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The static and dynamic fusimotor fibres – their present status

P. B. C. MATTHEWS

It is now nearly ten years since it was demonstrated experimentally that there are two functionally distinct types of motor fibres to the mammalian muscle spindle, namely the static and the dynamic fusimotor fibres. It seems a good moment therefore to stand back and take stock of where we are and how we got here, for as usual the stream of advancing knowledge has taken a tortuous course. In so reviewing the field I shall be referring to the contributions of many different workers without always giving them detailed recognition since most of the older work has already been reviewed several times (GRANIT, 1953, 1970; MATTHEWS, 1964, 1972). In particular, Professor LAPORTE has done far too many important experiments for it to be possible to do them justice in the present space.

Structural considerations

To appreciate the present state of affairs we need to go back to the beginning and look at the muscle spindle as it was known for the first half of the present century. The importance of the spindle was demonstrated in 1894 by SHERRINGTON's observation that about half the medullated fibres to a muscle are afferent and not efferent, and that the majority of these afferent fibres are devoted to supplying the muscle spindles. Fig. 1 shows the structure of the muscle spindle as it was seen by RUFFINI in 1898. The bundle of fine intrafusal muscle fibres is supplied with three morphologically distinct kinds of nerve terminal. These are the central primary ending, the juxta-equatorial secondary endings, and numerous polarly placed plate endings. By around 1900 the primary and secondary endings had become accepted as sensory terminals and the plate endings as motor. The investigation of their functional properties had to await the arrival of the electronic era. Then a series of elegant investigations proved that the sensory endings are stretch receptors and that the motor plates are supplied in the main by the specialised small γ efferent fibres which are purely fusimotor and do not supply the ordinary extrafusal muscle fibres. Activity of the γ efferent fibres elicits a contraction of the intrafusal muscle fibres which leads to an excitation

of both kinds of afferent ending. This happens because the endings lie on intrafusal regions which are less strongly contractile than the rest of the fibre and which are therefore stretched by contraction in much the same way as they are by an externally applied stretch.

RUFFINI'S analysis of the nerve endings provided the basis for most physiological thinking for the first 60 years of the century, and has been very fruitful in this respect. Fig. 2 shows that RUFFINI'S picture does not perhaps do full justice to the true length of the intrafusal muscle fibres and fails to show what a small proportion of their length is occupied by the afferent terminals. But this is a detail. Quite surprisingly, however, continued work in the 1950's with the light microscope particularly by BARKER, by BOYD and by COOPER and DANIEL showed that the classical picture had failed to include the important feature that the spindle contains two quite distinct kinds of intrafusal muscle fibre. These are illustrated diagrammatically in Fig. 3 which shows one intrafusal fibre of each kind, though the normal spindle contains several. The nuclear bag fibres are characterised by having their equatorial regions stuffed quite full of nuclei whereas the nuclear chain fibres have their equatorial nuclei arranged in single file with rather more cytoplasm around them. In addition, the bag fibres are usually longer and thicker than the chain fibres. Recent work with the electron-microscope has now added to this by showing ultrastructural differences between the two kinds of intrafusal fibre. The most notable of these are that the chain fibres contain far more mitochondria and have a much better developed M line in the middle of the sarcomere than do the bag fibres (ADAL, 1969; CORVAJA, MARINOZZI and POMPEIANO, 1969). These ultrastructural differences are probably more important and more consistent than the details seen with light microscopy. They are also found in the rabbit spindle where with ordinary microscopic observation all the intrafusal fibres appear to be of the bag type (CORVAJA and POMPEIANO, 1970).

Independent variation in the decerebrate preparation of the responsiveness of the primary ending to static and to dynamic stimuli

In his original detailed description of the bag and chain intrafusal fibres BOYD (1962) described them as being supplied by completely separate motor fibres as illustrated in Fig. 3. This has proved to be something of a simplification though it can still be taken to express the essence of the matter. It originally had the tremendous advantage that by its very dogmatism it simplified and thereby encouraged speculative thinking about the teleological purpose of having two kinds of intrafusal fibre. At about the same time the functional differences between the primary and the secondary afferent ending were being elucidated experimentally. This work allowed the generalisation that in response to stretches of large amplitude the primary ending responds to the instantaneous values of both the length and the velocity components of the stimulus, whereas the secondary ending

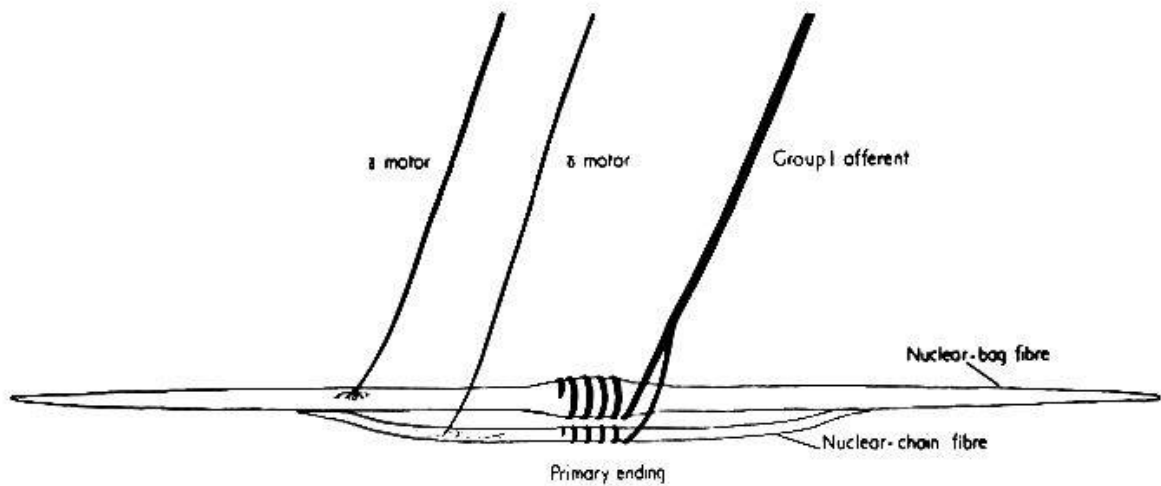


Fig. 3. Greatly simplified diagram of the structure of the muscle spindle to illustrate the existence of two kinds of intrafusal muscle fibres. The normal cat spindle contains several of each (CROWE and MATTHEWS, 1962a).

responds solely to the length component. Put another way, the two kinds of ending were found to be about equally sensitive to static stimuli while the primary ending is very much the more sensitive to dynamic stimuli. The superadded velocity sensitivity of the primary ending seems to be of some importance in thinking about its function for it has been likened to the velocity feedback provided in many human engineered position control systems. As is well known the primary ending is reflexly responsible for the stretch reflex of the decerebrate preparation which would appear to be the response of a biological position control system.

