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ANALYSIS OF AFFERENT AND EFFERENT SYSTEMS IN THE MUSCLE NERVE OF THE TOAD AND CAT

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The method of isolating single nerve fibres (Kato, Kaku & Tasaki, 1935; Tasaki & Takeuchi, 1941) enables us to survey all the nerve impulses, afferent and efferent, carried by individual nerve fibres, myelinated and unmyelinated. This series of experiments was designed to contribute, by means of this direct method, to the analysis of afferent and efferent nerve systems by which the skeletal muscle is connected with the spinal cord.

On the large afferent fibre system in the muscle nerve, a considerable amount of work has already been done by previous investigators (Forbes, Campbell & Williams, 1924; McCouch, Forbes & Rice, 1928; Adrian & Zotterman, 1926; Bronk, 1929; Matthews, 1931*a*,*b*, 1933). Through these investigations, the physiological properties of the sensory nerve endings located in the belly of the muscle, i.e. the muscle spindles, have been fully elucidated. Matthews (1933) further describes the behaviour of the sensory endings lying in the fascia associated with muscle. According to the results of our investigation, however, there are at least three other types of sensory endings in the muscle, including those corresponding apparently to the tendon organs.

Turning now to the analysis of the efferent systems in the muscle nerve, the well-known work of Adrian & Bronk (1929) gives almost complete information as to the behaviour of the large, quick motor nerve fibres. More recently, the physiological properties of the small, slow motor nerve fibre (Tasaki & Kano, 1942; Kuffler & Gerard, 1947) have been repeatedly investigated (Tasaki, 1942; Tasaki & Tsukagoshi, 1944; Kuffler, Laporte & Ransmeier, 1947). There is, however, another efferent fibre system in the muscle nerve, namely the unmyelinated efferent fibre system.

We propose in this paper to present the summary of all the results we have so far obtained. The main part of this work was done in 1944 at the

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Physiological Institute, Keio University. The paper was originally written in 1949 before we had seen the work of Kuffler and his collaborators on the small efferent fibres of mammals (Kuffler, Hunt & Quilliam, 1951; Hunt & Kuffler, 1951*a*, *b*). Our conclusions differ from theirs, but we still believe that our view represents one function of these fibres even if not the only one. Since we have had no opportunity to repeat either our own experiments or theirs, we have thought it best to present our conclusions in their original form.

METHODS

The experimental arrangements and the technique used for recording the nerve impulses from single nerve fibres are essentially the same as those by which the afferent fibre systems in the skin nerve were studied (Maruhashi, Mizuguchi & Tasaki, 1952). For the analysis of the afferent nerve systems in the toad's muscle nerve, excised sciatic-sartorius or sciatic-semitendinosus preparations were used. In these preparations, the operation for isolating single nerve fibres can be done at a point on the nerve 10–20 mm away from the muscle.

For the study of the efferent nerve systems in the toad, the muscle nerves entering either the gastrocnemius or the tibial muscle were employed. The muscle was carefully dissected out leaving its nervous connexion with the spinal cord intact. Special care was taken to minimize bleeding during and after the operation. The animal was then fixed to the wooden plate and the operation for isolating a single nerve fibre was carried out on the muscle nerve.

For the experiments on the cat, the nerves innervating the tibialis anterior, flexor digitorum longus, gastrocnemius and soleus muscles were preferred. The animal, lying on its back, was rigidly fixed to the experimental table. By means of drills through both ends of the femur, the hind-limb was fixed at the desired position on the table. When the efferent nerve systems were to be examined, one of the muscle nerves was cut across close to its entrance into the muscle. The nerve twig was then separated from the main nerve bundle (peroneal or tibial nerve) for a length of about 2 cm, and the isolation of single nerve fibres was performed on this part of the nerve twig. In the investigation of the afferent systems, the operation for isolating single nerve fibres was done on the distal portion of a severed muscle nerve.

Action currents from single nerve fibres were led directly from the operated region of the nerve either by means of a bridge-insulator or by suspending the operated region in the air with one of the lead electrodes. To record the action currents, an oscillograph of the Duddell type or a cathode-ray oscillograph was used. The amplified action current was tapped and was made to operate a loud-speaker by means of an auxiliary amplifier.

RESULTS

Afferent nerve systems of toad muscle

The fact that all the previous studies on the frog's muscle afferents have been concerned exclusively with the behaviour of the muscle spindles gave us formerly the impression that there was no other afferent system in frog muscle. When, however, we started the present investigation, we at once noticed that there are several afferent systems other than those originating at the muscle spindle.

The results of our investigation indicate that we may roughly divide the afferent nerve fibres in the toad's muscle nerve into four groups.

Tonic muscle afferent fibres. In the first, best-known group come those which for simplicity we designate the *tonic muscle afferent fibres*, originating apparently in

the muscle spindles. These fibres are in general between 8 and 12 μ in diameter. When the muscle is subjected to a sustained stretch, the afferent fibre of this type continues to carry a succession of impulses, and this discharge does not stop until the muscle is released. In some preparations an irregular discharge at a low frequency (below 10/sec) persists in the absence of applied tension (Fig. 1). The nerve endings from which these fibres arise are extremely

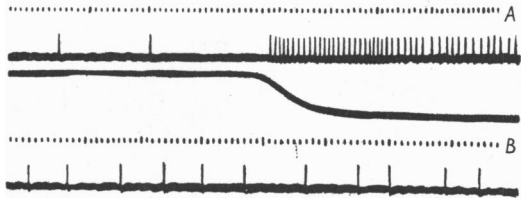

Fig. 1. Discharge of impulses in a 'tonic muscle afferent fibre' of the toad induced by stretching the muscle. The upper record (*A*) shows the discharge at the onset of the stimulus, and the lower record (*B*) the discharge observed about 30 min after the onset of stretching. The diameter of the isolated fibre was 8·5 μ. 25° C. The time marks are 10 msec apart.

