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RESPONSE CHARACTERISTICS OF MUSCLE AFFERENTS IN THE DOMESTIC DUCK

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SUMMARY

1. Response patterns of 116 muscle stretch receptor units isolated from the sciatic nerve of the duck have been studied, and the units classified as muscle spindles and tendon organs.

2. Units classified as spindles had low threshold tensions for maintained discharge. From conduction–velocity measurements, the calculated fibre-diameter spectrum appears to be unimodal, ranging from 5 to 11–12 μm.

3. Spindle units showed essentially 'in parallel' behaviour, though increase in initial tension often led to the appearance of 'in series' responses. Although apparent 'α-excitation' during maximal tetanic contractions was a common occurrence, no direct evidence of α-innervation of spindles was obtained.

4. Evidence has been obtained for motor innervation of spindles by fibres distinct from those constituting the alpha supply to extrafusal muscle fibres. Afferent response attributable to this fusimotor innervation is influenced by initial tension and stimulus-frequency. Electrical thresholds for fusimotor responses ranged from 1·1 to 4·03 times α maximum.

5. Tendon organ units consistently showed 'in series' response patterns during muscle contractions. They were not influenced by stimulation of the high-threshold efferent nerve supply to the muscles.

6. Threshold tensions required for maintained discharge in tendon organ units from m. gastrocnemius pars lateralis were characteristically high; however, many units from m. flexor perforans et perforatus d. 3 had unexpectedly low mechanical thresholds. The calculated fibre-diameter spectrum for tendon organ units is unimodal, ranging from 4–7 to 10–11 μm. As in mammals, they contribute to the coarse-fibre component in the muscle nerve and include the fastest fibres present.

INTRODUCTION

Despite the wealth of information available about the properties of mammalian muscle receptors, no equivalent electrophysiological investigations have been reported in birds. Histological studies of Huber & DeWitt (1898) describe an afferent innervation in the dove spindle resembling more closely that in the frog than that in mammals, although recent work of Barker (1968) reports that some chicken spindles receive a small-fibre fusimotor supply in addition to a collateral innervation derived from efferent axons supplying extrafusal fibres.

In the present investigation, the response-patterns of stretch-receptors have been studied in two muscles of the duck's hind limb. It will be shown that both these muscles contain receptors with properties in general similar to those of mammalian spindles and tendon organs. Spindle units receive independent motor innervation from fibres of high threshold, as in mammals; however, the calculated afferent fibre-diameter spectrum for spindle units appears to be unimodal, and no other indication has been obtained of their separation into two types corresponding to mammalian primary and secondary endings. Tendon organ units behaved in general like their mammalian counterparts, except that some had very low mechanical thresholds.

METHODS

Preparation. Experiments were performed on fourteen ducks which were anaesthetized with sodium pentobarbitone (60 mg/kg, Sagatal, May & Baker) by intramuscular injection, supplementary doses being administered intravenously as required. Because the anaesthetic depressed respiration, the animals were artificially ventilated by way of a tracheal cannula. A dissection exposed the nerves and muscles to be studied and exposed tissue was covered with liquid paraffin at 40 °C, retained by skin flaps. Single muscle afferent units, supplying receptors in m. gastrocnemius pars lateralis (GPL) and m. flexor perforans et perforatus digiti 3 (FPP 3), were isolated from the sciatic nerve. All nerves joining the sciatic, other than that to the muscle studied, were cut to reduce input. The sciatic nerve was severed, desheathed, supported on a small black disc and subdivided under a dissecting microscope until functionally single unit preparations were obtained, a total of 116 units being studied. The leg was immobilized by a pin in the distal end of the femur and a clamp at the tibia–tarsometatarsal junction. Tension changes were recorded isometrically by a strain gauge (Grass or Statham), mounted on a rack and pinion which allowed changes in resting tension to be applied to the muscle. The output of the strain gauge was amplified and displayed on the lower beam of a cathode ray oscilloscope.

Stimulation. The short length of the spinal roots necessitated stimulation of the mixed muscle nerve to produce muscle contraction and to excite the fusimotor nerve supply. Square wave pulses of 0·2 msec duration were used. Voltage values required to produce maximal twitch contractions of the muscle were determined frequently, as they could be altered by small changes in the position of stimulating electrodes. A maximal twitch was produced by a stimulus strength 1·43–1·75 times that required for a threshold contraction. Fusimotor efferents were routinely excited by

stimuli of 10 × maximal strength. The electrical thresholds for many of these fibres were determined and expressed as multiples of the voltage giving maximal contractions.