This line of thought immediately led to the speculation that the purpose of having the two kinds of intrafusal fibre is to allow the independent control of the two facets of response of the primary ending, namely its response to static stimuli and its response to dynamic stimuli. This was the idea that Dr. JAN JANSEN and I had ten years ago when we were engaged on spindle experiments which were actually started with quite other objects in mind. In these we were stretching the soleus muscle of the decerebrate cat while recording from single spindle afferents. Fig. 4 shows in a grossly simplified way the increase in spindle firing with stretching and illustrates how we assessed the dynamic sensitivity of the ending by measuring the so-called dynamic index. This is simply the decrease in the frequency of firing of the ending occurring in the first 0.5 sec after completing the dynamic phase of a stretch and holding the muscle at a new longer length. We also measured the frequency of firing at the new length and called this the static response. This was done first with the ventral roots intact when the endings were being excited by the spontaneous fusimotor discharge of the decerebrate preparation, and again after cutting the ventral roots to eliminate fusimotor activity. Fig. 5 shows the effect of eliminating the fusimotor activity on the dynamic sensitivity of a number of primary endings. For each one the resulting change in its dynamic index is plotted against the corresponding effect on its

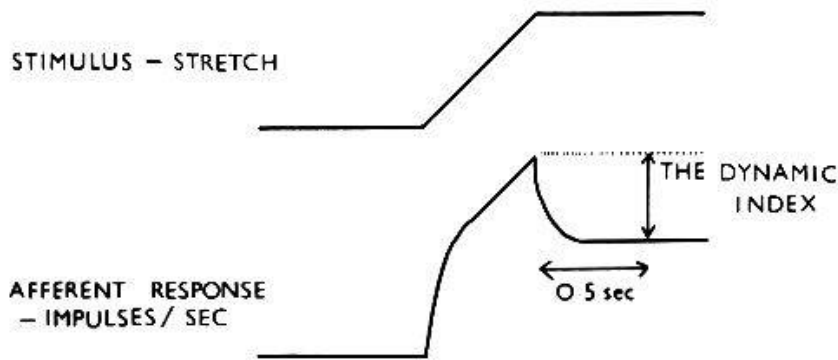


Fig. 4. The measurement of the "dynamic index" shown on a grossly simplified diagram of the spindle afferent discharge elicited by a ramp stretch.

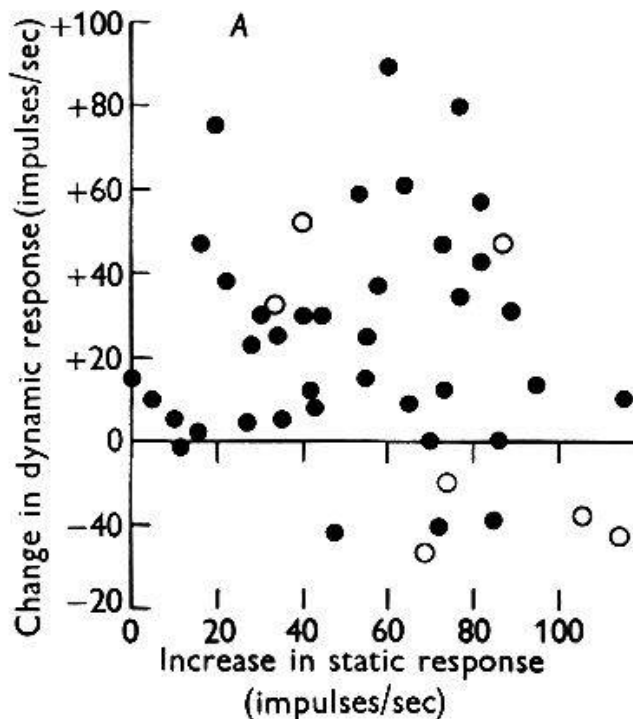


Fig. 5. The effects of the "spontaneous" fusimotor activity of the decerebrate preparation on the responsiveness of the spindle primary to static and to dynamic stimuli. Each point shows the effect on an individual ending of removing all fusimotor action by cutting the ventral roots; both the ordinate and the abscissa show the amount by which the responses of the fusimotor activated endings exceeded their passive values. The «dynamic response» is an older term for the «dynamic index». The static response is the frequency of firing of the ending 0.5 sec after completing a stretch at constant velocity. The results were obtained from a number of different preparations. Their variability demonstrates that these two parameters of afferent responsiveness can be controlled independently by fusimotor action (JANSEN and MATTHEWS, 1962).

static responsiveness. Clearly for the population of endings from a number of different preparations there is no correlation between the static and dynamic parameters of response. This suggests that these two facets of spindle behaviour were being independently controlled by the varying amounts of fusimotor activity in the different preparations.

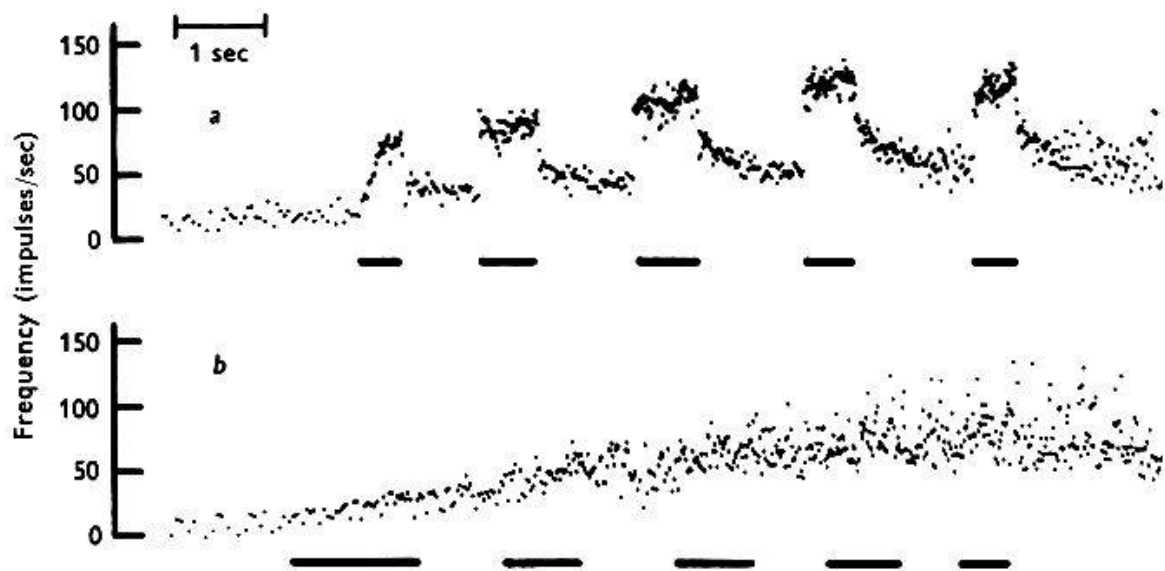


Fig. 6. Alteration of the dynamic sensitivity of a primary ending produced by stimulation within the central nervous system in the decerebrate cat. - a) Response to successive small stretches; the horizontal bars mark the periods of dynamic stretching during which the muscle was being stretched at 3 mm/sec. - b) Response of same ending to similar stretching applied during repetitive stimulation of the anterior lobe of the cerebellum (JANSEN and MATTHEWS, 1962).

