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Stockholm 60, Sweden

**The Pause During Contraction
in the Discharge of the Spindle Afferents from Primary
End Organs in Cat Extensor Muscles**

By

RAGNAR GRANIT and J. P. VAN DER MEULEN¹

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Abstract

GRANIT, R. and J. P. VAN DER MEULEN. *The pause during contraction in the discharge of the spindle afferents from primary end organs in cat extensor muscles.* Acta physiol. scand. 1962. 55. 231—244. — Recently much detailed information has become available about the structural design of the muscle spindles. It seems highly pertinent that the large spindle-afferents from primary end organs possess two kinds of terminals, one set deriving from the nuclear bag of special 'nuclear bag'-fibres, another from purely muscular, short, so-called 'nuclear chain'-fibres. Also spindles may vary in length over more than a tenfold range (cat). The pause in the discharge of the muscle spindles in isometric contraction has been studied and the findings evaluated from the point of view of spindle anatomy. The primary end organs were found to fall into two groups, long-pause spindles and short-pause spindles. This grouping is assumed to express their anatomical length. This may vary between 2 and 22 mm. The pause either ended with a phasic burst, often succeeded by a brief, secondary pause, or else the discharge was resumed in a tonic fashion. Thus spindles were 'phasic' or 'tonic' with respect to how they resumed firing after the 'pause'. Nearly all the 'tonic' spindles were found among the long-pause spindles. The hypothesis adopted to explain the phasic-tonic differentiation is that phasic spindles are dominated by 'nuclear bag'-fibres, tonic ones by 'nuclear chain'-fibres. Spindles are also known to vary considerably with regard to the relative number of these two different fibre types.

¹ Visiting special Trainee of the National Institute of Neurological Diseases and Blindness Bethesda, Md., U. S. A.

B. H. C. MATTHEWS (1933), who discovered the pause in the discharge of the muscle spindle afferents during contraction, also gave it an explanation that has been generally accepted. Despite isometric recording, the tendinous portion of the muscle elongates in contraction and allows some shortening (1—2 mm) of the extrafusal fibres. The intrafusal fibres of the spindle, being situated 'in parallel', are thereby unloaded and their stretch receptors become silenced, as had been anticipated by FULTON and PI-SUÑER (1927—28). This, no doubt, is a still valid generalization but what shall concern us below is how the primary end organs are re-excited after a contraction or, in other words, how long the pause is and in what way the discharge recommences. In this respect spindles vary a great deal and the question is what these variations suggest when they are reproducible and independent of gamma control.

In the past it seemed an unprofitable task to systematize and try to explain the variations alluded to because too little was known about spindle anatomy. This deficiency has now been remedied, largely owing to the work of BARKER and his associates, and of BOYD, work that was preceded by some pioneer studies of SYBIL COOPER and lately confirmed by SWETT and ELDRED (ref. below). The new picture of the organization of the muscle spindle that has emerged from these studies is detailed enough for the first time to make a study of the pause worth while. It will be easier to follow the arguments of the present paper if the salient features of spindle anatomy are given already at this stage.

It has been known for a long time, and often confirmed, that there are long and short spindles and also that the intrafusal fibres of one and the same spindle have different length and thickness (see *e. g.* SHERRINGTON 1894, CUAJUNCO 1927, and summaries by HINES and TOWER 1928, BARKER 1948, COOPER 1960). New is the knowledge that there are two kinds of intrafusal fibres, nuclear bag-(NB) and nuclear chain-(NC) fibres, the latter being shorter and thinner with nuclei in chains, the former identical with the nuclear bag-fibres known from the classical literature. The new information is found in a note by COOPER and DANIEL (1956), in papers by BARKER and CHIN (1960), BARKER and GIDUMAL (1961), BARKER and IP (1961), preceded by preliminary reports, as well as in a number of brief reports by BOYD (1956, 1958, 1959, 1960, 1961) and in two papers by SWETT and ELDRED (1960 *a, b*). The large-fibre afferents, previously held to terminate as annulospirals in the nuclear bag are now known also to dispatch branches to the purely muscular NC-fibres which are lacking bags. This means that these afferents derive information from an NB elastic structure in series with muscular poles of more viscous, contractile material as well as from short purely muscular NC-fibres and hence from two different structures provided with contractile fibres 'in parallel' with one another. The whole spindle structure is 'in parallel' with the extrafusal fibres. There is also some histological evidence (COOPER and DANIEL 1956, BOYD 1959, 1961) for differences in motor innervation of NB- and NC-fibres. According to the new findings it is legitimate to differentiate between

'nuclear bag'- and 'nuclear chain'-terminals of the primary afferents from muscle spindles.

The new knowledge also means that the term 'nuclear bag-organ' is too restricted to describe the primary end organs adequately nor can they be called 'annulospirals' because they are not always provided with annulospiral endings. We have therefore returned to RUFFINI's (1897, 1898—99) alternative term *primary endings*. The *secondary endings*, according to the same recent authors, are chiefly found on the NC-fibres but also in the myotube region of the long NB-fibres. None of them have terminals on the nuclear bag.

The new knowledge makes it imperative to reconsider known spindle properties, among them the pause in the discharge of the primaries during contraction. An evaluation of the general situation (GRANIT) as well as detailed information will be found summarized in the Proceedings of the Hong Kong Symposium on Muscle Receptors (to be edited by BARKER 1962).

Methods

In the present experiments cats were used, the majority of which were decerebrated by precollicular suction. The remainder were anesthetized with a mixture of chloralose-pentobarbitone (20 mg/kg of each I. P.). A laminectomy was performed, exposing the spinal cord and roots from L₅ to cauda equina. Single fibres in the appropriate dorsal roots (L₇, S₁) were split until single spike discharges could be recorded from spindles in the gastrocnemius or soleus muscles of the left leg. These fibres gave conduction velocities in the Gr. I afferent range, as calculated from the latent period, sometimes recorded photographically, but often merely observed on the screen at high sweep speed.