Estimation of the degree of afferent unit excitation during tetanic contractions. Because of the large tension developed during tetanic contraction of GPL, the smaller FPP 3 muscle was used for these experiments. Action potentials from the units isolated were amplified and displayed on the upper beam of the oscilloscope. The necessity of stimulating the mixed muscle nerve to excite the efferent supply to the muscle resulted in the concurrent stimulation of the majority of afferent units studied. The presence of these direct spikes caused a continual resetting of the firing pattern of a unit, by antidromic invasion of its terminals, so that its response bore a temporal relation to the direct spike stimulus artifact complex. An attempted estimation of the firing frequency of a unit was made from the interval between direct spike and response spike. However, this was not successful at high stimulus frequencies as small inaccuracies in the interval measurements greatly influenced the calculated firing frequencies. The degree of unit excitation was therefore estimated from the discharge occurring after the last stimulus to the muscle, including the burst of spikes during the falling phase of the tetanic tension. When a pause occurred before resumption of resting discharge, the number of spikes between the last stimulus and the pause were counted. When no pause occurred, the number of spikes were counted in a fixed time interval after the last stimulus, normally until the end of the burst associated with the falling phase of tension (see Fig. 6).

Conduction velocity measurements. Conduction velocities of the units studied were determined, by a slope method, along the muscle nerve distal to its junction with the sciatic. The nerve was stimulated at regular intervals of 2 or 4 mm by a movable cathode mounted in a micromanipulator, and the equivalent latency measurements were determined from photographic records of the unit action potentials, a timer scale being displayed on the lower beam. The slope of the graph gave the conduction velocity along the length of nerve studied and was taken as characteristic of the unit. In each case, identity of the unit responses to electrical stimulation with those evoked by muscle stretch was established by 'occlusion' of the former by stretch-evoked unit responses, as in previous studies (Hunt, 1954; Hunt & McIntyre, 1960). The alternative method of using single latency/over-all distance measurements was found to be inadequate in this kind of preparation (Dorward, 1966). Calculated fibre-diameter spectra of muscle spindle and tendon organ units were determined from the conduction velocity measurements, assuming the conversion factor of 6 (Hursh, 1939). Evidence has been found for a similar factor in the duck (Dorward, 1966).

RESULTS

Units were classified as muscle spindles or tendon organs on the following grounds. Spindle units showed some form of 'in parallel' behaviour during active twitch contractions of the muscle while tendon organs gave 'in series' response patterns during twitch and tetanic contractions (Matthews, 1933). The behaviour of spindle units during tetanic contractions was often less clear-cut, because of apparent α-excitation, as discussed later. Spindle units situated in FPP 3 were influenced by the excitation of high-threshold efferent fibres while tendon organs were unaffected. In both muscles studied, all spindle units had characteristically low mechanical thresholds. 90 % of the units showed a background discharge at zero tension; the

remaining units discharged in response to small tensions not exceeding 50 g. In GPL most tendon organs could be distinguished from spindles by their high mechanical thresholds: in FPP 3, however, unexpectedly low thresholds for tendon organs prevented this criterion from being used.

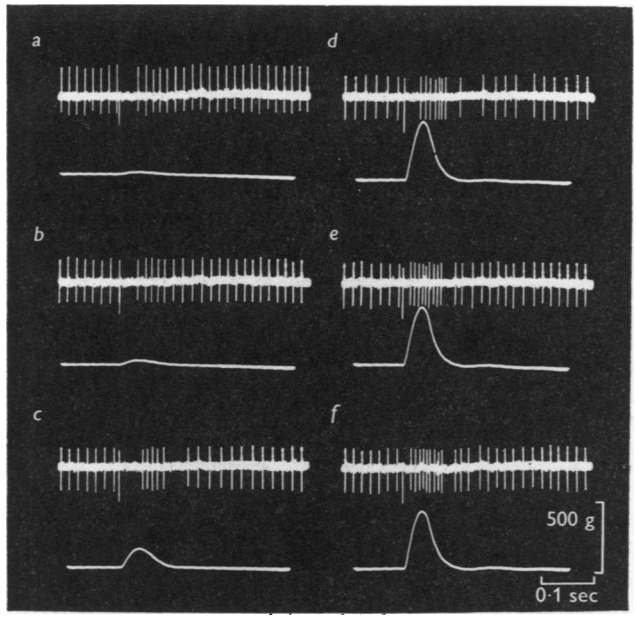

Fig. 1. Responses of a spindle unit to increasing stimulus strength with 5 g resting tension applied to the muscle. *a*, twitch threshold; *b*, 1·02 × threshold; *c*, 1·05 × threshold; *d*, maximal twitch at 1·4 × threshold; *e*, 2·1 × maximal, electrical threshold for the fusimotor fibre supplying this spindle; *f*, 2·8 × maximal. Downward deflexions on upper traces are stimulus artifacts. Records retouched.

Muscle spindle units

Responses of spindle units during twitch contractions

Submaximal and maximal stimulation. Spindle units showed several response patterns during muscle twitches which were regarded as modification of the 'in parallel' behaviour predicted from their anatomical relationship to the extrafusal muscle fibres. At low resting tensions, background discharge ceased during the development of twitch tension. In some units, this pause extended throughout the twitch, while others showed an increase in firing rate during the falling phase of twitch tension, commonly followed by a second pause before the resumption of resting discharge. The kind of response obtained was affected by the strength of contraction as shown in Fig. 1*a–d*, where changes in the response occurred as the stimulus strength was increased from threshold to maximal.