The next stage was to make sure that any one particular primary ending could be made to change its dynamic responsiveness at the behest of the central nervous system. Fig. 6 shows that this is indeed so. The top trace shows the response to successive short periods of stretching at 3 mm/sec (during bars) of a primary ending which was under the influence of the steady background fusimotor discharge of the decerebrate cat. The ending shows a characteristically high dynamic sensitivity. The bottom record shows the response of the same ending to the same pattern of stretching applied while the anterior lobe of the cerebellum was being stimulated, thereby producing an unknown change in the degree of fusimotor firing. The ending is then virtually insensitive to this particular dynamic stimulus. It is easy to see how this sort of thing could be brought about by having two kinds of fusimotor fibre which had different actions on the static and the dynamic sensitivity of the primary ending, and no other explanation seems readily available. So JAN JANSEN and I proposed that this was the function of the two kinds of fusimotor fibre which had been suggested on histological grounds (JANSEN and MATTHEWS, 1962). Accepting this view the original evidence also shows that the two kinds of fusimotor fibre can be individually controlled by the central nervous system.

Isolation of static and dynamic fusimotor fibres

The obvious thing to do next was to see if one could isolate the postulated two kinds of fusimotor fibre in ventral root filaments in the way introduced

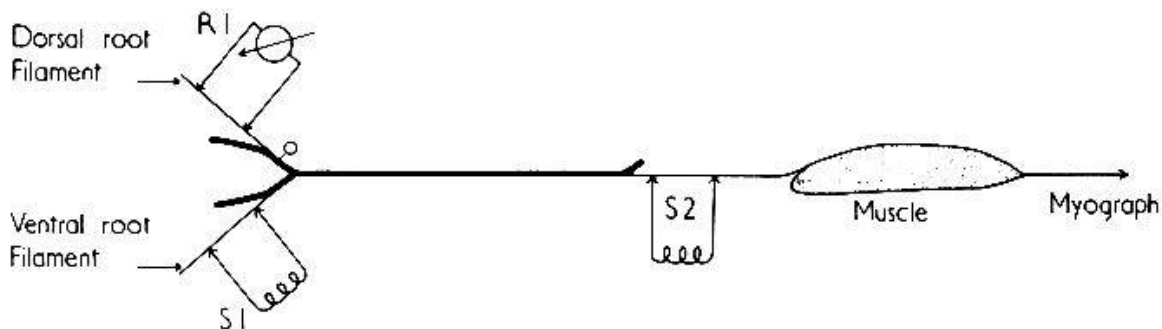


Fig. 7. Diagram of the usual preparation for studying the action of a single fusimotor fibre, isolated in a ventral root filament, on the behaviour of a single afferent fibre, isolated in a dorsal root filament. Each filament, however, consists of far more than an anatomically single fibre for as well as the fibre in question it also contains a goodly number of fibres to muscles other than the one studied; these other fibres are rendered functionless in the particular experimental context by denervation of their muscles.

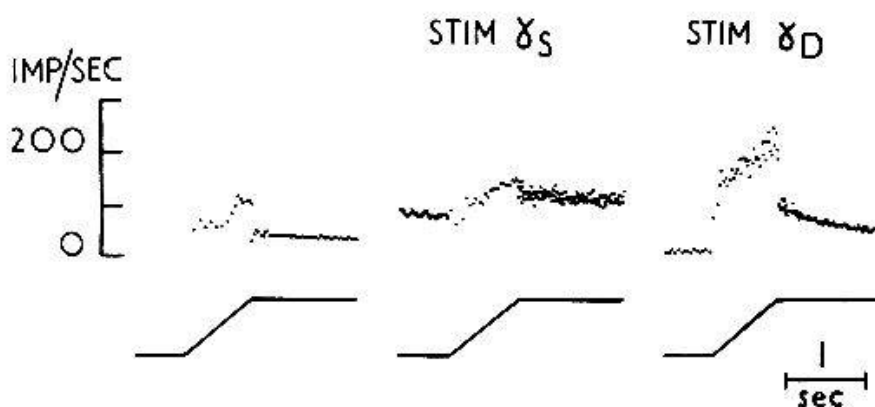


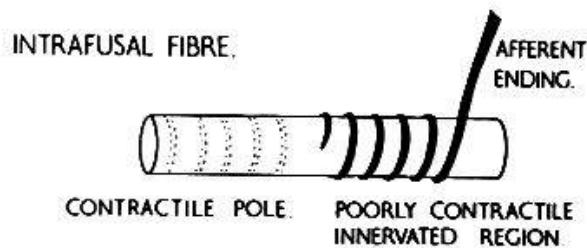
Fig. 8. The contrasting effects of static and dynamic fusimotor stimulation on a primary ending. - a) Response to stretching in the absence of fusimotor stimulation. - b) Response to similar stretch applied during repetitive stimulation of a single static fusimotor fibre. - c) Response during stimulation of a single dynamic fusimotor fibre (BROWN and MATTHEWS, 1966).

afferent is isolated by splitting dorsal root filaments. A single motor fibre is by KUFFLER et al. (1951). Fig. 7 shows the preparation. A single spindle then isolated by splitting ventral root filaments until a fibre is found which influences the particular spindle studied; the singleness of the γ motor fibre is assured by stimulating the muscle nerve while recording from the ventral root filament and observing a single all-or-none potential with the appropriate velocity. This preparation showed just what was hoped for, namely that individual fusimotor fibres had one or another of two quite different kinds of action on the primary ending (MATTHEWS, 1962). This is shown in Fig. 8. Some γ fibres, which were named static fusimotor fibres, had a powerful excitatory action on the primary ending when the length of the muscle was constant and at the same time decreased the normally high dynamic responsiveness of the primary ending. Other γ motor fibres, which were called dynamic fusimotor fibres, had a rather weaker action on the ending when the muscle length was held constant, but in spite of this their stimulation

tremendously increased the sensitivity of the primary ending to the dynamic component of a stimulus (CROWE and MATTHEWS, 1964a; LENNERSTRAND and THODEN, 1968a). When a range of more or less randomly selected fusimotor fibres was studied there was usually little trouble in deciding whether each one was a static or a dynamic fibre and intermediate forms were virtually absent. More importantly, when it was found possible to test the action of an individual fusimotor fibre on several different primary endings then it was always found to have the same kind of action on all of them. This shows that a fusimotor fibre has a static or dynamic specificity in its own right rather than by virtue of some chance relation that it enters into with one particular spindle. In conjunction with the now amply supported finding that the static and dynamic fibres can be influenced independently from the CNS this guarantees that the static/dynamic classification is physiologically meaningful. The classification has thus been widely accepted for at least the last six years (BROWN and MATTHEWS, 1966; BESSOU and LAPORTE, 1966).