The left leg was denervated except for the medial and lateral gastrocnemius nerves which were used for stimulation at knee level and in the decerebrate preparations the right leg was denervated. The soleus or gastrocnemius muscles were separated so that their tendons could be attached individually to the recording apparatus. A strain gauge myograph and an inductance length recorder connected to the tendon allowed for alternate or simultaneous recording of tension or length during either isometric or isotonic contraction. The muscle was pulled out by weights from 100 to 500 g on a short lever. For isometric contractions the lever was clamped at the length thus attained, for isotonic recording it was allowed to lift the weight. Since only the early onset of the discharge was of interest in this work, oscillations after complete relaxation in isotonic recording were of no importance.

In some experiments gamma efferents were selectively blocked with dilute procaine solution in the manner of P. B. C. MATTHEWS and RUSHWORTH (1957 *a, b*, 1958). For cocainization xylocaine (lidocaine) was used.

Results

General remarks on the pause. The ensuing descriptive sections should be read with two points of view in mind: (i) a pause in the discharge is taken to mean that the spindle is relatively too long compared with surrounding extrafusul elements so that in isometric contraction we are concerned with the time it

takes for a spindle to become matched in length with the latter; (ii) is this matching process initiated by a phasic burst or not?

To (i): both gastrocnemius and soleus spindles fall into two groups clearly distinguishable in the extremes; these are the short pause (SP) and the long pause (LP) spindles (see *e. g.* Fig. 1). There is, of course, an arbitrary element in these distinctions owing to border line cases. Actually, however, when the muscles are properly stretched, from some 5 to 7 mm, there has been no overlap in our material which consists of 11 LP- and 10 SP-soleus spindles, 15 LP- and 19 SP-gastrocnemius spindles, in all, 55 analyzed at different extensions out of 61 isolated.

With double shocks, exceptionally three shocks, the average pause of the LP-spindles in soleus was 310 msec, the range from 270 to 340 msec; for the SP-spindles the average was 150 msec, the range 100 to 200 msec. In gastrocnemius the average was 180 msec with range from 130 to 300 msec for LP-spindles; corresponding values for SP-spindles averaging 70 msec with range from 40 to 110 msec. With single shocks, the LP-average for soleus was 220 msec (range 170—320), the SP-average was 90 msec (range 58—130); for gastrocnemius the corresponding figures were: LP-spindles 110 msec (90—200), SP-spindles 60 msec (30—83). In general, when the pause is long, it also tends to be labile and influenced by muscle length and stimulus strength; the shorter it is, the better reproducible despite variations in extension of the muscle and stimulus strength.

There was one soleus spindle which in the beginning of the experiment belonged to the SP-category with a double-shock pause of 130 msec; later it suddenly changed type and the pause lengthened to values around 300 msec. The others maintained their character except at extreme extensions when some spindles lost their early component and gave pauses of long duration. In others the pause tended to shorten somewhat with extension (values below 5 mm extension not considered), the majority being fairly stable. The values given do not refer to extremes of extension and cases when this has led to an alteration of the duration of the pause.

The effect of stimulus strength, whether just maximal or supramaximal, proved to be of little importance with SP-spindles, even when brief tetani were used so as to activate gamma fibres. The SP-spindles, on the whole, had more definite 'time constants' than LP-spindles though, in response to gamma activation, frequency might change within the burst by which they tended to resume function. With the LP-spindles we were surprised to find a number of them to have longer pauses with supramaximal stimuli, even when the silent period then was sprinkled with spikes owing to gamma activation. In others the pause shortened somewhat, in the majority it proved to be uninfluenced. We have no cue to these differences. The fact that by sufficient gamma activation it is possible to fill out the pause in extended spindles (MATTHEWS 1933, KUFFLER, HUNT and QUILLIAM 1951), recently again

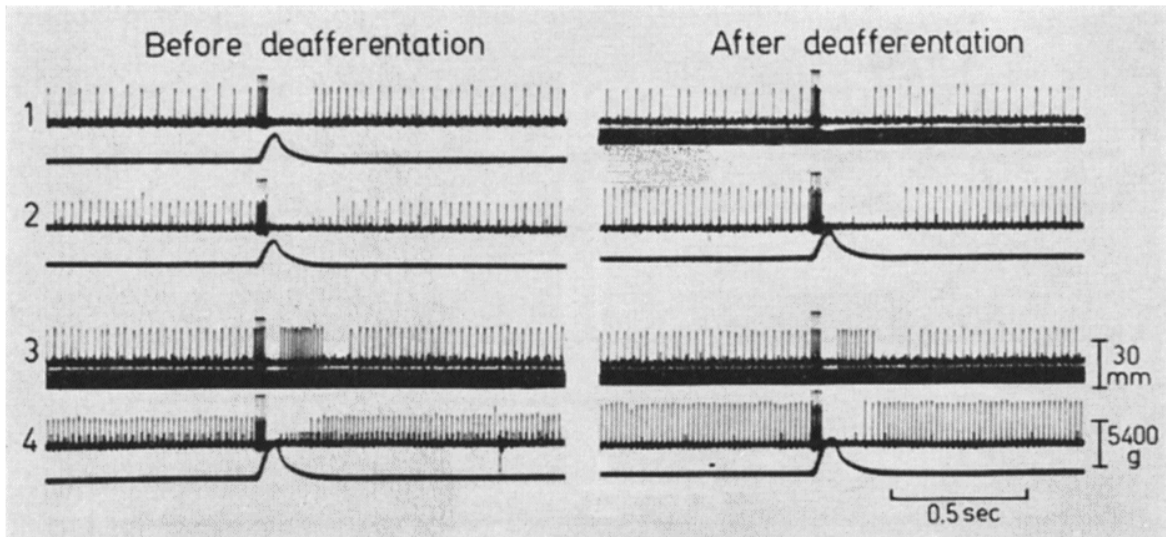


Fig. 1. Pentobarbitone-chloralose, intact preparation. Two primary gastrocnemius afferents stimulated by brief tetanus. Isometric recording, sometimes with length-measuring device. Muscle at 4.5 (1, 2) and 9.5 (3, 4) mm extension. Spike responding in 1 and 3 became 'short-pause', phasic upon extension to 9.5 mm; spike responding in 2 and 4 remained 'long-pause' and tonic. The phasic spike (1, 3) started firing to pull at 2 mm extension, the tonic (2, 4) fired 15–20 per sec already at zero extension. The curves in a diagram plotting discharge frequency against extension were roughly parallel, merely shifted by the threshold difference given. Conduction velocity of phasic spike 115 m/sec, of tonic spike 90 m/sec.

studied by HARVEY and P. B. C. MATTHEWS (1961 *a*), does not enter into our considerations. Very strong stimuli of longer duration than we have used are required to demonstrate it. More extension may be necessary with de-efferented spindles than with intact ones to define their properties.