Response patterns were influenced by the resting tension applied to the muscle. Increased tension usually produced a reduction in the duration of the pause and/or an increase in the burst associated with the falling phase of the twitch. The larger unit in Fig. 2 shows an initial lengthening of the pause on increasing tension from 8 g to 50 g (Fig. 2*a*, *b*) followed by a reduction at 180 g (Fig. 2*c*). In several units, high tensions resulted in responses resembling the 'in series' behaviour of tendon organs. The smaller unit in Fig. 2*a–c* can be seen to fire during the rising phase of the twitch at 50–180 g. Other units showed an increase in firing throughout the contraction at high resting tensions.

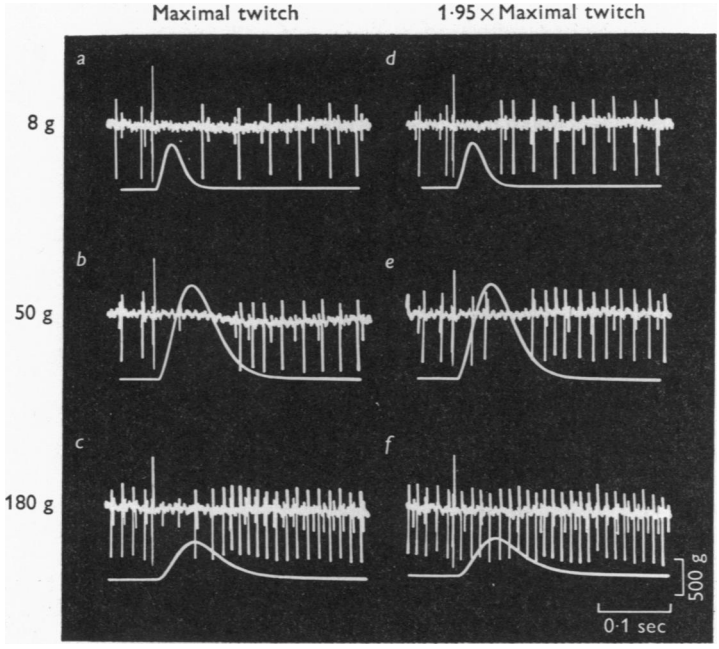

Fig. 2. Effect of resting tension on responses of two spindle units to maximal and supra-maximal stimulation. 1·95 × maximal is the electrical threshold for fusimotor effect on the larger unit. Increase in resting tension causes an initial increase in twitch tension (*a–b*) followed at high resting tension (*c*), by a reduction. (*a–c*) Effect of different resting tensions on responses to maximal twitch contractions; (*d–f*) effect of these same initial tensions on responses of the larger unit to fusimotor stimulation. Resting tension indicated on left. Large diphasic deflexions on upper traces are stimulus artifact–direct spike complexes. Records retouched.

An early discharge (Hunt & Kuffler, 1951*a*) was found in about 40 % of the spindle units, normally consisting of one spike (occasionally two) occurring shortly after the stimulus artifact-direct spike complex, at about

the time the initial tension rise was registered by the strain gauge (see Fig. 3). This response was unpredictably affected by resting tension, some units requiring a certain tension for it to appear, while in others it was abolished by an increase in tension.

Supra-maximal stimulation. In about two thirds of the units studied, extra impulses occurred during the twitch when the stimulus strength was raised above that required for a maximal contraction, although no detectable change in twitch tension was recorded. In some units, supra-maximal stimulation caused an earlier resumption of firing after the initial

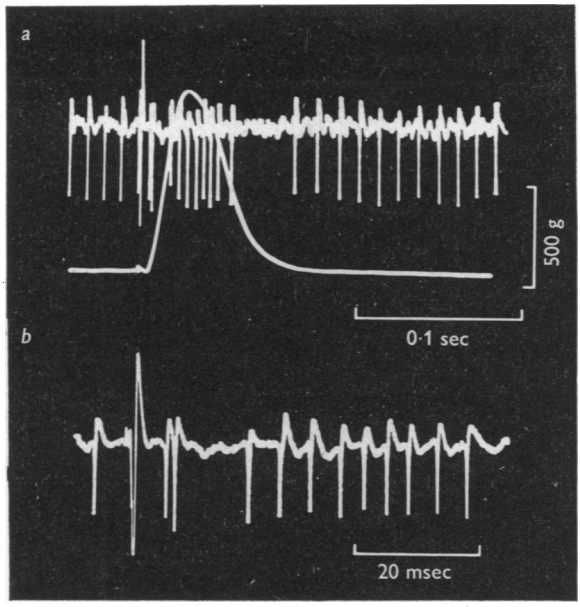

Fig. 3. Early discharge of a spindle unit. *a*, Normal sweep with tension record; *b*, expanded sweep to show details of early discharge. Large diphasic deflexions on upper traces are stimulus artifact–direct spike complexes. Records retouched.

pause in base line discharge (compare Fig. 1*d*, *e*) while in others impulses occurred on the rising phase of the contraction (see Fig. 2*e*, *f*). A certain amount of resting tension was normally required to show this response and its pattern was often modified by increasing tension. An example of this can be seen in Fig. 2. At 8 g, supra-maximal stimulation causes only a slight change in the behaviour of the larger unit, the base line discharge resuming at a faster rate after the pause than was found during a maximal twitch (compare *a* and *d*). At 50 g, two extra spikes appear on the rising phase of the contraction, while at 180 g the pause is filled with four extra spikes (compare *c* and *f*).