Intrafusal mechanisms

The understanding of what is actually happening inside the spindle has, however, proceeded rather less smoothly and universal agreement has yet to be achieved. This is simply because of the continuing lack of suitably direct evidence. The original suggestion was that the dynamic fibres achieved their particular action by virtue of supplying the nuclear bag intrafusal muscle fibres and the static fibres by virtue of supplying the nuclear chain fibres. On its inception this hypothesis ran far ahead of the available evidence and in certain respects the arguments then advanced in its favour have not proved entirely correct. Even so, this original suggestion has gradually come to be established as the most likely state of affairs. The hypothesis has two separate components. First, that the two kinds of fusimotor fibre achieve their separate actions by each supplying one or other of the two different kinds of intrafusal muscle fibre. Second, that the correspondence between static and dynamic action and the bag and chain intrafusal fibres falls out one particular way round. Apart from histological observation, BOYD (1971) has produced direct evidence that stimulation of individual fusimotor fibres usually produces contraction of one or other kind of intrafusal fibre and not of both. He did this by watching single living spindles under the microscope. Thus the first component of the original hypothesis appears reasonably validated. It should be noted, however, that on about 10% of occasions BOYD observed that a single fusimotor fibre produced contraction of both kinds of intrafusal fibre; it would be surprising if this cross-innervation did not also prove to be of physiological significance. Fig. 9 illustrates how by having different contractile properties the two kinds of intrafusal fibres might produce the two types of action. It is assumed that the velocity response of the primary ending arises because the contracting intrafusal poles behave more viscously than the non-contracting equatorial



<u>NATURE OF CONTRACTION.</u>	<u>RESPONSE OF ENDING</u>
A. SHORTENING WITH INCREASE OF 'VISCOSITY' (i.e. SLOW).	DYNAMIC TYPE.
B. SHORTENING WITH 'VISCOSITY' UNCHANGED (i.e. FAST).	STATIC TYPE.

Fig. 9. Diagrammatic illustration of how the static and dynamic fusimotor actions might be mediated by different types of intrafusal muscle fibre with different speeds of contraction (BROWN and MATTHEWS, 1966).

Fusimotor fibre	Intrafusal fibre
γ_d Slow intrafusal system Excites primary alone Mimicked by S. Ch.	N-Bag Slow contraction Primary innervation alone More strongly excited by S. Ch.
γ_s Fast intrafusal system Excites primary and secondary	N-Chain Fast contraction Primary and secondary innervation

Ergo: $\gamma_d \rightarrow NB$ and $\gamma_s \rightarrow NC$

Fig. 10. Summary of the arguments for the dynamic and static fusimotor fibres achieving their actions by predominantly innervating the nuclear bag and nuclear chain fibres respectively.

region where the primary ending lies. If so, then a contraction which is accompanied by an increase of intrafusal viscosity would give the dynamic type of response and a contraction with a decrease of intrafusal viscosity would give the static type of response. It seems likely that an increase of viscosity can be equated with a slow type of contraction and a decrease with a fast contraction.

Fig. 10 summarises the current arguments in favour of the dynamic fibres supplying the bag fibres and the static fibres the chain fibres rather than the other way round. The first argument is based on estimates of the speed of intrafusal contraction. Direct observation of isolated spindles shows that the bag fibres contract relatively slowly while the chain fibres contract rather rapidly (BOYD, 1966; SMITH, 1966). Recording of spindle afferent discharges, notably by Professor LAPORTE and his colleagues, has shown that the static fibres produce a much more rapid action than do the dynamic fibres (BESSOU et al., 1968). Second, there is the matter of the secondary afferent ending.

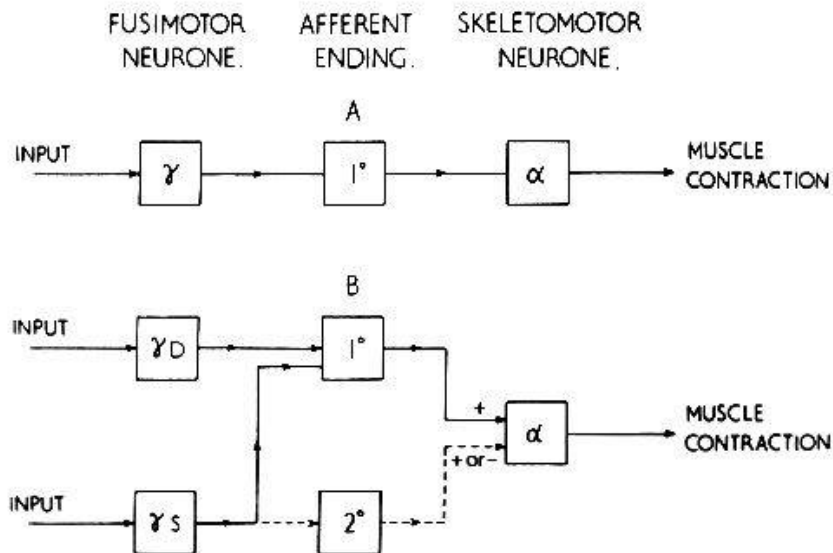


Fig. 11. Diagram showing possible routes for the activation of muscle via the fusimotor fibres and the spindle afferents. - A. Classical scheme. - B. Modified scheme incorporating some of the newer findings (BROWN and MATTHEWS, 1966).

Histology shows that this ending lies almost entirely upon the nuclear chain fibres and hardly at all on the nuclear bag fibres. It would thus be expected that the secondary ending should be excited on chain contraction but not on bag contraction. Experiment shows that the static fibres regularly excite secondary endings whereas the dynamic fibres fail to do so even though they can be shown to be influencing the particular muscle spindle in which any particular ending studied happens to lie (APPELBERG et al., 1966). The third argument is based on the study of the action of succinylcholine (suxamethonium). This drug has a powerful dynamic action on the primary ending and direct observation shows that it has a much more powerful action on the nuclear bag than on the nuclear chain fibres (SMITH, 1966; RACK and WESTBURY, 1966). Thus a correspondence may be drawn between dynamic fusimotors and bag intrafusals and between static fusimotors and chain intrafusals; and certainly no better scheme would appear to be currently available.