To (ii): the pause either ends with a phasic burst, often followed by a secondary pause and a 'tonic' discharge, or else resumption of activity is 'tonic' from the beginning. We shall speak of phasic and tonic spindles, since the terms 'dynamic' and 'static' discharge have been defined with respect to fast stretch (*cf.* KATZ 1950, HARVEY and MATTHEWS 1961 *b*). There were 51 % phasic spindles in gastrocnemius, hence 49 % tonic; 67 % phasic spindles in soleus, hence 33 % tonic. These figures refer to the total number of 61 spindles of which 37 were in gastrocnemius, 24 in soleus. The general tendency is for the SP-spindles to be phasic and for the tonic spindles to belong to the LP-category. This rule held for all the gastrocnemius spindles, but a few LP-spindles in soleus had a phasic component. Among the 55 spindles, analyzed in detail, there was one tonic spindle in gastrocnemius (after ventral root section) which had a short pause (SP-spindle). The other tonic spindles were all LP-spindles.

The comparison of pause durations in isometric and isotonic contraction, the former more of an internal adjustment, the latter a response to stretch by the falling weight, showed that, with a couple of exceptions, all spindles responded phasically to the pull of the weight. For LP-spindles the isotonic

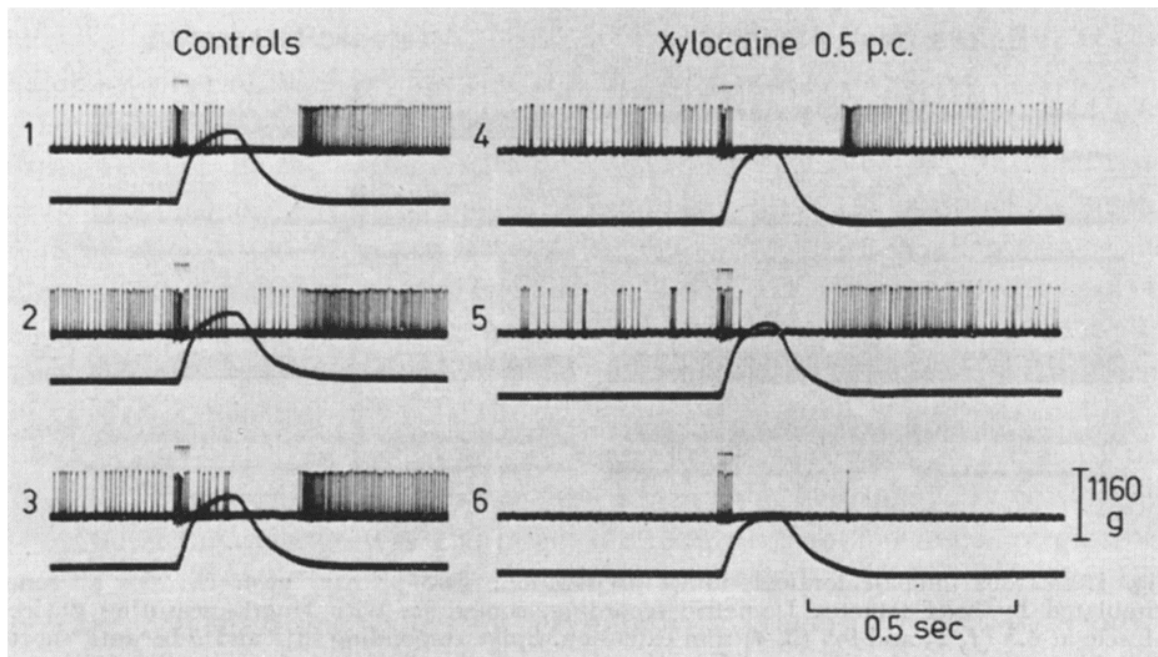


Fig. 2. Decerebrate animal with good stretch reflex and spindle response to twist of pinna. Soleus spindle 1—3, repeated supramaximal stimulation by brief tetani illustrating pause partially filled out by gamma activation of spindles. 4—6, gradually increasing effect of xylocaine applied below stimulating electrodes. In record 6 also some effect on alpha motor fibres. Conduction velocity of spike was 100 m/sec.

values for the pause also tended to vary considerably less in duration than the isometric ones. As is to be expected, the SP- and LP-character of a spindle was less in evidence with isotonic contractions; when the isometric pause was long, the isotonic was definitely shorter, and, vice versa, when the isometric pause was short, the isotonic pause was longer or of much the same length. The main role of the isotonic tests in this work has been to demonstrate that nearly all the spindles have been potentially capable of giving a dynamic response to pull, and this finding adds emphasis to the question of why so many of these same spindles have not been able to respond phasically after isometric contraction.