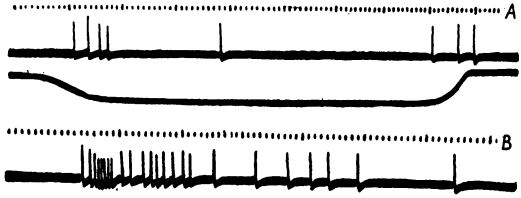

Fig. 2. Impulse discharge in a 'phasic muscle afferent fibre' of the toad induced by stretching and relaxing (*A*) and by pricking the muscle (*B*). The isolated fibre was 7 μ in diameter. 25° C. Time, 10 msec.

sensitive to stretching of the muscle. A discharge in this type of fibre can be evoked not only by pulling on the tendon but also by applying light pressure to the belly of the muscle. But pricking the surface of the muscle with a pin was always ineffective.

Phasic muscle afferent fibres. The second group, which we call the phasic muscle afferent fibres, are those arising from nerve endings that respond to a sustained stretch with only a short, transient discharge of impulses. As no continued discharge can be evoked in these fibres by a steady tension, their presence in the frog's muscle nerve has been overlooked by previous investigators. When the muscle is suddenly released after sustained stretching, the nerve endings of this type respond again with a short discharge (Fig. 2); a discharge on relaxation of the muscle can never be observed in the tonic afferent fibres described above.

The size of these fibres is not much different from that of the tonic muscle afferent fibres. During an experiment to determine the quantitative aspects of

the discharge in the tonic afferent fibres (which will be published in a subsequent paper) we made a thorough investigation of twenty-four single afferent fibres of over 7 μ diameter, and we found that five of these fibres were of the phasic afferent type.

The most important characteristic of these afferent fibres is that their nerve endings are distributed in the perimysium and possibly in the substance of the muscle. The receptive field of a single afferent fibre of this type spreads

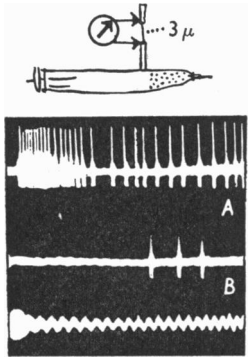

Fig. 3.

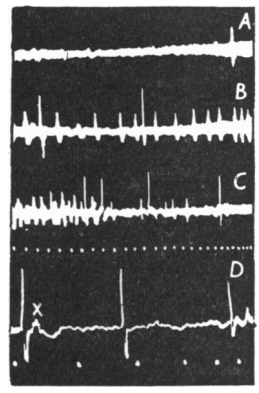

Fig. 4.

Fig. 3. Impulse discharges in a 'small myelinated muscle afferent fibre' of the toad. The receptive field on the sartorius muscle is shown on the top. The upper oscillograph record (*A*) shows the discharge provoked by stretching. The lower record (*B*) was obtained by pressing the receptive field with a glass rod. Time, 50 c/s. 26° C.

Fig. 4. Afferent impulses recorded from a small bundle of nerve fibres containing a number of unmyelinated fibres arising in the sartorius muscle of the toad. (*A*), spontaneous discharge; (*B*), discharge induced by stretching the muscle; (*C*), discharge caused by pricking the muscle; (*D*), a record taken at a high transit speed. The cross marks the action current from an unmyelinated fibre. Time, 20 msec. 24° C.

generally over an area covering about one-third to two-thirds of the entire surface of the muscle. A light touch on the receptive field, or scratching the surface of the muscle, with a sharp needle gives rise to a short discharge of impulses. One can readily distinguish phasic afferent fibres from tonic fibres by means of this property.

Small myelinated afferent fibres. The third group we may call the small myelinated afferent fibres. These are 2·5–5 μ in diameter, and the endings give rise, on stretching the muscle, to an impulse discharge which lasts for a considerable period of time but generally for less than 1 sec. The interval between the impulses was between 5 and 50 msec at 23° C. The endings of these fibres, unlike those of the tonic afferent fibres, are sensitive to pin-pricks applied to the surface of the muscle (Fig. 3). The receptive field

determined by light pin-pricks was as a rule below 3×5 mm. In some cases the endings had so high a threshold to injurious stimuli that it was not possible to determine the receptive field very accurately. We have succeeded in isolating single fibres of this type in six cases.

Unmyelinated afferent fibres. The fourth group consists of the unmyelinated afferent fibres. There are a number of unmyelinated fibres in the muscle nerve (see below). Most of them are efferent fibres coming from the sympathetic chain. It seems certain, however, that some of the unmyelinated fibres are sensory, transmitting a long train of impulses when the muscle is stretched. The frequency of the discharge is generally less than 50/sec at 24° C (Fig. 4). As all our observations on unmyelinated fibres were done with multi-fibre preparations, the character of the endings of these fibres could not be examined very accurately.

Afferent nerve systems in cat muscle

The types of sensory nerve endings found in muscles of the cat do not seem to differ a great deal from those present in toad muscle. We have thus divided

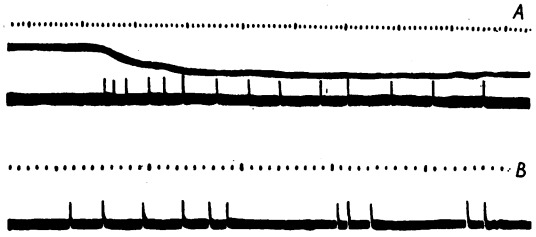

Fig. 5. Afferent impulses recorded from a single 'tonic muscle afferent fibre' of the cat. Discharge was induced by stretching (*A*) and by pressing the belly (*B*) of the tibialis anterior muscle. The isolated fibre was 15 μ in diameter. Time, 10 msec.

the myelinated muscle afferents into tonic, phasic and small myelinated afferent fibres. Matthews (1933) divides the tonic afferent fibres in our classification further into A_1, A_2 and B, according to the behaviour of the nerve endings during the active contraction of the muscle.

Tonic afferent fibres. These fibres arise in the nerve endings lying in the belly of the muscle near the entry of the nerve. They not only give rise to a tonic discharge of impulses on stretching the muscle but also respond to a light pressure stimulus applied to the belly of the muscle (Fig. 5). One can readily locate tonic afferent endings by pressing various parts of the muscle with a blunt glass rod. When the pressure stimulus is applied to a definite point in the muscle, a tonic discharge of impulses is observed which ceases as soon as the pressure stimulus is withdrawn. Pin-pricks on the surface of the muscle are ineffective in eliciting afferent impulses.