Possible functional roles of the fusimotor fibres, particularly in relation to the servo-control of muscle

So much for the periphery where the residual problems may reasonably be expected to be unravelled by the continued application and refinement of the present methods of experimentation. A much more serious problem is to achieve understanding of how the central nervous system uses the static and dynamic fusimotor fibres. This also involves understanding just how the central nervous system uses the information it receives from the muscle spindle. Fig. 11 shows in diagrammatic form the best way of thinking about things we have at the moment, namely the employment of the fusimotor

fibres for the servo-control of movement or more probably for its servo-assistance; this is an idea which we originally owe to MERTON (1953) and to GRANIT (1955). The particular schemes so far proposed are undoubtedly gross simplifications of the real state of affairs but the whole idea has had the merit of stimulating experimental work. The upper part of Fig. 11 shows the now classical γ route for muscle excitation in which movement is seen as commanded by the higher centres channelling activity onto γ motoneurons in the first instance rather than directly upon the α motoneurons. The γ motoneurons excite the primary endings which then in their turn monosynaptically excite the α motoneurons and so produce an overt contraction. The supposed advantage of this roundabout way of producing muscle contraction is that it employs the valuable stabilising properties of the stretch reflex. Unfortunately, we cannot continue to think in terms of such a simple scheme for it ignores the two kinds of fusimotor fibre. The lower half of Fig. 11 shows the currently more realistic scheme. This also includes the secondary ending, but in the present talk I shall ignore its contribution as the matter is still controversial, but to make such an omission is undoubtedly to leave a serious gap in understanding. Slightly indirect evidence suggests that when the spinal centres are suitably facilitated the secondary ending provides an excitatory contribution to the stretch reflex arc which is quite as important as that provided by the primary ending (MATTHEWS, 1969).

The main question about the newer scheme is whether only one or other of the two kinds of fusimotor fibre provides the input command to the servo. The answer appears to be that the static fibres are chiefly if not wholly responsible. This can be said because only the static fibres elicit an intrafusal contraction which is fast enough to keep up with the extrafusal muscle fibres. They alone seem able to make the spindle fire faster during shortening of the main muscle and thereby allow it to continue to reflexly excite the α motoneurons (LENNERSTRAND and THODEN, 1968b). The dynamic fibres appear to produce an intrafusal contraction which is just too slow to be effective in this respect. A wealth of experimentation now leaves no doubt that the spindle does fire faster during many a physiologically evoked muscle contraction and thus is able to play a role in reflexly aiding contraction. Fig. 12 shows the recent dramatic example of such acceleration obtained by VALLBO during a voluntarily induced muscle contraction in the co-operative human subject who has a micro-electrode pushed into his median nerve. The spindle acceleration during the contraction shows that the static fusimotor fibres must have been firing more rapidly than before because otherwise the spindle would have slowed down. However, the contraction was not initiated solely via the fusimotor fibres, because the increase in spindle firing begins after the beginning of the movement and so cannot have been its cause.

What then is the function of the dynamic fusimotor fibres? The original suggestion was that by increasing the sensitivity of the primary ending to velocity they served to damp the stretch reflex arc and hence reduce its

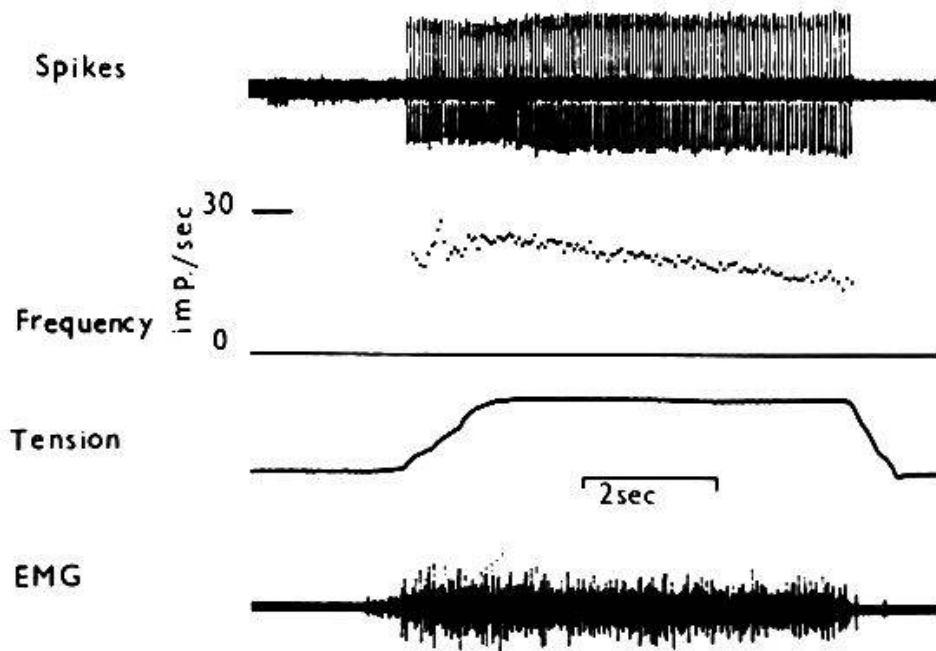


Fig. 12. The discharge in man of a presumed spindle afferent during a weak voluntary isometric contraction of the muscle which it supplied (flexor of index finger) (VALLBO, 1970).

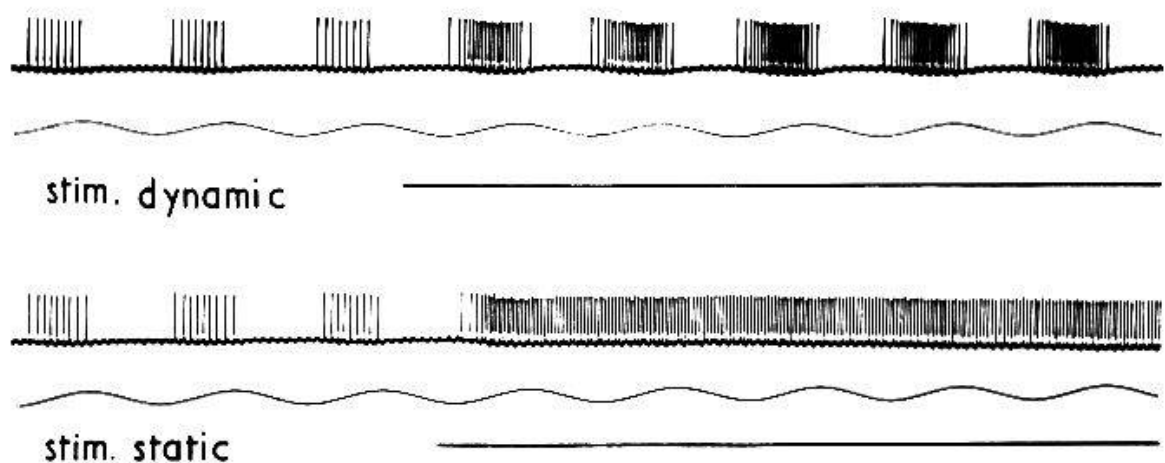


Fig. 13. The effect of fusimotor stimulation on the response of a primary ending to sinusoidal stretching of medium size (1 mm peak to peak at 3 Hz) (CROWE and MATTHEWS, 1964b).