Samples analyzed. Fig. 1 shows two spindle afferents whose primary end organs by pressure were localized to the upper portion of the medial gastrocnemius muscle. The results reported in Fig. 1 were obtained both with just-maximal and supramaximal stimulus strength. The spindles were in the same thin filament and first recorded together. Separation proved possible and the experiment was repeated by studying them alternately, as in Fig. 1. Records 1 and 3 belong to the first spindle (phasic), at 4.5 and 9.5 mm extension respectively, 2 and 4 to the second spindle (tonic) at the same extensions. The pause of the first spindle, which had the higher threshold (see legend), was considerably shortened by extending the muscle to 9.5 mm. This shortening is of an unusually high order. The pause now ended with a burst of impulses

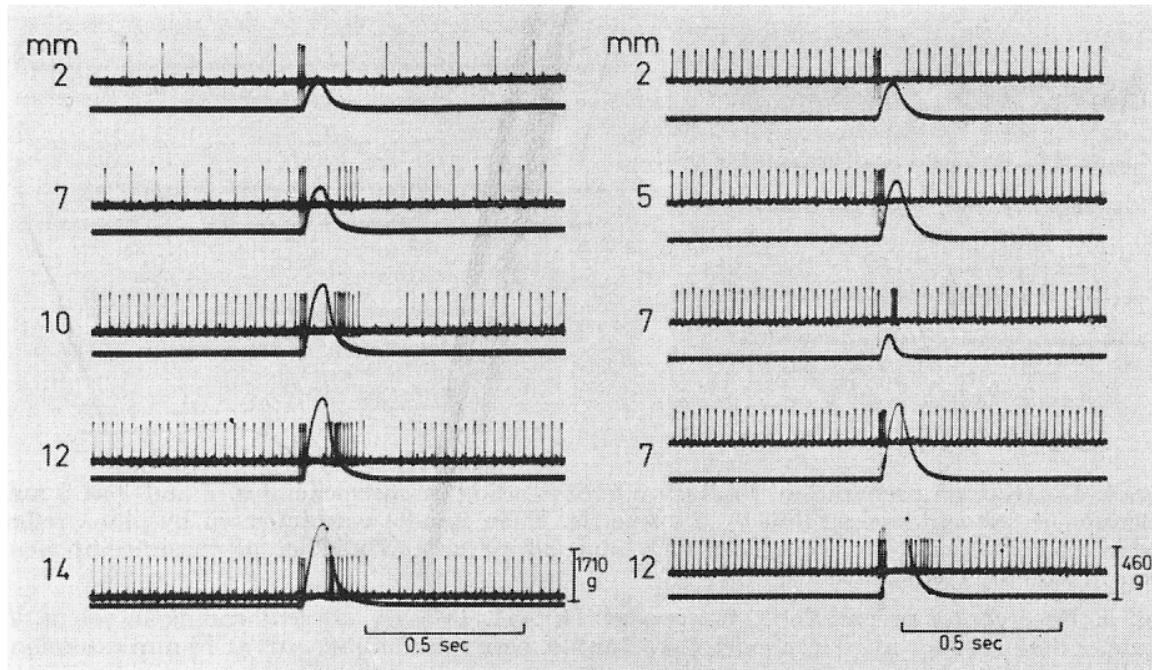


Fig. 3. De-efferented, chloralose-pentobarbitone preparation. Two phasic gastrocnemius spindles studied at different extensions, as marked on films. Third record on the right is a single-shock response, the others brief tetani. Spindle on the left studied with submaximal, spindle on the right, with maximal stimuli. Five similar spindles were isolated in the same preparation. Their conduction velocities were between 90 and 100 m/sec.

at the turning point of contraction. The secondary pause, seen here, is typical of the majority of spindles with an early phasic burst. The second spindle — active even at zero length — always responded tonically and resumed firing at the original rate when contraction was over, even when this rate was high as in the present case (records 4). (In record 4 there is also another phasically responding spindle, the small spike.) The experiment was repeated after de-afferentation (on the right) to remove a possible reflex component with preservation of whatever tonic gamma bias remained after anaesthesia (chloralose-pentobarbitone).

Fig. 2 illustrates a soleus spindle, under some gamma activation, because in the controls a supramaximal brief tetanus was used (1, 2, 3). The pause is sprinkled with some spikes induced by a varying contribution of gamma activity. Then xylocaine was applied (below the stimulating electrodes) to remove the contribution from this source (MATTHEWS and RUSHWORTH 1957 *a, b*, 1958). This also influenced the course of the contraction, which in the intact preparation is determined by rivalry between inhibitory and excitatory impulses from stimulated muscle afferents and end organs (GRANIT 1950). The end of the pause, however, should be considered with respect to the end of the contraction. As xylocaine successively took effect from records 4 to 6, it is seen that, in spite of a very large drop in 'gamma bias', the length of the pause changed but little, when measured in relation to the falling phase of contrac-

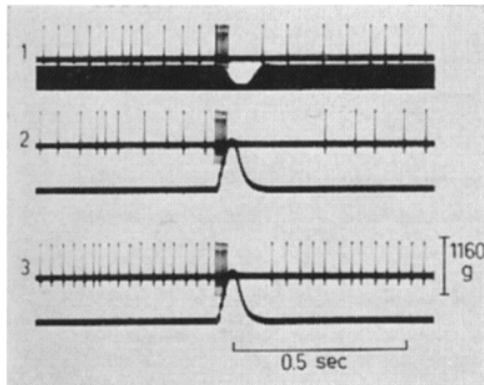


Fig. 4.

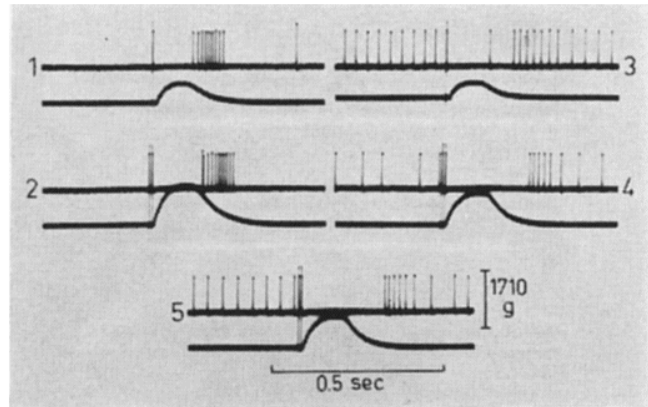


Fig. 5.