Responses to supra-maximal stimulation occurred at critical electrical thresholds and were not modified by increases in stimulus strength above these thresholds (compare Fig. 1*e* and *f*). With the exception of one high value (4·95 × maximal), all thresholds obtained fell between 1·4 and 2·4 × maximal. These results provide evidence for a specific fusimotor innervation of the duck spindle by fibres of a higher electrical threshold, and presumably smaller diameter, than those supplying the extrafusal fibres. Although the actual diameter ranges of these two efferent types are not necessarily the same in the duck as in mammals, for convenience, they will be referred to as γ and α efferents respectively.

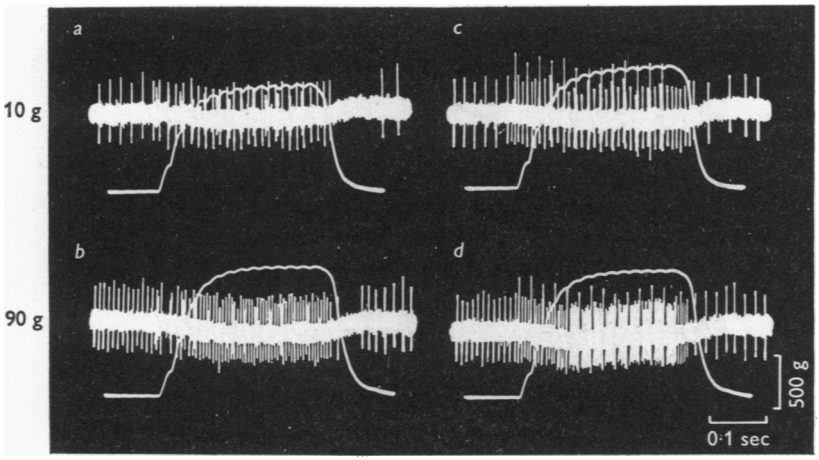

Fig. 4. Effect of resting tension on responses of a spindle to tetanic stimulation at 45/sec. *a*, 10 g resting tension, stimulus strength slightly less than maximal; *b*, 90 g resting tension, maximal tetanus; *c*, 10 g resting tension, 10 × maximal tetanus; *d*, 90 g resting tension, 10 × maximal tetanus. Small diphasic deflexions on upper traces in *a* and *b* are stimulus artifacts; large diphasic deflexions on upper traces in *c* and *d* are stimulus artifact-direct spike complexes. Records retouched.

Responses of spindle units during tetanic contractions

Further information on the nature of fusimotor innervation in the duck was gained from the responses of spindle units from FPP 3 during tetanic contractions. As previously indicated by work on the cat (Kuffler, Hunt & Quilliam, 1951; Hunt & Kuffler, 1951*b*; Harvey & Matthews, 1961*a*), modifications in afferent discharge were most easily demonstrated when a train of stimuli were given to the fusimotor fibres.

In the absence of applied tension, two thirds of the spindle units showed a cessation of resting discharge during maximal tetanic contractions, as expected from mammalian studies. At resting tensions of 100 g only a

quarter of the units continued to show a pure 'in parallel' response. The remaining units fired during the tetanus at a rate influenced by tetanic tension, a phenomenon resembling the α-excitation described by Harvey & Matthews (1961*a*) in the cat. In the duck, α-excitation was a common occurrence, forming a background discharge against which the responses to γ efferent stimulation had to be studied. It often resembled the pattern of excitation produced by γ efferent stimulation, thus raising the possibility of specific α-innervation of the spindle.