tendency to go into spontaneous oscillation or tremor. This remains a perfectly reasonable idea in the qualitative plane though it has yet to be tested in any quantitative manner. In addition, however, more recent experiments have put the matter in a different light by emphasising the striking effect of fusimotor stimulation on the response of the primary ending to rhythmic stretching of small amplitude. Fig. 13 shows the effect of fusimotor stimulation on the response to sinusoidal stretching of 1 mm peak to peak amplitude and emphasises again the tremendous difference between the two kinds of fusimotor fibre. During dynamic stimulation the ending was highly sensitive to the mechanical stimulus whereas during

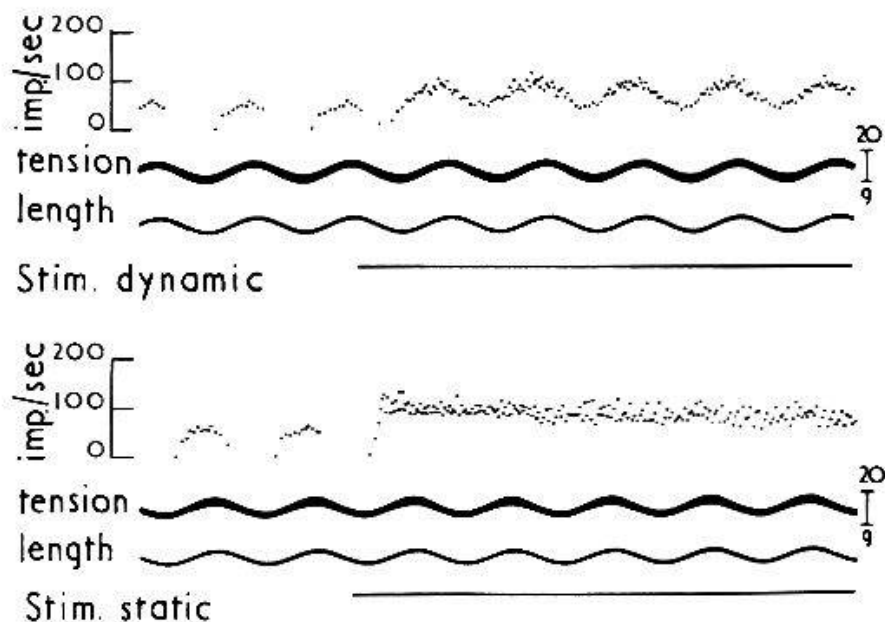


Fig. 14. The effect of fusimotor stimulation on the response of a primary ending to small amplitude sinusoidal stretching (0.1 mm peak to peak at 2 Hz; different experiment from that of Fig. 13) (CROWE and MATTHEWS, 1964b).

static stimulation the ending barely noticed the sinusoidal stretching. Fig. 14 shows similar differences in the responses when the amplitude of stretching was made ten times smaller, namely 0.1 mm peak to peak. With such a reduction of the sinusoidal stimulus the response lends itself to a more rigorous analysis because the ending now fires throughout all phases of the cycle of stretching. The ending can also be shown to be behaving "linearly" in that doubling the amplitude of the stretching doubles the depth of the modulation of the afferent firing. This allows us to measure what may be called the "spindle sensitivity" for each frequency of stretching. This is simply the change in afferent firing, measured in impulses/sec, divided by the size of the stimulus, measured in mm (MATTHEWS and STEIN, 1968). During dynamic stimulation in the particular example of Fig. 14 stretching of $\frac{1}{10}$ mm amplitude gave a response modulation of about 50 impulses/sec so that the sensitivity was about $500 \text{ impulses sec}^{-1} \text{ mm}^{-1}$. Using averaging procedures Mr. GOODWIN and I have been determining the sensitivity of the primary ending to a range of frequencies of stretching. Fig. 15 shows the typical effects of static and of dynamic stimulation. At low frequencies the sensitivity during static stimulation is around $10 \text{ impulses sec}^{-1} \text{ mm}^{-1}$ whereas during dynamic stimulation it is some ten times higher. From about 0.3 to 3 Hz the curves run rather flat, but they then begin to rise. The static curve rises much more steeply than the dynamic curve so that they progressively converge. This is very interesting from the point of view of intra-fusal mechanisms, but it is presumably unimportant from the point of view of physiological function because frequencies above about 10 Hz probably fall outside the physiological range and because the extent of the "linear range" then becomes rather small. Thus the functionally important feature

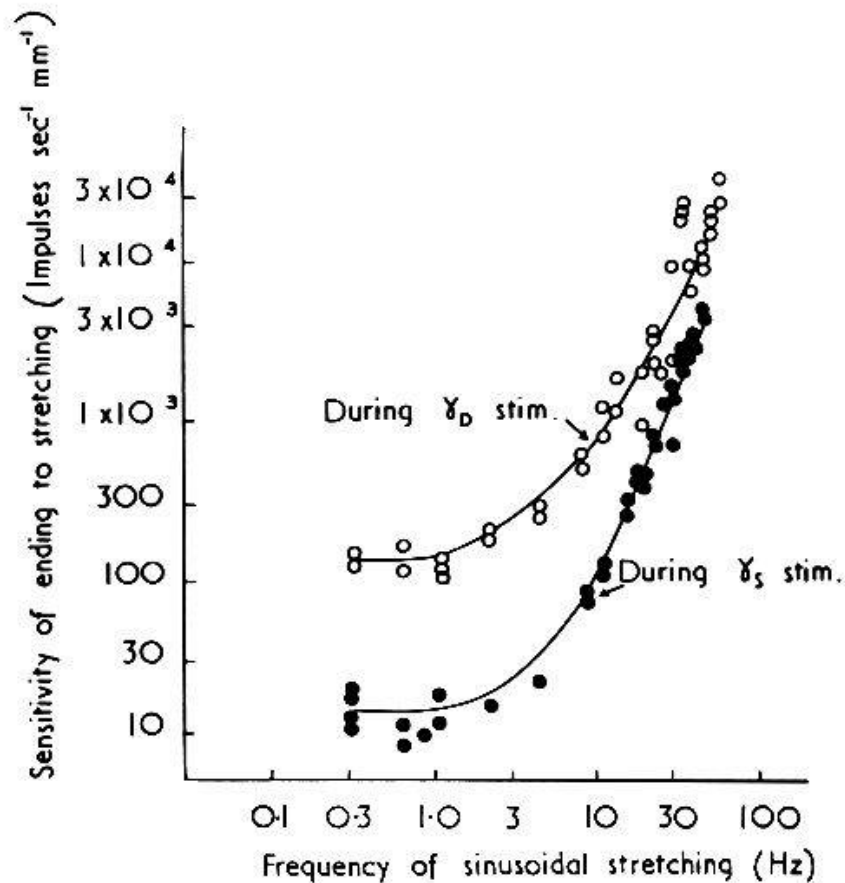


Fig. 15. The effect of fusimotor stimulation on the sensitivity of the spindle primary ending to sinusoidal stretching of various frequencies. The «sensitivity» is the amplitude of the modulation of the afferent discharge (in impulses/sec) divided by the amplitude of the sinusoidal stretching (in mm). The measurements were made with the amplitude of stretching reduced sufficiently to ensure that the response was linearly related to the stimulus. The two sets of data were obtained from two different preparations, but each was typical of its kind. Curves drawn by eye. Upper points obtained during stimulation of a single dynamic fibre at 47/sec for periods of about 5 sec for each frequency of stretching; lower points obtained during similar stimulation of a static fibre (results obtained with G. M. GOODWIN, technique broadly similar to that of MATTHEWS and STEIN, 1969).