Fig. 4. Decerebrate preparation. Primary efferent ending in gastrocnemius. 1 and 2 at 3 mm extension, 1 isotonic (weight 100 g), 2 isometric. Then spindle was activated by pinna reflex and record 3 taken. Note, persistent long isometric pause and absence of phasic component even in isotonic contraction.

Fig. 5. Decerebrate preparation, *spinalized* at Th XII. Primary afferent ending in soleus. 1, single, 2 double shock at 10 mm extension, 3 and 4, corresponding records at 13 mm extension; 5 is repetition of 4.

tion. Clearly the length of the pause was a property of the peripheral instrument, merely modulated by variations in 'gamma bias'.

Fig. 3 illustrates for different extensions two gastrocnemius spindles (de-efferented) starting to discharge with typical phasic bursts followed by a secondary pause. As always, some extension of the muscle was needed to reveal the phasic component (as expected here in view of the de-efferentation). For the spindle on the right it should be noted that in the upper record 7 the phasic burst was emphasized by using a single shock instead of a brief tetanus. This may be seen with a fast muscle like gastrocnemius. The slow soleus often required a double shock or brief tetanus to show up spindle properties of the kind studied.

By contrast, Fig. 4 presents a gastrocnemius spindle which even isotonic contraction (record 1) could not make phasic. Record 2 gives the isometric equivalent at the same length. When shifting from isotonic to isometric contraction many spindles displayed very long pauses for the first few tests with contraction. This slow adjustment is not what is illustrated in record 2 which had been preceded by several tests in the isometric condition. Activation of this spindle was then attempted (record 3) and, though successful, to judge by the greatly increased rate of firing, the discharge still started *after* contraction and in a tonic fashion.

Fig. 5 has been chosen to illustrate what sometimes can be seen, namely that the pause greatly lengthens at great extensions. It is a soleus spindle with an early phasic burst in records 1 and 2 (single and double shock) at 10 mm extension. Adding 3 mm to the length of the muscle (records 3 to 5) possibly led to some over-extension of the spindle to judge by the diminution of the

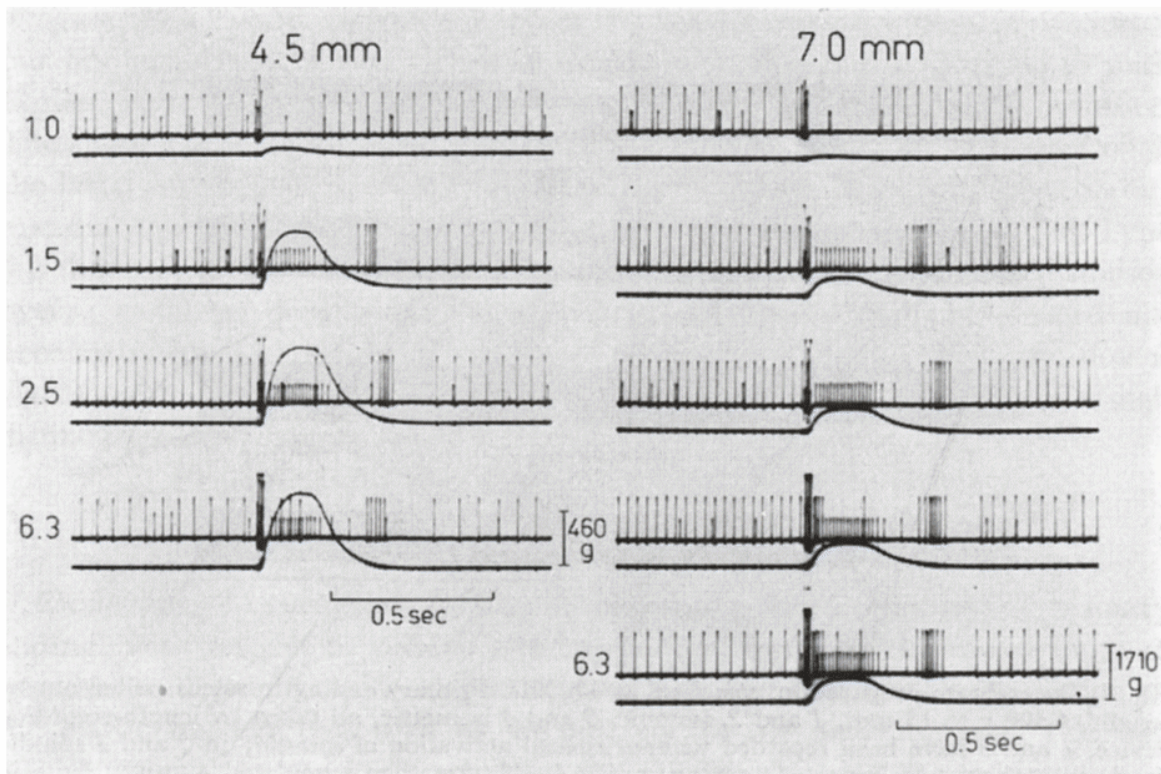


Fig. 6. De-efferented chloralose-barbitone preparation. Primary afferent ending in soleus, studied at two extensions, as marked in figure. Stimulus strength in multiples of lowest value on the left. Activation of gamma fibres by stimuli from 2.5—6.3 times the just suprathreshold uppermost value (1.0) shows some filling-in of the pause but no shift of major phasic burst relative to contraction. Note, tension-recording sense organ filling out the pause with stronger contractions.

contraction in 3, 4 and 5, to be compared with 1 and 2 respectively. Record 5 is a repetition of 4. The discharge now began when contraction was nearly over. Some spindles have behaved in this manner.

Fig. 6 shows with a soleus spindle the effect of increasing stimulus strength at two extensions, 4.5 and 7.0 mm. It was a de-efferented animal. The discharge from another sense organ, a tension-recording instrument sensitive to contractile tension only, is seen to fill out the pause. The interesting feature here is that, in spite of the relatively late discharge at the end of contraction, the spindle responded phasically with a secondary pause followed by the tonic component of the discharge. (LP-spindles in gastrocnemius have not shown up a phasic component.) This mode of behaviour was very little influenced by gamma bias and extension. In fact, gamma activation has to be very strong to alter the fundamental features of the response obtained at the end of contraction and even then these features mostly shine through, thereby supporting our general conclusion that they reflect some basic organizational principles in the design of individual spindles.