It was shown with multi-fibre preparations that afferent fibres of this type

exist in all the limb muscles examined. Single afferent fibres from the nerve entering the tibialis anterior muscle were successfully isolated on three occasions. The diameters of these fibres were 12·5, 15 and 16·5 μ. The endings were found to be situated at a point slightly above the middle of the muscle. We did not examine the behaviour of the endings during contraction.

Phasic afferent fibres. These can most readily be distinguished from the tonic fibres by the sensitivity of their endings to light injurious stimuli. A short discharge of impulses was caused by scratching the surface of the

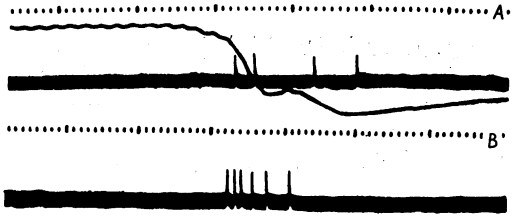

Fig. 6. Impulse discharges in a single 'phasic afferent fibre' arising in the tibialis anterior muscle of the cat, induced by stretching (*A*) and by pricking (*B*) the muscle. The fibre diameter was 11 μ. Time, 10 msec.

muscle with a needle, a procedure which did not stimulate the tonic afferent endings. The receptive field of a single fibre determined by this method was found to spread over one-third to two-thirds of the surface of a whole muscle. This should also be contrasted with the limited size of the tonic afferent ending. Another property of the phasic afferent endings which served to distinguish them from the tonic endings was quick adaptation to constant stretch stimulation; the discharge generally came to an end within about 0·1 sec from the onset of a sustained pull on the tendon (Fig. 6). When the muscle was suddenly released after a constant stretch a short discharge of impulses was observed, just as in the phasic afferent endings of the toad.

The diameters of isolated fibres of this type were 11, 8·5, 9 and 10 μ (fibres from the tibialis anterior muscle) and 7 μ (from the soleus muscle).

These endings seem to correspond to the type C endings of Matthews (1933).

Small myelinated afferent fibres. Fibres of this group originate in endings which occupy a restricted area on the surface of the muscle. Their properties were investigated mainly with multi-fibre preparations obtained after operative attenuation of the nerve entering the tibialis anterior muscle. When a small number of myelinated fibres of below 7 μ in diameter were isolated from one of the nerve branches entering the muscle, it sometimes happened that pressing a definite, restricted part of the muscle with a wooden pin gave rise to a relatively long discharge of impulses in one of the nerve fibres left uncut. To a sustained pull on the tendon, endings of this type responded with

a long tonic discharge. These endings did not seem to exist near the ends of the muscle.

It is very interesting to note that afferent fibres of this type have been demonstrated in 'deafferented' muscle nerves. In connexion with our investigation of the small myelinated efferent fibres (see below) and the 'wide-receptive' skin afferent fibres (Maruhashi *et al.* 1952), we carried out a careful operation to resect five lumbar dorsal root ganglia (4th to 8th ganglia according to the nomenclature of Eccles & Sherrington, 1930)

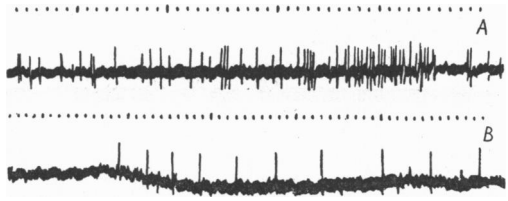

Fig. 7. 'Afferent' impulses recorded from a 'deafferented' muscle nerve of the cat. The dorsal root ganglia had been resected 21 days before the experimentation. Tibialis anterior muscle. The upper record (*A*) was taken from a small nerve branch entering the muscle. The lower record (*B*) was obtained after the number of the active fibres was reduced until only four fibres of 4–7 μ in diameter were left uncut. Discharges were induced by tendon-pulls. Time, 10 msec.

on one side of the spinal cord. In two out of five cats in which the operation seemed satisfactory, we looked for afferent impulses in the nerves entering the tibialis anterior and soleus muscles. In each muscle nerve examined we could observe a tonic discharge of impulses in fibres between 4 and 6 μ in diameter (Fig. 7). Since no discharge could be observed in the large myelinated fibres in those cases, it seemed certain that the ordinary afferent fibres of dorsal root origin had suffered degeneration. Histological examination of these muscle nerves, in comparison with the nerves on the unoperated side, showed that approximately 50 % of the total nerve fibres had disappeared on the operated side (see below, p. 167).

As to the origin of the small myelinated 'afferent' fibres demonstrated in the 'deafferented' animals, it seems that there are two possibilities: (1) they reach the muscle through the ventral roots, or (2) they are derived from dorsal roots above or below those cut. But, as we could record afferent impulses from the ventral roots of the cat and the toad (Maruhashi *et al.* 1952), the first possibility seemed to us more probable than the second. In this connexion, it may be pointed out that Allen (1925) has demonstrated proprioceptive fibres in the motor root of the trigeminal nerve.

Tendon afferent fibres. These originate in the tendinous part of the muscle. Our observations on their properties were made exclusively with the 'non-motor muscle nerve' entering the extensor digitorum muscle (Kato *et al.*

1935). The uppermost branch of the nerve entering this muscle generally contains no motor nerve fibres. It consists of fifteen to forty myelinated fibres which can roughly be divided into two groups, one 9–13 μ in diameter and the other below 7 μ (Fig. 8, top). This bundle leaves the main muscle nerve 2–3 cm away from the muscle and approaches the tendinous part of the muscle. Such a 'non-motor' nerve bundle is found also in the extensor digitorum muscle of the rabbit.