would appear to be that dynamic stimulation leads the primary ending to have a high sensitivity to small amplitude sinusoidal stretching of moderate and low frequency. However, the sensitivity during dynamic stimulation may be no larger than that found for the passive ending in the absence of intrafusal contraction, but a high passive sensitivity is found only when the muscle is pulled out rather taut. In contrast, during dynamic stimulation a high sensitivity is preserved over a wide range of physiologically significant lengths.

Fig. 16 shows the occurrence of a high spindle sensitivity under reasonably physiological conditions and helps illustrate its likely functional importance. The records show the behaviour of three different spindle afferents from the soleus muscle of the decerebrate cat while it was taking part in a crossed extensor reflex elicited by stimulating a contralateral nerve. The contraction



Fig. 16. Physiological manifestation of a high sensitivity of the primary ending to small amplitude rhythmic stretching. The two primary endings show an obvious response to the small irregularities in the contraction. This was taking place under the nearly isotonic conditions produced by connecting the muscle to the myograph via a weak spring (peak tension about 120 g). The preparation was the soleus muscle of the decerebrate cat with intact ventral roots, severed dorsal roots, and spontaneously occurring fusimotor activity. The contraction was evoked reflexly by stimulating the lateral popliteal nerve of the other hindlimb for the period indicated. The discharges of the three afferents were recorded simultaneously (previously unpublished record of JANSEN and MATTHEWS, 1962).

was occurring under nearly pure isotonic conditions, produced by connecting the muscle to a myograph via a weak spring, so that the reflex was primarily producing shortening rather than tension and was thus better able to allow the endings to show off certain features of their behaviour. The ventral roots were intact so the endings were under the influence of whatever particular spontaneous fusimotor firing that the preparation had, but the dorsal roots were cut so the spindle firing could not reflexly alter the course of the contraction. The secondary ending behaved very simply and slowed down as the muscle shortened and then gradually speeded up again as the muscle returned to its original length. The two primary endings slowed down much less during the shortening; during the lengthening they showed a marked increase in firing, presumably in response to the dynamic stimulus of being stretched. In addition, however, they fired somewhat irregularly with short periods of alternating higher and lower frequencies of discharge. These were synchronised for the two primary endings and can be recognised as the response to the small irregularities in the length trace which are about 0.1 mm in extent. Thus these records demonstrate the high sensitivity of the primary ending to a physiologically occurring type of sinusoidal stretching. Moreover, there can be little doubt that if the reflex arc had been intact the rhythmic alteration in primary firing would have reflexly counteracted the irregularities of movement and so tended to smooth out the muscle contraction.

Thus the dynamic fusimotor fibres may be thought of as having a two-fold action. On the one hand, they increase the sensitivity of the primary ending to small stretches. On the other hand, they increase its response to the velocity component of large stretches. It would be invidious to attempt to decide between the relative importance of these two actions, and their separation is useful as much as anything to achieve verbal clarity while we are still continuing to talk about the spindle in relatively simple terms. In life, both actions will help to make the primary more effective at resisting an externally applied deformation irrespective of whether it is large or small. Hence the dynamic fusimotor fibres appear to have as their role the sensitising of the primary ending so as to control the sensitivity of the stretch reflex servo. The static fibres, however, would appear to allow for the servo-assistance of movement, but in so doing they appear to be decreasing the sensitivity of the spindle. It would seem reasonable that the gain of the spindle should be set to a high value during holding and postural reactions and to a low value during phasic movements.

Thus ten years of progress may be summarised as follows. First, it is now well established that the static and dynamic fusimotor fibres are functionally distinct entities. Second, there is a fair measure of agreement about how they act inside the spindle to achieve their separate actions. Third, it is possible to make tentative suggestions on their functional role in the body as servants of the central nervous system. Future work seems likely to be concerned progressively with attacking the regulatory aspects of their func-

tion and in so doing should help us to understand better the central nervous system itself, and its functional derangements in disease.

Summary

In the late 1950's light microscopy established that the small muscle fibres inside the muscle spindle are of two distinct kinds. These are now called nuclear bag and nuclear chain intrafusal muscle fibres. It then became natural to enquire into their respective functions and whether they were supplied by separate motor nerve fibres. This led in 1962 to the subdivision of the small γ efferent fibres to the spindles into two functionally distinct groups which were named the static and the dynamic fusimotor fibres. The two kinds of fusimotor fibre were originally distinguished by their very different actions on the response of a spindle primary ending to a large stretch applied at a constant velocity. Stimulation of a dynamic fibre enhances the normal dynamic responsiveness of the ending to this form of stimulus whereas stimulation of a static fibre reduces the dynamic responsiveness of the ending even though it powerfully excites the ending. Dynamic stimulation also leads the primary ending to be highly responsive to sinusoidal stretching of small amplitude and low frequency (100 μm extent at 0.3–10 Hz). In contrast, static stimulation makes the primary ending largely insensitive to this form of mechanical stimulation. The dynamic fibres were originally suggested to achieve their particular actions by supplying the nuclear bag intrafusal muscle fibres and the static fibres to achieve theirs by supplying the nuclear chain fibres. This view can now be supported by reasonably direct evidence.

The central nervous system has been shown to be able to exert an independent control over two kinds of fusimotor fibre. The use it makes of such a facility is still highly speculative. The static fibres may be suggested to be used in conjunction with the α motor fibres to provide a "command signal" to the stretch reflex arc and thereby produce a "servo-assistance" of movement. The dynamic fibres may be suggested to be used to control the sensitivity of the stretch reflex loop. In this respect equal importance may be attached to their increasing the velocity responsiveness of the primary ending to large stretches and to their increasing its responsiveness to small amplitude rhythmic stimuli.