This statement is best illustrated by Fig. 7, records 3 and 4 (isometric, but recorded with length-measuring device). Strong spindle activation in record 4

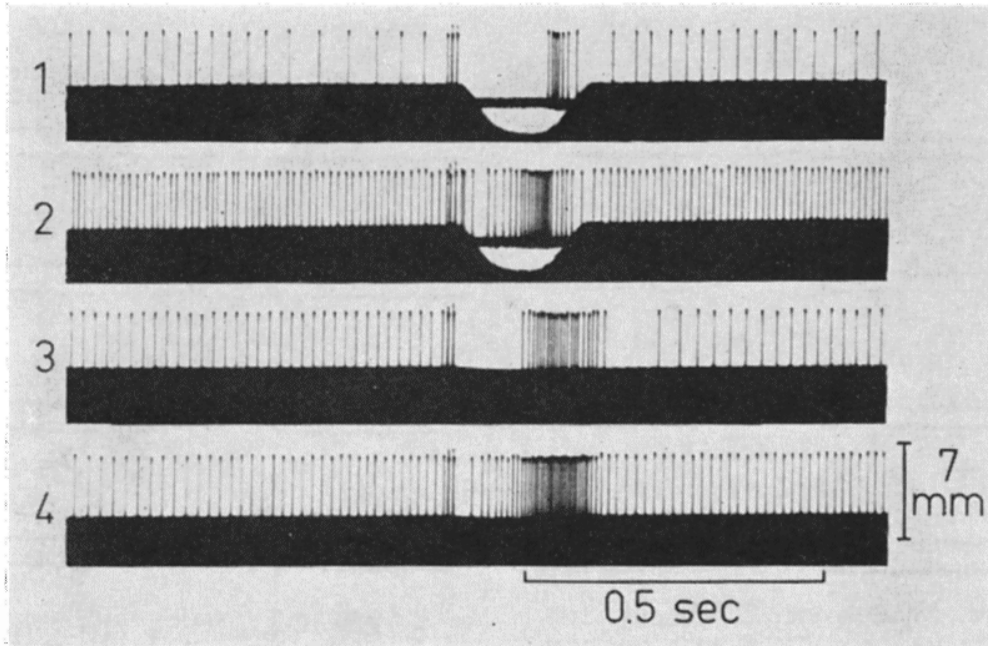


Fig. 7. Decerebrate preparation, *spinalized* at Th XII. Primary ending in soleus pulled out by weight of 500 g to 13 mm. 1 and 2, isotonic, 3 and 4 isometric, all taken by length-recording device. 1 and 3 have been recorded without special activation of spindle; in 2 and 4 spindle has been activated by repeated taps on muscle itself (skin then stimulated as well). Note in 4 that, despite filling-out of pause, the phasic burst is located much as in the control (3).

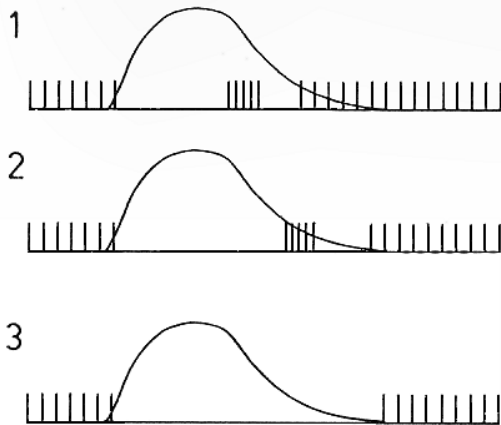


Fig. 8. Schematic. Diagram of the minimum of spindle types needed to account for the results obtained. 1 and 2 are two versions of phasic spindles the second 'long-pause' (LP); 3 is the LP-tonic spindle.

shortened the pause, if it be measured as duration of full silence, by comparison with the control in record 3. But the basic length of the pause, inherent in the spindle design, is clearly set off as a burst at maximal frequency in record 4 beginning in the same place there as in record 3. The pause in isotonic contraction (active re-stimulation) is shown to be dependent on gamma bias in the pair 1 and 2 which are otherwise equivalent with 3 and 4. Incidentally the isotonic record 2 shows how strong gamma bias can make spindle length shift together with extrafusal muscle length so as to fill out the pause over a considerable range of shortening, as concluded by ELDRED, GRANIT and MERTON (1953).

Spindle types needed. It is necessary to restrict a diagrammatic presentation of our findings to major types since at the moment it is hardly possible to push explanations based on spindle anatomy too far. Fig. 8 will have to suffice. The spindle with the marked phasic component may occur in versions 1 or 2, the latter — we believe — not uncommon in soleus as it has been seen in our material of 21 soleus spindles but not among the 34 gastrocnemius spindles. Type 3 is the tonic spindle which only exceptionally is of the SP-variety when studied over a range of extensions. The discharge in spindles of Type 1 need not necessarily start at the turning point of contraction; it may be shifted downwards on the falling phase, but it serves no obvious purpose to make such distinctions in a diagram of this sort.

Discussion

Phasic-tonic. MATTHEWS (1933), in discussing the properties of primary endings with respect to sudden stretch, pointed out that the initial burst of impulses underwent rapid adaptation and ascribed this to the interaction of the elastic nuclear bag with its viscous, contractile polar regions. The bag would respond to quick stretch by a quick extension but its tension would thereafter be released by the secondary adjustment to the new length of the pliant material in the viscous poles. The initial burst of impulses and the semi-stationary state of the 'adapted' discharge have been identified (GRANIT 1955, JANSEN and P. B. C. MATTHEWS 1961) with KATZ's (1950) dynamic and static phase of the terminal (generator) potential in frog spindles, as since justified by the observations of LIPPOLD, NICHOLLS and REDFEARN (1960) on similar terminal potentials in the spindles of the cat. It is of considerable interest to note that the dynamic phase is absent in direct electrical stimulation of cat spindles (LIPPOLD, NICHOLLS and REDFEARN 1960).