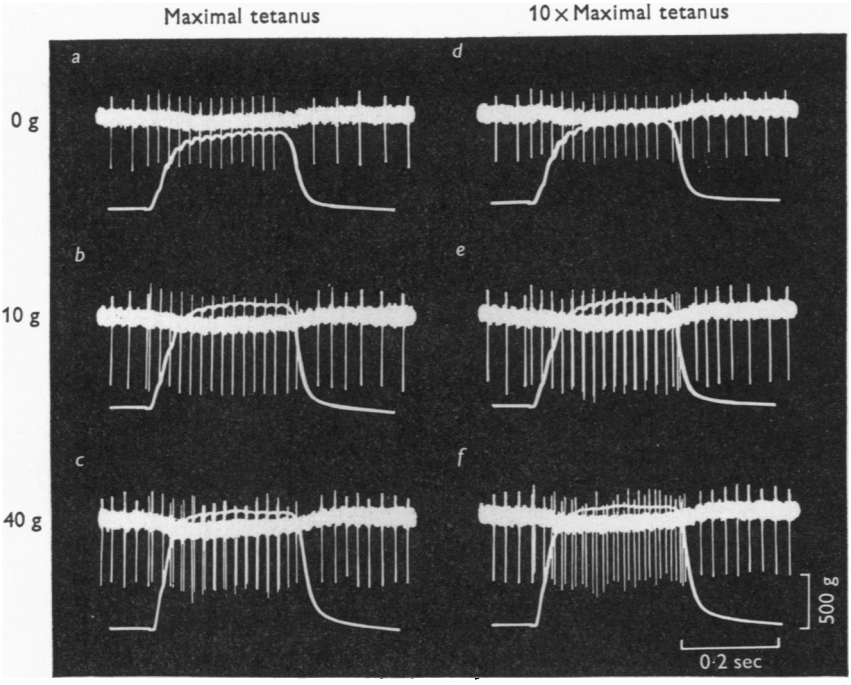

Fig. 5. Effect of resting tension on responses of a spindle unit to maximal and supra-maximal tetanic stimulation at 45/sec. The afferent fibre was directly excited by each of the thirteen stimuli to the muscle nerve (see *a*). Responses of the unit were recognized as additional impulses occurring after the last direct spike (*b–f*) and just before the direct spikes during the tetanus (*c*, *e* and *f*). Analysis of the response was done on enlarged records. *a–c*, Effect of different resting tensions on responses to maximal tetanic contractions; *d–f*, effect of these same initial tensions on responses to fusimotor stimulation. Resting tension indicated on left. Records retouched.

Characteristics of α-excitation. The effects of tension on α-excitation are most clearly seen in Fig. 4, which shows the responses of a unit whose axon was not excited by stimulation of the muscle nerve sufficient to give a maximal tension record. An increase in resting tension from 10 g (*a*) to 90 g (*b*), almost doubles the firing rate during the tetanus. In the majority

of units, direct stimulation of the afferent axon was unavoidable and the weakest detectable form of α-excitation was an extra impulse appearing just before some of the direct spikes and/or a discharge following the last direct spike. An increase in resting tension caused these extra impulses to appear throughout the tetanus and increased the discharge after the last direct spike. Fig. 5*a–c* demonstrates some of these effects. In two units, the persistence of the early discharge throughout the tetanus formed another kind of α-excitation. This response was converted into the typical α-excitation pattern on increasing resting tension. Normally an early discharge was only found after the first stimulus of the train. α-excitation was also affected by stimulus frequency below the fusion frequency of the muscle (between 120 and 140/sec). This effect was probably due to the higher tetanic tensions developed by the muscle on increasing frequency over this range. Above 105/sec (producing 94% of tetanic tension at fusion frequency) α-excitation was not influenced by frequency. Fig. 6 demonstrates these findings, the firing after the last stimulus artifact being used to estimate the degree of spindle excitation (see Methods). The number of spikes occurring in the time interval indicated by the horizontal bars are 11, 15, 15 and 14 respectively for stimulus frequencies 52/sec, 105/sec, 140/sec and 195/sec. Average values obtained from four records of each stimulus frequency were 9·5, 15, 14·75 and 14·75.

Characteristics of fusimotor stimulation. A response was obtained to fusimotor stimulation (i.e. stimulation at strengths greater than that required for maximal contraction) in all units studied. Extra spikes appeared in units which were silent during a maximal tetanus, while the remaining units showed an increase in the firing due to α-excitation. This response was influenced by resting tension, stimulus frequency and exhibited facilitation.

Normally, a small amount of tension (8–50 g) was required to elicit the response and typical results of increasing tension are seen in Figs. 4, 5. In Fig. 4, a rise in tension from 10 g (*c*) to 90 g (*d*) causes an increase from two to six in the number of impulses occurring between the direct spike/stimulus artifact complexes during the tension plateau. In Fig. 5, a weak response is seen at 0 g (*d*), in the form of two impulses following the last direct spike. At 10 g (*e*), four impulses occur on the falling phase of the tetanus and extra impulses appear just before the next direct spike, from the fourth stimulus onwards. At 40 g (*f*), six impulses follow the last direct spike and the extra impulses during the tetanus are seen to occur earlier.