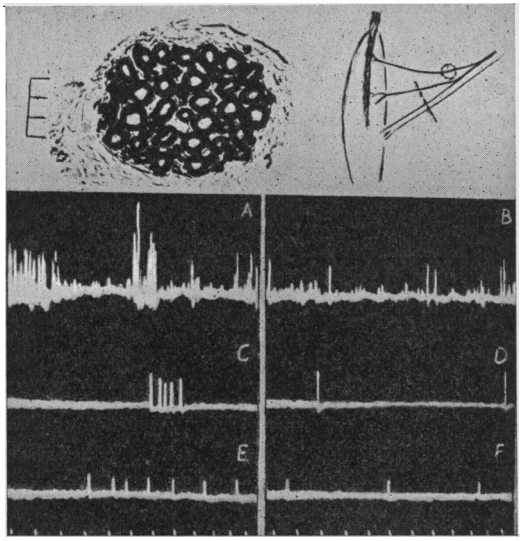

Fig. 8. Impulse discharges in 'tendon afferent fibres' in the 'non-motor muscle nerve' of the cat. The sketch at the top, right, shows the course of the non-motor muscle nerve from the peroneal nerve to the tendinous part of the extensor digitorum longus muscle. The photomicrograph at the top, left, shows the cross-section of this nerve bundle, the scale on the left indicating 10 μ. Oscillograph records *A* and *B* show afferent impulses taken from the whole nerve bundle. Records *C* and *D* were taken from a single fibre of 12 μ in diameter: the discharge was induced, in record *C*, by the start of sustained stretching, and the two impulses in record *D* were taken during a constant tendon-pull. Records *E* and *F* were obtained when a single fibre of 5·5 μ in diameter was isolated from this muscle nerve; record *E* shows the discharge at the onset of a stretch stimulus, and record *F* the discharge observed 1 min later. Time, 20 msec.

When afferent impulses were led from this special nerve bundle, it was immediately found that both large and small fibres transmit impulses when the muscle is stretched. The discharge in small fibres lasts longer than that in large fibres. When most of the fleshy part of the muscle was cut off with a pair of scissors, the spontaneous discharge in these fibres increased markedly. The stretching of the remaining tendinous portion of the muscle still brought about a pronounced increase in the frequency of discharge in both kinds of afferent fibres.

On several occasions we investigated the discharge in a single fibre isolated from this nerve bundle. Fig. 8 shows one example of each of the two kinds of tendon afferents. It can be clearly seen that the discharge in the smaller fibre lasts much longer than that in the larger one.

Unmyelinated afferent fibres. We have not succeeded in recording centripetal impulses from the unmyelinated fibres in muscle nerves of the cat.

Unmyelinated efferent fibres

Toad. When we tease with fine needles the nerve entering the gastrocnemius or other limb muscles of the toad, we easily see a number of unmyelinated fibres under a low-power microscope. These fibres have a very high threshold for induction shocks, about one hundred times as high as that of the large motor nerve fibres. The velocity of transmission along these fibres at room temperature is less than 1 m/sec and the configuration of their action currents is typically slow (see Fig. 9).

If we lead action currents from a small bundle of nerve fibres containing unmyelinated fibres which are in physiological connexion with the spinal cord, we find immediately that groups of efferent impulses are recurring periodically in the unmyelinated fibres. The interval between such outbursts of impulses in these fibres is somewhat irregular, as can be seen in records *A*, *B* and *E* of Fig. 10.

Following faradic stimulation of the ipsilateral peroneal nerve, the discharge in unmyelinated fibres innervating the gastrocnemius muscle seemed to increase to some extent (records *C* and *D*, Fig. 10). The discharge was almost completely stopped by removal of all the visible sympathetic ganglia around the lumbar nerve plexus, but not by crushing the whole spinal cord if the sympathetic chain was left intact.

Cat. On a few occasions we have examined such efferent discharges in unmyelinated fibres in muscle nerves of the cat. These discharges were found to be markedly depressed by a hypodermal injection of 2–4 g of ethyl urethane.

According to Suda and his collaborators (Suda, Abe, Uchiyama & Mizuno, 1944), injection of various organic salts into the cerebellum induces pronounced autonomic reactions, such as rise of blood pressure, acceleration of the respiratory movements, etc. This procedure was found to induce discharges in fine nerve fibres, entering rabbit or cat muscle, which developed action currents of long duration and low conduction velocity.

Impulse discharges in two kinds of myelinated efferent nerve fibres from the spinal cord

The impulse discharge from the spinal cord in the large and small motor nerve fibres of the toad and frog has already been subjected to repeated study by Tasaki (1942), taking nerve action currents as index, and by Tasaki &

Tsukagoshi (1944) and also by Kuffler *et al.* (1947), taking muscle action potentials as index. We are concerned in this paper mainly with what we have

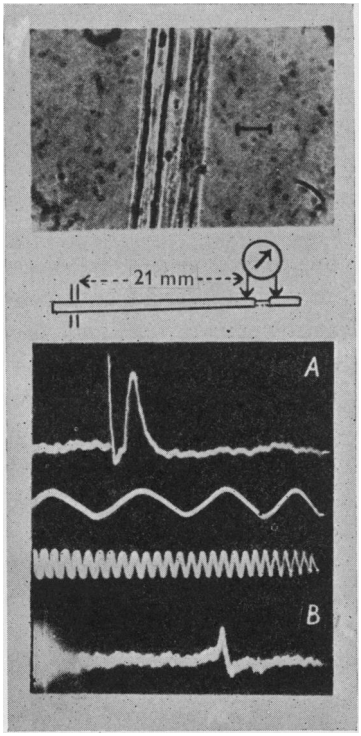

Fig. 9.

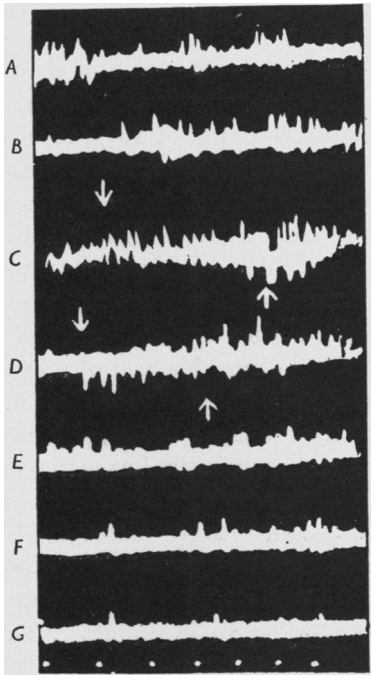

Fig. 10.