The hypothesis of MATTHEWS should to-day be confronted with the fact, first noted by COOPER (1959, published in full 1961) and then confirmed by LUNDBERG and WINSBURY (1960), HARVEY and P. B. C. MATTHEWS (1961 *b*) and BESSOU and LAPORTE (1962), that secondary endings, which are restricted to NC-intrafusal fibres and never terminate on bags, possess a very insignificant, if any, phasic response to stretch. Only primary endings have both NB- and NC-terminals (much as the large fibres from the retina pick up messages both from rods and cones). We have therefore cogent reasons for modifying MATTHEWS' hypothesis to include these facts. At the moment it merely states that the phasic burst on cessation of contraction is a response from the NB-component. The modified version suggests that the drawn-out tonic discharge is likely to be a response from the NC-component. JANSEN and P. B. C. MATTHEWS (1961), basing their argument on experiments in which they found differentiation of dynamic and static sensitivity of primaries with respect to gamma control, have explained this along similar lines. It is also quite in

keeping with what we know from other sense organs to find separate transducers for phasic and tonic responses.

Let us now see what a hypothesis on such lines can do for our findings. Spindles are known to vary with respect to relative number of NB- and NC-fibres. BARKER and GIDUMAL (1961) report from *one* to *three* large NB-fibres and from *one* to *eight* small NC-fibres in different spindles. The NC-fibres which are about half the length of the NB-fibres divide somewhat, twist among themselves and cross over the large fibres. If the NB-fibres of a given spindle are few in number and the NC-fibres many, the slack will first be taken up by the latter slow, 'tonic' structure and the discharge will be tonic. Our results suggest that basic spindle design suffices to explain the differentiation described in the present work. The common phenomenon of a secondary pause in phasic spindles, followed by a tonic discharge, suggests a change-over from NB- to NC-terminals and makes it necessary seriously to consider the possibility that the NB-component never may be able to respond tonically. The present results cannot, of course, be conclusive on this point. The hypothesis also provides a satisfactory explanation for the cases in which at great extensions spindles lose their phasic response. The one case in which a perfectly good spindle (in an animal useful for several hours afterwards) lost its phasic component and merely responded tonically may be due to selective loss of bias with respect to NB- and NC-intrafusal musculature (*cf.* JANSEN and P. B. C. MATTHEWS 1961).

Long pause — short pause. The question of why matching of intrafusal to extrafusal length sometimes is slow, sometimes fast, concerns the relative length of the spindle and not only whichever component responds first, the NB- or the NC-terminal apparatus. Single spindles in the rectus femoris of the cat vary in length from 2.4 to 13.7 mm while tandem spindles run up to 22.3 mm (BARKER and IP 1961). Of the latter there is a significant number, 21 % in soleus, 44 % in gastrocnemius (SWETT and ELDRED 1960 *a*). In the tandem spindles the intrafusal NB-fibres run through from end to end of the whole structure. Unless heavily biased by gamma activation these are likely to show up a considerable number of LP-responses. The spindle in Fig. 4 which even in the isotonic test failed to give a phasic burst is likely to be a tandem spindle. Similarly it seems likely that when there are long pauses undergoing large variations the responsive structure is likely to be a tandem spindle. The longer pause of the long spindle may favour the slower NC-elements. One of the most striking correlations in the present material was that the tonic spindles were found among the LP-spindles.

The length of the pause ultimately must emerge as a compromise between anatomical length (relative to adjacent extrafusal fibres) and whatever element is dominant, NB- or NC-fibres. A reservation must be made here for the possibility that some spindles are likely to possess fast motor fibres (GRANIT, POMPELANO and WALTMAN 1959 *a, b*, RUTLEDGE and HAASE 1961) which means

that the spindle is co-contracted and pulled up to a shorter length together with the extrafusal fibres. As a consequence the NB-fibres are ready to respond at an early moment in the turning point of contraction. This reservation does not concern the principle of our explanation. It merely means that such spindles are provided with a length correction operating in parallel with the changes of length in the surrounding extrafusal tissue.

Our work originally began as an attempt to use the length of the pause as an index of autogenetic gamma inhibition. However, this line soon proved unprofitable because the great differences in the length of the pause, discovered by systematic analysis, persisted when the findings were controlled by de-efferentation or gamma blocking by xylocaine. Hence it followed that the predominant factor was peripheral and inherent in the design of the spindles and their attachment to connective tissue, fascia or tendons. Against this background possible minor effects of autogenetic inhibition could not be demonstrated by the index used.

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References

- BARKER, D., The innervation of the muscle spindles. *Quart. J. micr. Sci.* 1948. *89*. 143—186.
- BARKER, D., Editor, Muscle Receptors. Hong Kong Golden Jubilee Symposium. Hong Kong and Oxford Univ. Press. To be publ. 1962.
- BARKER, D. and N. K. CHIN, The number and distribution of muscle-spindles in certain muscles of the cat. *J. Anat. (Lond.)* 1960. *94*. 473—486.
- BARKER, D. and J. L. GIDUMAL, The morphology of intrafusal muscle fibres in the cat. *J. Physiol. (Lond.)* 1961. *157*. 513—528.
- BARKER, D. and M. C. IP, A study of single and tandem type of muscle-spindle in the cat. *Proc. roy. Soc. B.* 1961. *154*. 377—397.
- BESSOU, P. and Y. LAPORTE, Responses from primary and secondary endings of the same neuromuscular spindle of the tenuissimus of the cat. In Barker, D., Editor (1962).
- BOYD, I. A., The tenuissimus muscle of the cat. *J. Physiol. (Lond.)* 1956. *133*. 35 P.
- BOYD, I. A., The innervation of mammalian neuromuscular spindles. *J. Physiol. (Lond.)* 1958. *140*. 14—15 P.
- BOYD, I. A., Simple and compound mammalian muscle spindles. *J. Physiol. (Lond.)* 1959. *145*. 55 P.
- BOYD, I. A., The diameter and distribution of the nuclear bag and nuclear chain muscle fibres in the muscle spindles of the cat. *J. Physiol. (Lond.)* 1960. *153*. 23—24 P.
- BOYD, I. A., The motor innervation of mammalian muscle spindles. *J. Physiol. (Lond.)* 1961. *159*. 7—9 P.
- COOPER, S., The secondary endings of muscle spindles. *J. Physiol. (Lond.)* 1959. *149*. 27—28 P.
- COOPER, S., Muscle spindles and other muscle receptors. In BOURNE, G. H. Editor, Structure and Function of Muscle. Vol. I. 381—420. Acad. Press New York and London 1960.
- COOPER, S., The responses of the primary and secondary endings of muscle spindles with intact motor innervation during applied stretch. *Quart. J. exp. Physiol.* 1961. *46*. 389—398.
- COOPER, S. and P. M. DANIEL, Human muscle spindles. *J. Physiol. (Lond.)* 1956. *133*. 1 P.
- CUAJUNCO, F., Embryology of the neuromuscular spindle. *Carnegie Inst. Contrib. Embryol.* 1927. *19*. 45—93.