Frequency of stimulation influenced the response to fusimotor stimulation above the fusion frequency of the muscle and hence independently of tension changes in the extrafusal muscle fibres. An example is seen in Fig. 6 *e–h*. The number of impulses occurring in the time interval indi-

cated by the horizontal bars are 16, 17, 19 and 22 respectively for the tetanic frequencies 52/sec, 105/sec, 140/sec and 195/sec (fusion frequency, between 120/sec and 140/sec). Average values from four records of each stimulus frequency were 15·25, 17·5, 19·5 and 22. Maximal responses of units to fusimotor stimulation occurred at frequencies between 140/sec

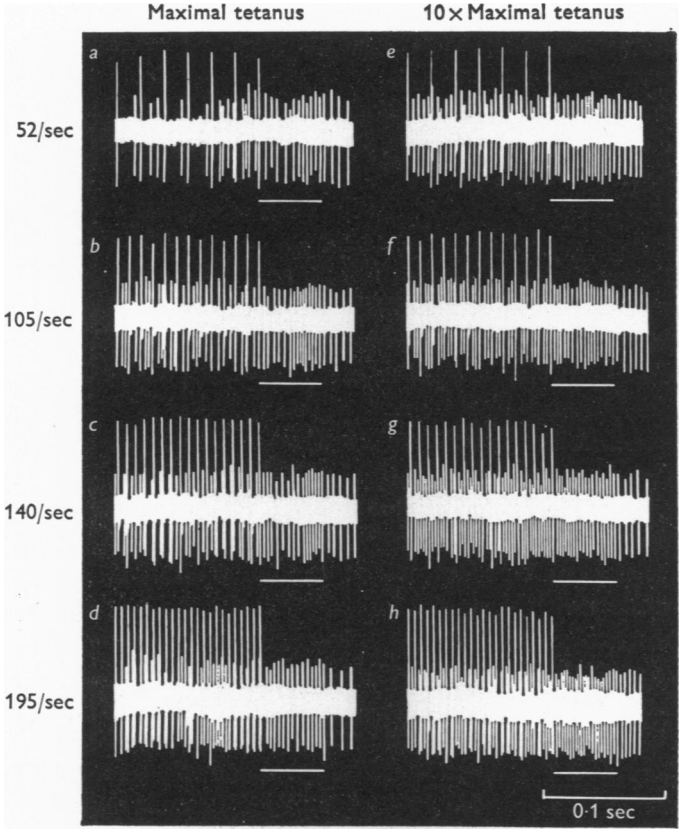

Fig. 6. Effect of stimulus frequency on responses of a spindle unit to maximal and supra-maximal tetanic stimulation. Records show the response to the last half of the tetanus and the discharge occurring after the last stimulus. Stimulus frequencies of 52/sec and 105/sec gave tetanic contractions which were 50 % and 94 % of the maximum tetanic tension; 140/sec and 195/sec were above the fusion frequency of the muscle. 100 g resting tension was applied throughout. The number of spikes occurring in the time interval indicated by the horizontal bars were counted to give an indication of the excitation of the spindle afferent. Analysis of responses was done on enlarged records. *a–d*, Effect of different frequencies on responses to maximal tetanic contractions. *e–h*, Effect of the same frequencies on responses to fusimotor stimulation. Frequencies indicated on left. Large diphasic deflexions are stimulus artifact–direct spike complexes. Records retouched.

and 195/sec, giving some indication of the fusion frequency range of intrafusal muscle fibres.

During a response, the firing rate of a unit increased with successive stimuli until a steady level was reached indicating that facilitation was occurring. This phenomenon can be seen in Fig. 5*e–f* at different levels of resting tension. In *e*, the first few stimuli fail to produce a response before the next direct spike, while in *f*, the response comes in progressively earlier until a steady interval is reached.

Electrical thresholds for the above fusimotor effects ranged from 1·1 × maximal to 4·03 × maximal. In a few units it was possible to see a second increment in the response when the voltage reached another higher critical

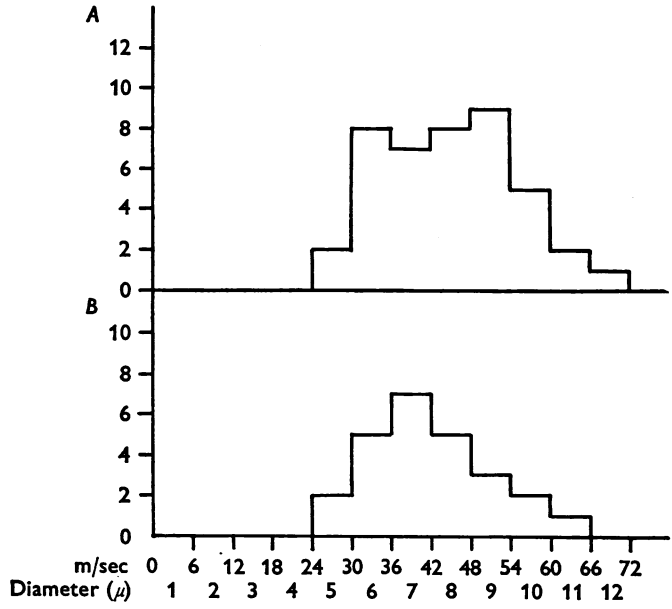

Fig. 7. Calculated diameter distribution of spindle units isolated from the nerves to m. gastrocnemius pars lateralis (*A*) and m. flexor perforans et perforatus d. 3 (*B*).

level, indicating that spindles could be innervated by more than one fusimotor fibre. As described above, with a number of spindle units it was possible to bring about a change in firing pattern during and after a maximal twitch by increasing the strength of shock above a critical level; for example, compare *d* and *e* in Fig. 1. Threshold values for such single-shock fusimotor action were slightly higher than threshold strengths for fusimotor action from tetanic stimulation in the same units. This suggests

that recruitment of more than one high-threshold fibre with action on the spindle under study may be necessary to reveal fusimotor effects from single stimuli.