Fig. 9. A large myelinated nerve fibre and a group of unmyelinated fibres isolated from a muscle nerve of the toad and their action currents. The bar in the photomicrograph at the top subtends 20 μ. The oscillograph record *A* was taken at a high transit speed. The record *B* was obtained with an induction shock about 80 times as strong as that in *A*: the transit speed in this case is so low, as can be seen from the time signal of 250 c/s in the middle, that the action current from the large myelinated fibre, together with the shock artifact, is seen as a faint straight line on the left. 28° C.

Fig. 10. Centrifugal impulse discharges in a group of unmyelinated nerve fibres entering the gastrocnemius muscle of the toad. *A* and *B*, spontaneous discharge; *C* and *D*, the effect of nerve stimulation upon the discharge (faradic stimuli to the ipsilateral peroneal nerve were started at the moment marked by the first arrow and withdrawn at the second arrow); *E*, spontaneous discharge; *F*, discharge observed after crushing the whole spinal cord; *G*, record taken immediately after nerve section. Time, 0·1 sec. 29° C.

learnt of the roles played by large and small myelinated efferent nerve fibres in the spinal reflexes of the cat.

In tibialis anterior, gastrocnemius and vastus muscles, which we have used in the present investigation, the diameter of large motor nerve fibres was in

most cases between 15 and 20μ (Tasaki & Tsukagoshi, 1944). An induction shock sent into a single nerve fibre of this type sets up in the muscle a quick twitch which can well be observed with the naked eye. In the present investigation, we have first examined whether or not there are efferent discharges of impulses from the spinal cord in the myelinated nerve fibres smaller than the large motor fibres referred to above.

Spontaneous discharges. For the study of the spontaneous efferent discharge in myelinated fibres, we used cats under light urethane narcosis (subcutaneous injection of 5–10 ml. of 10 % urethane solution) or, sometimes, unanaesthetized cats. One of the small branches of a muscle nerve was cut across near its entry into the muscle, and a bundle with one to five nerve fibres of varying sizes was isolated from this branch. To preserve the afferent pathway from the muscle under investigation to the spinal cord, care was taken not to injure other branches of the nerve innervating the rest of the muscle. The diameters of the fibres isolated were measured *in situ* with a medium power microscope attached to a movable arm of a heavy iron stand. Action currents were led off directly from the operated region of the nerve. Under these experimental conditions it was, of course, possible that some of the fibres left uncut were afferent and not efferent, but as the connexion of these fibres with the muscle had already been severed, we could not examine afferent discharges in those fibres.

It was immediately discovered by this method that there are efferent discharges in small myelinated fibres innervating the extensor muscles. We found in fact that such spontaneous efferent discharges are in general limited to fibres below 8μ in diameter. The frequency of discharge in these small efferent fibres innervating the vastus or gastrocnemius muscles was as a rule 10 to 40/sec. Massage of the plantar region of the animal, or pinching the dorsal skin, was found to increase the frequency of such spontaneous discharge or sometimes to induce long-lasting discharges in new elements.

It was quite seldom that a spontaneous discharge was observed in a large myelinated fibre. In two out of sixteen preparations we observed irregular spontaneous discharges (at a frequency below 8/sec) in large fibres, but the discharges lasted for only a few minutes (Fig. 11 *B*). When visible voluntary contractions were taking place in the neighbouring limb muscles in unanaesthetized animals, discharges in large fibres were in most cases observed, and the frequency of discharge then rose to 10–25/sec.

When both large and small fibres were taking part in the spontaneous discharge, we could demonstrate that the discharge in the large fibre could be inhibited by nocuous stimuli applied to the skin of the foot or by induction shocks sent into one of the ipsilateral nerves (record *B*, Fig. 11). As a rule the discharge in small fibres was not inhibited by ipsilateral stimulation. In a few cases the spontaneous discharge in small fibres to the gastrocnemius medialis muscle was enhanced by ipsilateral stimulation.

The spontaneous discharge in a small nerve fibre was much more regular than that in a large fibre. In five out of twenty-three preparations, groups of impulses at 50–100/sec appeared rhythmically with a frequency of 5–10/sec. In record *A* of Fig. 11 it is seen that two small fibres are discharging groups of impulses. We have seen a similar phenomenon in both the quick and slow motor units of the strychninized toad.

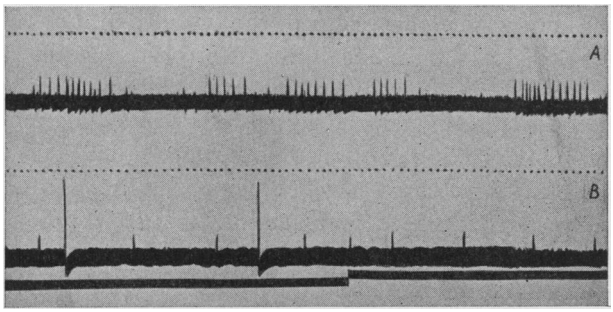

Fig. 11. *A*, discharge of impulses from the spinal cord in small myelinated nerve fibres. Action currents were led from six myelinated nerve fibres between 15 and 4 μ in diameter, innervating the gastrocnemius muscle of a cat under urethane. Two fibres below 6 μ are discharging groups of impulses in rotation. *B*, effect of ipsilateral stimulation on the spontaneous discharge in two kinds of nerve fibres from the spinal cord. Cat under urethane. Action currents were led from four fibres (15, 8, 7 and 6 μ in diameter) innervating the lateral head of gastrocnemius. Time, 10 msec.

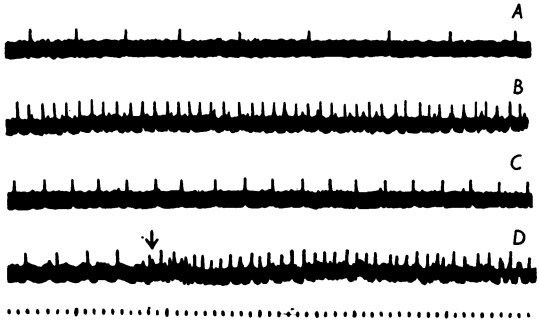

Fig. 12. Cat under urethane. Action currents recorded from three myelinated fibres of below 5 μ in diameter innervating the medial head of gastrocnemius. *A*, spontaneous efferent discharge from the spinal cord; *B*, increase in the frequency of discharge by decerebration; *C*, record taken about 10 min after decerebration; *D*, increase of the frequency by repetitive induction shocks applied to the contralateral sciatic nerve (started at the arrow). Time, 10 msec.

