaxation (see Fig. 1b). In these cases the end of stimulation was often accompanied by a return to the initial state. This sort of relationship between the height of response and the stimulus intensity was recorded in 22 out of 29 instances. The minimum stimulus intensities at which relaxation of the muscle below the initial level occured were 2–3.2 times the threshold intensity in most cases. In response to more intense stimuli, inhibition became more profound, and reached its greatest depth at stimulus intensities of 4–8 times threshold, or more.

In some animals reflex contractions was more pronounced, in others reflex inhibition, and in a third group both the positive and negative reactions were marked. This is indicated by the wide scatter of stimulus intensities marking the transition from contractions to relaxations. In five cases, there was no clear-cut display of inhibition, even when the stimulus intensity became very great. In some experiments, on the other hand, the contractions were very weak, but profound inhibition of the quadriceps developed readily.

In order to establish the connection between the character of reflex responses and stimulation of particular groups of afferent nerve fibers, it was necessary to compare thresholds for reflexes with those of afferent fibers of muscle nerves.

For observation of dorsal root action potentials, the animals were placed in a special stand, in the prone position. After laminectomy of the lumbar vertebrae, repeated determinations of the thresholds of reflex excitability were made. Then the dura mater was opened and a bundle of fibers from the fifth or sixth lumbar dorsal root was lifted with a ligature and placed across the recording electrodes. The roots were covered with liquid petrolatum. Then the thresholds of excitability of these afferent fibers were determined several times. Action potentials were recorded with the sweep frequency of the cathode-ray oscillograph synchronized with the rhythm of stimulation at 100 per second. Distances between the stimulating cathode and the recording electrode were measured on isolated nerves while they were tightly stretched.

It was found that when decerebrate rigidity was sufficiently marked, the thresholds of reflex responses were only slightly greater than those of the most excitable afferent fibers. In four experiments, the following mean values were obtained for the differences between these thresholds (in percents): 5, 1.5, 0, and 2. These differences are within the error of the determination of stimulus intensities corresponding to the different forms of reflex responses. We can therefore suppose that in most experiments the thresholds of reflex excitability rather closely reflected the thresholds of the afferent fibers. We might mention that for single stimulations of muscle nerves the differences between these thresholds are far greater [7].

The fact that the compound dorsal root action potential clearly displays several peaks when the muscle nerve is stimulated (Fig. 2) is in agreement with published data [7]. The relationship between the amplitude of the dorsal root action potential and stimulus intensity is shown in Fig. 3 (data from five experiments; the three middle curves show the relationship most frequently encountered, and the other two show extreme variations). The stimulus threshold was determined from the appearance of potential variations resulting from the excitation of fibers with a conduction velocity of 100-125 m/sec (fibers of Group I). As the stimulus intensity increased, this potential variation rapidly grew in size. At a stimulus intensity of 1.2 times the threshold intensity, the height of these potentials was usually 30 per cent of the maximum height (in individual experiments, from 20 to 50 per cent). At the same time, fibers with lower conduction velocities were brought into action, as shown by the broadening of the foot of the peak, which included action potentials being propagated with a velocity of 80–60 m/sec. In most experiments the amplitude of the first peak reached a maximum at stimulus intensities of 1.8–2 times threshold intensity. At these and greater stimulus intensities, all the fibers in Group I were active.

At stimulus intensities as low as 1.2–1.3 times threshold, a second peak appeared that was barely perceptible, which corresponded to velocities of 70-40/m sec and represented fibers of Group II. But up to a certain stimulus intensity, the amplitude of this peak remained low. At a stimulus intensity of 1.8-2 times threshold, the amplitude and areas of the second peak increased sharply. The increase in amplitude was primarily due to impulses traveling with a velocity of 50-40 m/sec. With further increases in stimulus intensity, several more peaks (from two to six) appeared on the screen. At intensities three times threshold, those fibers which had conduction velocities greater than 45-26 m/sec (in different experiments) were active; at stimulus intensities of five times threshold, fibers with conduction velocities of 30-20 m/sec were active.

Thus, stimulation of the central ends of nerves to the quadriceps femoris, at high frequencies (100 per second), in decerebrate regidity, causes contraction of the remaining heads of this muscle. Spread of excitation to the centers for close synergists may occur in response to single stimuli [11], but it is far more pronounced in response to rhythmic stimulation [5, 15]. In form and duration, the observed contractions correspond to the muscle contractions that determine body position, and they are a manifestation of the static stretch reflex. Such reflexes do not develop under conditions where static reflexes are absent in response to