Conduction velocity measurements

Conduction velocity measurements were plotted as histograms, using the conversion factor of 6, to give an estimate of the fibre-diameter spectrum of the units studied. In Fig. 7 the diameter distribution is seen to be unimodal in both GPL (*A*) and FPP3 (*B*), with diameters ranging from 5 to 11–12 μ.

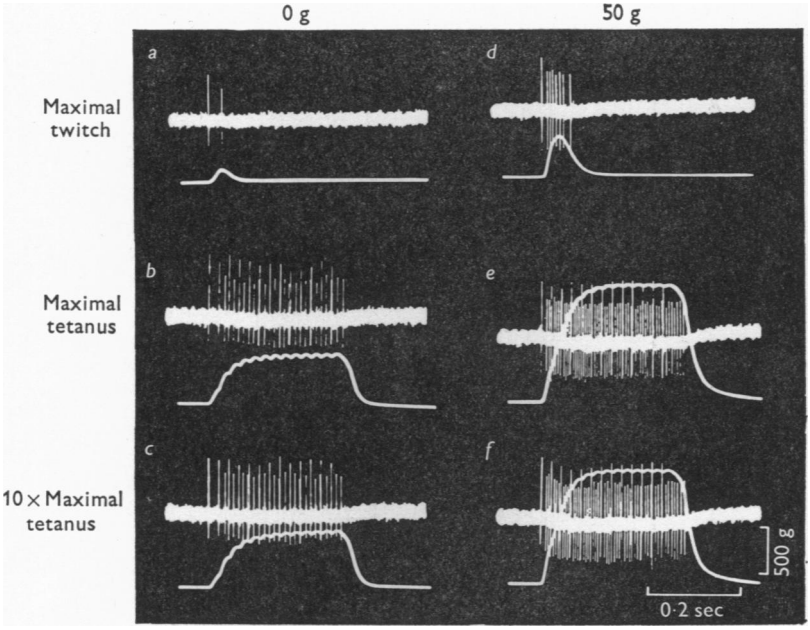

Fig. 8. Effects of resting tension on responses of a tendon organ to maximal twitch contractions (*a*, *d*), maximal tetanic contractions at 46/sec (*b*, *e*) and 10 × maximal tetanic contractions at 46/sec (*c*, *f*); resting tension indicated above. Large diphasic deflexions are stimulus artifact-direct spike complexes. Records retouched.

Tendon organ units

Responses of tendon organ units during contraction. Tendon organs showed typical 'in series' response patterns during muscle contractions. Units fired during the rising phase and peak of a twitch and throughout a tetanus if the active tensions reached were above the threshold levels required. Rises in resting tension, with consequent rises in the active tension developed, increased the firing rate as seen in Fig. 8*a*, *b* and *d*, *e*. Units were not influenced by stimulation at fusimotor strength (compare *b* and *c*; *e*

and *f*, Fig. 8). Some tendon organs showed an early discharge, although it was less common than in spindle units. It was distinguished from the 'in series' response by a slight pause, the latter only coming in when the active tension developed by the muscle had reached a certain level.

Threshold tensions for maintained firing. Most of the tendon organs from GPL required 100–300 g resting tension for maintained discharge. A few units had still higher thresholds while three units were found to fire at zero tension. Units from FPP 3 had lower thresholds, half the units showing resting discharges at zero tension while the remainder were excited by tensions below 150 g. The criteria of high resting tension threshold could not, therefore, be used to distinguish tendon organs from

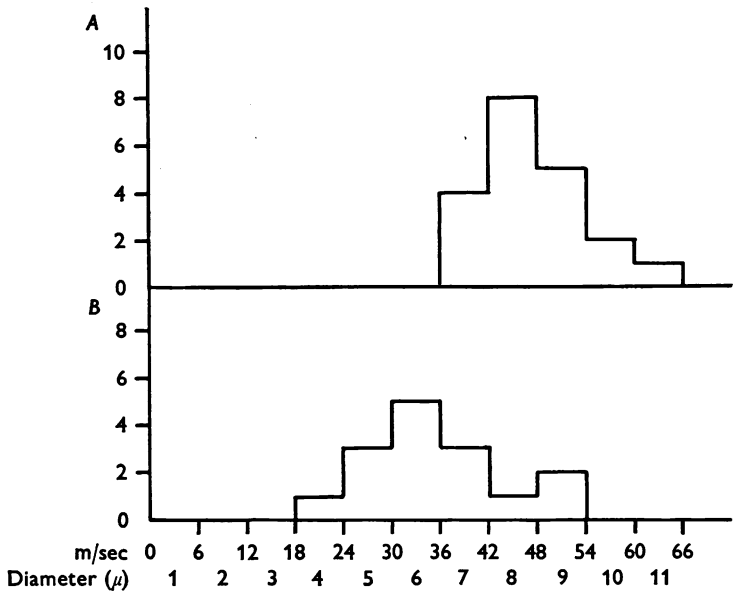

Fig. 9. Calculated diameter distribution of tendon organ units isolated from the nerves to m. gastrocnemius pars lateralis (*A*) and m. flexor perforans et perforatus d. 3 (*B*).