- ELDRED, E., R. GRANIT and P. A. MERTON, Supraspinal control of the muscle spindles and its significance. *J. Physiol. (Lond.)* 1953. *122*. 498—523.
- FULTON, J. F. and J. PI-SUNER, A note concerning the probable function of various afferent end-organs in skeletal muscle. *Amer. J. Physiol.* 1927—28. *83*. 554—562.
- GRANIT, R., Reflex self-regulation of muscle contraction and autogenetic inhibition. *J. Neurophysiol.* 1950. *13*. 351—372.
- GRANIT, R., Receptors and Sensory Perception. Yale Univ. Press. New Haven. 1955.
- GRANIT, R., O. POMPEIANO and B. WALTMAN, Fast supraspinal control of mammalian muscle spindles: extra- and intrafusal co-activation. *J. Physiol. (Lond.)* 1959 *a*. *147*. 385—398.
- GRANIT, R., O. POMPEIANO and B. WALTMAN, The early discharge of mammalian muscle spindles at onset of contraction. *J. Physiol. (Lond.)* 1959 *b*. *147*. 399—418.
- HARVEY, R. J. and P. B. C. MATTHEWS, Some effects of the muscle nerve on afferent endings of muscle spindles, and the classification of their responses into types A₁ and A₂. *J. Physiol. (Lond.)* 1961 *a*. *156*. 470—497.
- HARVEY, R. J. and P. B. C. MATTHEWS, The response of de-efferented muscle spindle endings in the cat's soleus to slow extension of the muscle. *J. Physiol. (Lond.)* 1961 *b*. *157*. 370—392.
- HINES, M. and S. S. TOWER, Studies on the innervation of skeletal muscles. II. Of muscle spindles in certain muscles of the kitten. *Johns Hopk. Hosp. Bull.* 1928. *42*. 264—308.
- JANSEN, J. K. S. and P. B. C. MATTHEWS, The dynamic responses to slow stretch of muscle spindles in the decerebrate cat. *J. Physiol. (Lond.)* 1961. *159*. 20—21 P.
- KATZ, B., Depolarization of sensory terminals and the initiation of impulses in the muscle spindles. *J. Physiol. (Lond.)* 1950. *111*. 261—282.
- KUFFLER, S. W., C. C. HUNT och J. P. QUILLIAM, Function of medullated small-nerve fibers in mammalian ventral roots: efferent muscle spindle innervation. *J. Neurophysiol.* 1951. *14*. 29—54.
- LIPPOLD, O. C. J., J. G. NICHOLLS and J. W. T. REDFEARN, Electrical and mechanical factors in the adaptation of a mammalian muscle spindle. *J. Physiol. (Lond.)* 1960. *153*. 200—217.
- LUNDBERG, A. and G. WINSBURY, Selective adequate activation of large afferents from muscle spindles and Golgi tendon organs. *Acta physiol. scand.* 1960. *49*. 155—164.
- MATTHEWS, B. H. C., Nerve endings in mammalian muscle. *J. Physiol. (Lond.)* 1933. *78*. 1—33.
- MATTHEWS, P. B. C. and G. RUSHWORTH, The selective effect of procaine on the stretch reflex and tendon jerk of soleus muscle when applied to its nerve. *J. Physiol. (Lond.)* 1957 *a*. *135*. 245—262.
- MATTHEWS, P. B. C. and G. RUSHWORTH, Relative sensitivity of muscle nerve fibres to procaine. *J. Physiol. (Lond.)* 1957 *b*. *135*. 263—269.
- MATTHEWS, P. B. C. and G. RUSHWORTH, The discharge from muscle spindles as an indicator of γ -efferent paralysis by procaine. *J. Physiol. (Lond.)* 1958. *140*. 421—426.
- RUFFINI, A., Observations on sensory nerve-endings in voluntary muscles. *Brain* 1897. *20*. 368—374.
- RUFFINI, A., On the minute anatomy of the neuro-muscular spindles of the cat, and on their physiological significance. *J. Physiol. (Lond.)* 1898—99. *23*. 190—208.
- RUTLEDGE, L. T. and J. HAASE, Flexor muscle spindles and reflex firing of early discharging units. *J. Neurophysiol.* 1961. *24*. 182—192.
- SHERRINGTON, C. S., On the anatomical constitution of nerves of skeletal muscles; with remarks on recurrent fibres in the ventral spinal nerve-root. *J. Physiol. (Lond.)* 1894. *17*. 211—258.
- SWETT, J. E. and E. ELDRED, Distribution and numbers of stretch receptors in medial gastrocnemius and soleus muscles of the cat. *Anat. Rec.* 1960 *a*. *137*. 453—460.
- SWETT, J. E. and E. ELDRED, Comparisons in structure of stretch receptors in medial gastrocnemius and soleus muscles of the cat. *Anat. Rec.* 1960 *b*. *137*. 461—473.