Decerebration. Decerebration of the cat at the intercollicular level was always found to increase the frequency of discharge in the small nerve fibres to an extensor muscle (Fig. 12). The frequency was generally as high as 30–90/sec immediately after decerebration and fell during about half an hour

to 15–30/sec. When the frequency of discharge had become steady, the muscle was gently stretched by pulling the tendon so as to send afferent impulses into the spinal cord through the tonic afferent fibres in the remaining muscle nerves. The procedure invariably increased the frequency of discharge in the small fibres.

Even in the decerebrate cat persistent discharges in large fibres were only rarely seen. Outbursts of efferent impulses in both large and small nerve fibres occurred during the transection of the brain stem, but the discharge in large fibres subsided within about 10 sec after the operation, and, when the limb muscles were in the state of decerebrate rigidity, discharge of impulses from the spinal cord was in general limited to the small nerve fibres.

We observed long-lasting spontaneous discharge in large fibres in only three out of twenty-three cases in which nerves entering extensor muscles of decerebrate cats were examined (we examined one multi-fibre preparation on each cat before, during and after decerebration). In these three cases, the frequency of discharge in the large fibres was between 8 and 25/sec. When a spontaneous discharge in the large fibres was absent in a decerebrated animal, stretching the muscle under investigation (so as to send afferent impulses through the remaining muscle nerves) or repetitive stimulation of the contralateral nerves was generally found to be effective in initiating a short, unstable discharge (see later).

Reflex discharges. We shall now turn to the role of these two kinds of efferent nerve fibres in the spinal reflexes. The ipsilateral flexion reflex was studied on one of the muscle nerves innervating the tibialis anterior muscle of the spinal cat. A nerve branch was cut near its entrance into the muscle and was freed from the surrounding tissue for a length of a few centimetres. Several fibres, large and small, were isolated from this freed portion of the nerve, and their diameters were measured with a low-power microscope. The ipsilateral tibial nerve was severed near the foot joint and a pair of stimulating electrodes was placed near its distal stump.

It was shown by this method that both the large and small fibres are brought into play in the flexion reflex. When the stimulus (repetitive induction shocks from a Porter coil) was strong enough, the spinal cord was found to discharge trains of impulses in both large and small nerve fibres. In all cases the impulse discharge in the small fibres could be induced more readily and its frequency was higher than that in the large fibres. Furthermore, it was observed that the discharge in the large fibres ceased immediately after withdrawal of the stimulus, whereas the small fibres continued to discharge for some time after cessation of ipsilateral stimulation (Fig. 13).

In many cases we saw spontaneous discharges of impulses at a frequency below 5/sec in the small fibres entering flexor muscles of the spinal animal. During the flexion reflex the frequency of discharge in the small fibres was

at times as high as 90/sec. We did not examine the relation between the frequency of discharge in the efferent fibres and the frequency of induction shocks applied to the ipsilateral nerve.

In the investigation of the roles of the two kinds of efferent nerve fibres in the crossed extension reflex we used decerebrate cats. Action currents were led from a few nerve fibres, large and small, entering one of the heads of the quadriceps or gastrocnemius muscle. When volleys of impulses were sent into

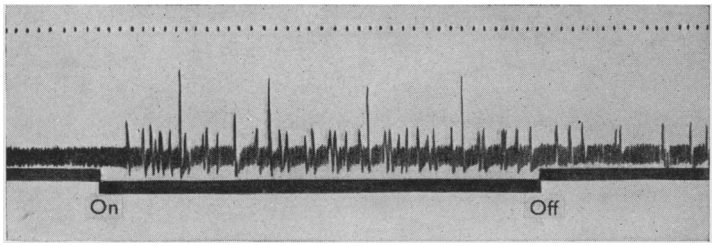

Fig. 13. Impulse discharges in large and small myelinated nerve fibres in the ipsilateral flexion reflex. Action currents were led from three fibres (20, 5 and 4 μ in diameter) innervating the tibialis anterior muscle of a spinal cat.

the contralateral sciatic nerve at a stage when the spontaneous discharge was not very conspicuous, it was observed that first the small fibres, and then the large fibres, were 'recruited' in the reflex (Fig. 14). When, at this stage of the reflex, repetitive induction shocks were delivered to one of the ipsilateral nerves, discharges in the two kinds of afferent fibres suffered immediate inhibition. It was thus found that both the large and small fibres take part in the crossed reflex (see also Fig. 15).

Motor effects of the impulses in efferent fibres

In 1930, Eccles & Sherrington carried out a thorough investigation on the contraction values of individual motor-units in several muscles of the limb. The method they adopted consisted in dividing the maximum tension developed by the whole muscle by the number of nerve fibres entering the muscle via the ventral roots. In this series of experiments, we tried to determine contraction values of the cat motor units directly by isolating individual motor nerve fibres and to compare the results with those obtained by the method of Eccles & Sherrington.

The hind-limb of the spinal cat was rigidly fixed to the experimental table by means of drills through both ends of the femur. One of the muscle nerves of the limb was cut across centrally and a single fibre of about 20 μ diameter was dissected out at a point 2–6 cm from the muscle. The distal one-third of the muscle was freed from the surrounding tissue and the maximum tension

developed by tetanic stimulation of the nerve fibre was measured by the method described previously (Tasaki & Mizutani, 1944). During the operation, care was taken not to impair the blood supply of the muscle. The initial tension imposed upon the muscle was in all cases 50 g. The room temperature was kept at 25° C.