Zusammenfassung

Ende der 50er Jahre konnte die Lichtmikroskopie zeigen, dass die Muskelspindel zwei Arten spezialisierter Fasern enthält. Heute werden diese als Kernsack- (nuclear bag) bzw. Kernketten (nuclear chain)-Fasern bezeichnet. Die weitere Forschung befasst sich nun mit den Funktionen und der efferenten Innervation dieser beiden intrafusalen Systeme. 1962 erfolgte die Unterteilung der γ -Fasern in zwei Gruppen: die statischen und die dynamischen

fusimotorischen Fasern. Diese Klassifizierung erfolgte ursprünglich auf Grund der verschiedenen Effekte auf die (afferenten) primären Endigungen bei starker Dehnung mit konstanter Geschwindigkeit. Die Reizung einer dynamischen γ -Faser verstärkt die Reaktionsbereitschaft, während die Reizung der statischen Fasern auch bei starker Rezeptorenreizung das Gegenteil bewirkt. Erregung der dynamischen γ -Fasern führt überdies auch zur erhöhten Empfindlichkeit der primären Endigungen auf sinusförmige Dehnungsreize mit kleiner Amplitude ($100 \mu\text{m}$) und niedriger Frequenz ($0,3\text{--}10 \text{ Hz}$). Im Gegensatz dazu macht die Stimulation der statischen Faser die primären Endigungen weitgehend unempfindlich auf diese Reizform. Es wurde angenommen, dass die dynamischen γ -Fasern diese Wirkung über die Kernsackfasern ausüben, während die statischen γ -Fasern die Kernkettenfasern versorgen. Diese Ansicht konnte nunmehr durch direkte experimentelle Beweise erhärtet werden.

Das Zentralnervensystem übt eine eigene Kontrolle über diese zwei fusimotorischen Systeme aus. Die Bedeutung dieser Kontrolle ist noch zum Teil Gegenstand von Spekulationen. Die statischen Fasern sollen vor allem im Zusammenhang mit sogenannten «Kommandosignalen» auf die α -Motoneurone des Rückenmarks einwirken und dabei eine Art «Servohilfe» des Bewegungsablaufes liefern. Die dynamischen Fasern dürften eine Empfindlichkeitskontrolle des Streckreflexes ausüben, indem sie die Empfindlichkeit der primären Endigungen einerseits auf kleinste Geschwindigkeitsänderungen bei starken Dehnungen und andererseits auf rhythmische Stimulation von geringer Amplitude erhöhen können.

Résumé

A la fin des années cinquante le microscope à lampe a permis de montrer que les petites fibres musculaires à l'intérieur d'un faisceau de muscle sont de deux types différents. Il est tout naturel d'étudier leurs fonctions respectives et de se demander si elles étaient innervées par des fibres motrices séparées. Ceci amena en 1962 à départager les petites fibres γ efférentes aboutissant aux faisceaux musculaires en deux groupes fonctionnellement distincts qu'on nomma les fibres fusimotrices statiques et dynamiques. Ces deux espèces de fibre fusimotrice avaient pu être distinguées au début par leurs actions différentes en réponse à une forte élongation appliquée à une vitesse constante d'un faisceau musculaire. La stimulation d'une fibre dynamique augmente la réaction dynamique normale à cette sorte de stimulus, alors que la stimulation d'une fibre statique diminue nettement la réaction dynamique de l'extrémité de cette fibre, bien qu'elle soit fortement excitée. Une stimulation dynamique rend l'extrémité des fibres extrêmement sensibles à une élongation sinusoïdale de petite amplitude et de basse fréquence ($100 \mu\text{m}$ d'élongation à $0,3\text{--}10 \text{ Hz}$). Par contre une stimulation statique rend l'extrémité fibrillaire très peu sensible à cette forme d'excitation mécanique. On a supposé tout d'abord que l'action spécifique des fibres dynamiques

était d'alimenter les fibrilles du fuseau musculaire dans le noyau, alors que les fibres statiques alimentaient les fibrilles en chaîne du noyau. Ce point de vue est aujourd'hui confirmé par des preuves suffisantes.

On a pu montrer que le système nerveux central était capable d'exercer un contrôle sur les deux espèces de fibres fusimotrices. On ne sait pas encore à quoi lui sert exactement cette capacité. On peut supposer que les fibres statiques sont excitées en même temps que les fibres motrices α afin de fournir un «signal commandé» à l'arc réflexe d'élongation, et en ce faisant de produire une «servo-assistance» pour le mouvement. Il est possible que les fibres dynamiques contrôlent la sensibilité de l'arc réflexe. En ce faisant ils ont une importance égale pour augmenter la rapidité de réaction à de fortes élongations et en augmentant leur réponse à des stimuli rythmiques de petite amplitude.

Riassunto

Verso la fine degli anni cinquanta, il microscopio a lampada ha permesso di dimostrare che le piccole fibre all'interno di un fascio muscolare sono di due tipi differenti. Sembra naturale quindi di studiarne le funzioni rispettive e di chiedersi se fossero innervate da delle fibre motrici separate. La conseguenza di queste considerazioni fu che nel 1962 si separarono le piccole fibre γ efferenti, trovando due gruppi di fasci muscolari funzionalmente distinti e che furono chiamati fibre fusimotrici statiche e dinamiche. All'inizio si arrivò a distinguere questi due tipi di fibre fusimotrici, grazie alle loro azioni differenti per quanto riguarda la risposta ad una forte elongazione applicata ad una velocità costante di un fascio muscolare. La stimolazione di una fibra dinamica aumenta la reazione dinamica normale a questo genere di stimolo, mentre la stimolazione di una fibra statica diminuisce nettamente la reazione dinamica dell'estremità di questa fibra, anche se è fortemente eccitata. Una stimolazione dinamica rende l'estremità delle fibre molto sensibile ad una elongazione sinusoidale di piccola amplitudine e di bassa frequenza (100 μ m d'elongazione a 0,3-10 Hz). Al contrario, una stimolazione statica rende l'estremità fibrillare poco sensibile a questa forma di eccitazione meccanica. Dapprima si pensò che l'azione specifica delle fibre dinamiche fosse di alimentare le fibrille del fascio muscolare nel nucleo, mentre le fibre statiche alimentavano le fibrille a catena del nucleo. Oggi, questo punto di vista è stato confermato da un numero sufficiente di prove.

Si è potuto dimostrare che il sistema nervoso centrale è capace di esercitare un controllo su i due tipi di fibre fusimotrici. Non si sa però ancora bene a che cosa serva esattamente questa facoltà. Si può supporre che le fibre statiche siano eccitate contemporaneamente alle fibre motrici α , allo scopo di fornire un «segnale comandato» all'arco riflesso d'elongazione, e così produrre una «servoassistenza» per il movimento. È possibile che le fibre dinamiche controllino la sensibilità dell'arco riflesso. Così facendo, hanno un'importanza uguale per aumentare la rapidità di reazione a forti elongazioni, aumentando la loro risposta a degli stimoli ritmici di piccola amplitudine.

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