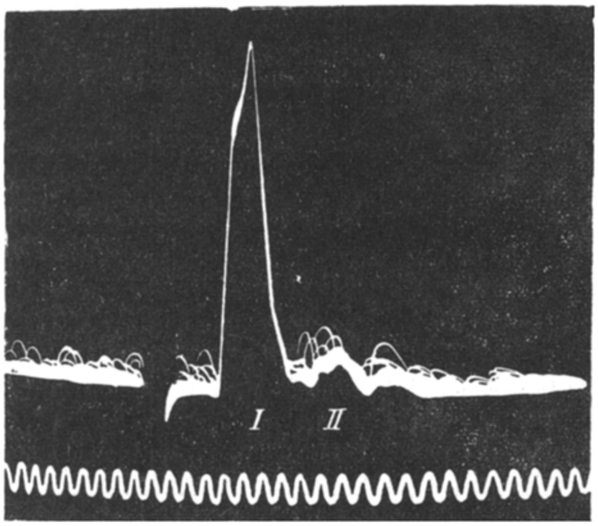

Fig. 2. Action potentials from the sixth lumbar dorsal root upon stimulation of the nerve to the deep and medial heads of the quadriceps. Stimulus intensity 4.5 times threshold. Frequency 100 per second. Distance between stimulating and recording electrodes 86 mm. Calibration 1 mv; time calibration 5000 c/s. I) first peak; II) second peak.

adequate stimuli [3, 12, 13]. Contractions of the quadriceps were observed following comparatively weak stimulation of the muscle nerves.

A comparison of the data obtained from recording of dorsal root action potentials and of reflex responses shows that muscle contractions occur principally in connection with the excitation of afferent fibers having the highest conduction velocities (90-125 m/sec), i.e., the fibers of the primary endings of the muscle spindles [6, 16]. Most of these fibers are active at a stimulus intensity of 1.5-1.7 times threshold intensity (Group Ia) [10]. But an increase in the height of contractions also occurs when stimulus intensities increase to values of 1.8-2 times threshold, where all the fibers of Group I are active. Proprioceptive inhibition in this instance is either weak or completely absent, although the fibers of the tendon receptors are known to be active (Group Ib).

The inhibition of quadriceps tone which was observed upon stimulation of muscle nerves was analogous to the inhibition which occurred when muscle stretch was increased. It was observed most frequently when the intensity of stimulation applied to the muscle nerve was sufficient (more than twice threshold) to excite a large number of afferent fibers in Group II (conduction velocity 70-35 m/sec). These are the fibers of the secondary endings of the muscle spindles, which are stretch receptors like the primary endings [6, 16]. These data indicate that impulses from the secondary endings are the principal factors producing inhibition when the muscle is lengthened. We have been unable to confirm the view that stimulation of tendon receptors plays the decisive role in the origin of stable autogenetic inhibition [4, 14].

It must be emphasized that in our experiments we stimulated not only afferent fibers, but also efferent fibers of muscle nerves, which, according to available published data [2], can inhibit motoneurons of the same muscle via reverse collaterals. At the present time, the character of such effects is not sufficiently understood. According to the data of P. G. Kostyuk [3], reverse collaterals are few

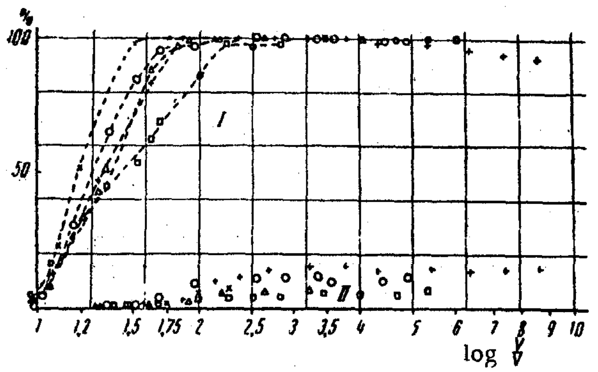

Fig. 3. Amplitude of action potential as a function of stimulus intensity. Abscissa) relative stimulus intensity (logarithmic scale); ordinate) amplitude of action potentials (maximum height of first peak taken as 100%). I) amplitude of first peak; II) amplitude of second peak. Data from five experiments shown (different symbols).

in number. Although theparticipation of antidromic impulses has not been completely excluded, the probability that strong inhibitory influences spread not only to "their own," but also to an extensive field of synergistic motoneurons via reverse collaterals is not very great.

Reflexes in response to stimulation of muscle nerves display wide variability, similar to that which is seen with adequate stimulation of proprioceptors [1]. In individual animals, we observed substantial differences in the character of reflex excitation and inhibition accompanying stimulation of the same nerve. We must suppose that these characteristics of reflex activity in individual animals depend to a large extent on facilitatory and inhibitory influences from the medulla.

SUMMARY

Experiments were performed on cats in decerbrate rigidity. Stimulation of the central ends of some nerves to the quadriceps femoris muscle (100 stimuli per second) evoked a steady contraction or relaxation of the other heads of this muscle. Contractions corresponding to the myotatic reflex are observed with comparatively weak stimuli. Contractions appeared and increased in amplitude in response to stimulation of afferent fibers of Group I (with stimulus intensities up to 1.8-2 times threshold intensity, and with conduction velocities of 70 m/sec and above). Proprioceptive inhibition developed with relatively strong stimuli (more than twice threshold intensity), and was connected with activity of afferent fibers of Group II (conduction velocity of 70-35 m/sec), although the possible importance of antidromic impulses in efferent fibers is not completely excluded. The idea that tendon receptors are of decisive importance in the origin of autogenetic inhibition has not been confirmed. Substantial differences are displayed in the character of reflex excitation and inhibition in individual animals.

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