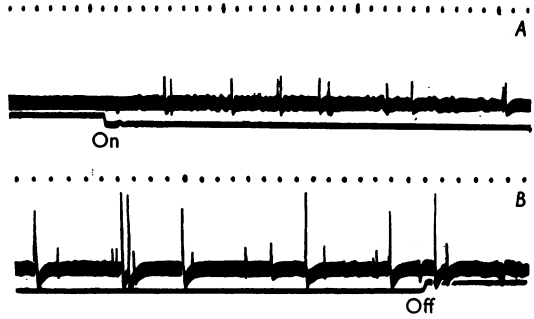

Fig. 14. Impulse discharges from the spinal cord in the contralateral extension reflex in a decerebrated cat. Action currents were led from five fibres of between 18 and 5 μ in diameter innervating the vastus medialis muscle. Induction shocks were applied to the contralateral peroneal nerve. In the record *B*, note a 'double response' (cf. Gilson & Mills, 1941) in one of the large fibres.

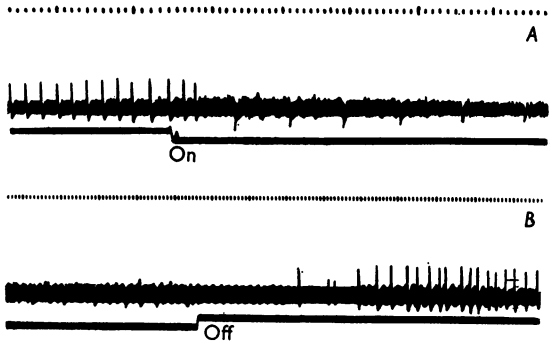

Fig. 15. Inhibition of contralateral extension reflex by induction shocks applied to the ipsilateral peroneal nerve. Action currents were led from five fibres, between 20 and 5 μ, innervating the lateral head of gastrocnemius of a decerebrated cat. The crossed reflex was maintained by continued stimulation of the contralateral peroneal nerve. Only one fibre of 5 μ is active in the crossed reflex. Time, 10 msec.

The results of our measurements were as follows:

M. tibialis anterior: 0·8, 1·0, 0·4, 1·7, 2·0 g.
M. gastrocnemius: 1·8, 1·0, 1·0, 0·6 g.
M. extensor digitorum longus: 1·0, 0·9 g.
M. soleus: 2·0, 0·9 g.

In all cases, the diameter of the nerve fibre isolated was between 18 and 20 μ.

The contraction values of individual motor units were, under the conditions of our experiments, far less than the values of 8–30 g predicted by Eccles & Sherrington.

We measured next, with somewhat primitive arrangements, the maximum tension developed by the muscle during tetanic stimulation of the *whole* muscle nerve under conditions similar to those in the preceding experiments. The results obtained are as follows, the first figure in each case being the tension in kg, and the bracketed figure the weight of the cat in kg:

M. tibialis anterior: 2·8 (3·5); 0·8 (1·8); 1·8 (2·0); 2·3 (2·5); 1·3 (1·7).
M. gastrocnemius medialis: 1·1 (1·5); 1·0 (1·6).
M. extensor digitorum longus: 0·8 (1·8); 1·6 (2·0); 1·2 (1·8); 1·5 (1·8).
M. soleus: 1·7 (2·0); 1·8 (2·9); 1·3 (2·8); 1·6 (2·0).

The contraction value of the whole soleus muscle in this table agrees well with the value obtained by Eccles & Sherrington. The value for the gastrocnemius muscle was much less in our results than in those of British workers, due at least partly to the low initial tension in our experiments. We adopted an initial tension of 50 g in all cases because we had carried out observations on individual motor units under that condition.

We also counted the myelinated fibres which reach the limb muscles through the ventral roots. Several muscle nerves were taken from the cats which survived for 3–4 weeks after resection of five dorsal root ganglia (from 4th to 8th lumbar roots according to the nomenclature of Eccles & Sherrington). The nerves were fixed in 15 % formal and were submitted for histological examination.

Fig. 16 gives an example of the results thus obtained, showing the fibre-size distribution in muscle nerves on the operated and unoperated sides. The ratio of the number of myelinated nerve fibres on the operated side to that on the unoperated side was approximately 1 : 2; in five out of the six cases it was between 0·4 and 0·55. The distribution on the operated side agrees well with the data obtained by Eccles & Sherrington. The difference between the two histograms in the figures gives an idea of the distribution of the fibres connecting the muscle with the spinal cord by way of the dorsal roots.

In estimating the average contraction value of single motor units, Eccles & Sherrington adopted the method of dividing the tension of the whole muscle by the total number of the myelinated fibres reaching the muscle by way of the ventral roots. It has now become evident that in the cat the contraction value obtained by this method gives a value much greater than that obtained by a direct measurement on the motor-unit preparation. For all the limb muscles mentioned above, the number of myelinated fibres of ventral root origin was between 200 and 400. The possibility that some of the small myelinated fibres may be afferent and that the small efferent fibres may develop only small

tension seems to aggravate the discrepancy between the calculated and observed contraction values. We cannot at present give any definite explanation for this discrepancy (cf. Tasaki & Tsukagoshi, 1944, p. 249.)

For the toad muscle the situation seems to be entirely different. The maximum tension developed by the toad sartorius muscle (on tetanic stimulation of the whole nerve) is on the average 300 g and the average tension caused by

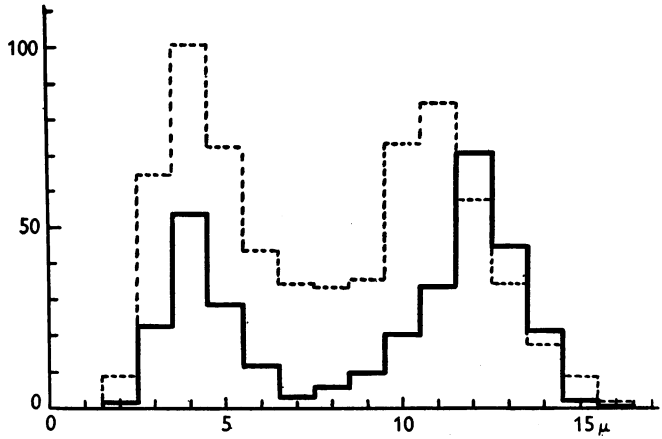

Fig. 16. Number of myelinated nerve fibres plotted against myelin sheath diameters in nerve of m. tibialis anterior of a cat of which five lumbar spinal root ganglia had been resected on one side. Spinal root ganglia were resected from No. 4 to No. 8: period of degeneration was 27 days. Solid line shows the data for the deafferented side, sampled by 359 fibres. Broken line, for the normal, control side sampled by 681 fibres. Counts were taken at a point about 2 cm away from the muscle. The outside diameters in the living nerve fibres appear to correspond to approximately 130 % of the diameters in these fixed and stained preparations.

stimulation of a single large motor nerve fibre is about 40 g. As the number of the myelinated fibres of above 8 μ in diameter entering into this muscle is approximately 14, it is possible to assume that the number of motor units is such that the whole muscle develops a tension which is given by simple addition of contraction values of individual motor units.

Turning now to the problem whether or not the small efferent fibres described above have motor functions, we made an attempt, on several deafferented cats, to cut all the large motor nerve fibres in a muscle nerve and to demonstrate either slow muscle action potentials or slow muscular contractions on stimulation of the remaining small nerve fibres. In spite of our strenuous efforts the attempt turned out to be unsuccessful.

DISCUSSION

The fact that we have failed to demonstrate slow muscular contraction by stimulation of single small efferent nerve fibres may seem to suggest that they do not have motor functions at all. There seems to us, however, good

reason to believe that they are motor nerve fibres, just as in the toad and frog. Our reasons are as follows:

(1) The behaviour of the impulse discharge in the small efferent fibres of the cat resembles, in a high degree, that in the small motor fibres of the toad. In decerebrate rigidity and in spinal reflexes of the cat, the strength of the tonic contraction of the muscle appears to vary as the frequency of discharge in the small efferent fibres.

(2) In the cat, as well as in the toad and frog, a single impulse in one large motor nerve fibre elicits in the muscle a quick, visible contraction. Therefore, a discharge at a low frequency in the large motor fibres would be expected to cause a tremor and not a smooth contraction.

(3) In the toad tetanic contraction of the muscle caused by a faradic stimulation of a single large motor fibre develops a tension as large as 50 g, and by faradic stimulation of a single small motor fibre, a tension of about 5 g (Tasaki & Mizutani, 1944). In the cat one large motor fibre can develop a tension of only a few grams. It is not surprising, therefore, if a contraction caused by a few 'small motor nerve fibres' in the cat is too weak to be observed directly.

(4) In excitation of a single motor nerve fibre, electric 'current' developed by the active muscle fibres spreads over surrounding inactive muscle fibres: the potential generated by this current on the surface of the muscle (i.e. the muscle-action potential) becomes smaller as the number of inactive muscle fibres, intervening between the active muscle fibres and the lead-off electrode, increases. This seems to provide a reasonable interpretation of the fact that in the cat the muscle-action potential resulting from excitation of a single large motor fibre is of small and variable magnitude (0·05–0·5 mV), and also to the fact that we could only rarely record muscle action potentials by stimulation of a fibre below 10μ in diameter (Tasaki & Tsukagoshi, 1944). As has been stated above, the number of quick motor units involved in one limb muscle of the cat is between 100 and 300, while the number in the toad muscle is generally between 10 and 30.

Thus we regard the difference in the experimental results for the cat and the toad to be merely quantitative, and not qualitative, and assume, as Häggquist (1940) does, the existence of a dual motor innervation in mammalian muscle.

In the spinal reflexes both large and small motor nerve fibres behave as if they served to develop tension in the muscle. The tonus of the muscle is considered to be caused mainly, if not exclusively, by the activity of the small fibre system.

The well-known experiments of Adrian & Bronk (1929) have elucidated the role of the large motor fibres in spinal reflexes and in decerebrate rigidity. The results they obtained seem to indicate that decerebrate rigidity is

maintained by the large motor fibre system. But, as their observation is considered to be made with preparations containing a relatively large number of large motor fibres, it seems possible to reconcile their results with ours. As has been described above, we have observed on a few occasions long-lasting discharges in large motor fibres of the decerebrated cat, and the frequency of discharge we observed (8–25/sec) is in good agreement with the value obtained in England. The discharge in the small fibres was much higher than that in the large fibres.

SUMMARY

1. By the method of recording action currents from individual nerve fibres, an attempt was made to survey the functions of all the nerve fibres contained in the muscle nerves of the toad and the cat.

2. Afferent nerve fibres arising in the toad muscle were classified into four groups. (*a*) *The tonic afferent fibres* arise in the belly of the muscle where the muscle spindles are located: they are 8–12 μ in diameter, and have been investigated extensively by previous workers. (*b*) The *phasic afferent fibres* are 7–11 μ in diameter and arise in the perimysium. (*c*) The *small myelinated afferent fibres* are 2·5–5 μ in diameter: some respond to an intense stretching or to injurious pin-pricks with only few impulses. (*d*) Slow afferent impulses were recorded which apparently travel along *unmyelinated fibres*.

3. In the muscle nerve of the cat there are also tonic, phasic and small myelinated afferent fibres, similar to those found in the toad muscle nerve. The small myelinated afferent fibres seem to reach the spinal cord, at least partly, by way of the ventral spinal roots. Large and small tendon afferent fibres were isolated from a 'non-motor' bundle entering the extensor digitorum muscle.

4. The toad's muscle nerve contains a large number of unmyelinated efferent fibres which transmit slow impulses from the sympathetic chain to the muscle. Similar slow efferent impulses were recorded from the rabbit and cat muscle nerves.

5. It was concluded that the tonus and the decerebrate rigidity in the cat muscle are maintained mainly by the activity of the small myelinated efferent nerve fibres. Both large and small efferent fibres take part in the spinal reflexes. In all cases, impulse discharges in small efferent nerve fibres are provoked more readily than discharges in large motor fibres, and the frequency of discharge is higher in the small fibres than in the large ones.

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Note added in Proof. Discovery of the slow motor nerve fibre in the frog was reported by Vereshchagin, Zhukov & Bogomolova (*J. Physiol., U.S.S.R.*, 1947, **33**; 1949, **35**) without knowing the report by Tasaki & Kano (1942).

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