muscle spindles in this muscle. However, the classification of these units as tendon organs on their 'in series' behaviour was confirmed by the absence of any response to efferent stimulation.

Conduction velocity measurements. Fig. 9 shows the calculated fibre-diameter spectra of tendon organs from GPL (*A*) and FPP 3 (*B*), obtained from single unit conduction velocity measurements. The distribution is unimodal and similar to that found for spindle units. Conduction velocity measurements of the leading edge of compound action potentials recorded from GPL and FPP 3 were 61–70 m/sec and 55–62 m/sec respectively,

giving calculated diameters of 10–12 μ for the fastest fibres present. The afferent fibres from muscle receptors are therefore amongst the largest fibres in the muscle nerves and must form a considerable proportion of their coarse-fibre component.

DISCUSSION

Muscle spindles

In general, duck spindles resembled their mammalian counterparts in their low mechanical thresholds, their 'in parallel' behaviour during twitch contractions and their response to stimulation of high-threshold, fusimotor efferents. The various response patterns found during twitch contractions in the duck resembled those described by Hunt & Kuffler (1951*a*). Both the early discharge and the appearance of 'in series' effects at high tensions are attributed by these authors to 'stray pulls' i.e. tensions exerted on the spindle by contraction of the extrafusal fibres. A similar explanation would apply in the duck.

α-excitation. α-excitation during maximal tetanic contractions occurred more frequently in the duck than in the cat (Harvey & Matthews, 1961*a*) and resembled the pattern of excitation caused by γ fusimotor stimulation, suggesting a possible α-innervation of the spindle. A generally accepted criterion for the existence of true α-innervation is an increase in afferent discharge with increasing frequency above the fusion frequency of the extrafusal fibres (Bessou, Emonet-Dénand & Laporte, 1963, 1965). In the present experiments, this criterion was not fulfilled when the effects of high frequency were studied. By contrast, responses to γ efferent stimulation did show high frequency dependency indicating that the fusion frequency of intrafusal fibres was higher than that of extrafusal fibres, as required for this criterion to operate. Barker (1968) reports a collateral plate innervation to spindles in posterior latissimus dorsi in the chick. However, this innervation was restricted to the slow fibres in the muscle; FPP3 appears to be predominantly a fast muscle which may explain the failure to demonstrate α-innervation in these experiments. Further studies on larger populations of units from a variety of muscles may yield functional evidence for α-innervation in the duck.

Fusimotor innervation. In this preparation, the small size of the lumbosacral spinal roots prevented the selective stimulation of fusimotor fibres. However, the presence of a fusimotor supply could be inferred from the following evidence. First, modification of spindle discharge at critical supra-maximal stimulus strengths indicated excitation of high-threshold, presumably small-diameter, fusimotor efferents. These responses were not accompanied by any change in the recorded tension, ruling out extrafusal

'stray pulls' as an explanation. Electrical thresholds of fusimotor fibres in the duck were in the same range as thresholds of γ efferents in the cat (Harvey & Matthews, 1961*a*). Secondly, characteristic features of the fusimotor response in the duck were similar to those described by Kuffler *et al.* (1951) and Hunt & Kuffler (1951*b*) in the cat. The response was dependent on stimulus frequency, as demonstrated free from accompanying tension changes above the fusion frequency of the extrafusal fibres. It also exhibited facilitation and was related to the resting tension applied to the muscle. These results are in agreement with the histological work of Barker (1968) in the chick, demonstrating the presence of a small-fibre, fusimotor supply to spindles in posterior latissimus dorsi.

Afferent fibre diameter. The fibre-diameter spectrum of spindle units found in these experiments differs from the characteristic distribution into Group I*a* (12–20 μ) and Group II (2–12 μ) found in the cat (Hunt, 1954). In the duck, spindle afferent distribution is unimodal (5 to 11–12 μ) and similar to that of the tendon organs (4–7 μ to 10–11 μ). The absence of small-fibre spindle afferents was not considered a technical artifact, as identical techniques of unit isolation using the interosseous nerve yielded a reasonable number of units in the 2–5 μ range (Dorward, 1966). Histological studies in mammals (Barker, 1948; Boyd, 1962) give diameter spectra similar to Hunt's and show that Group Ia fibres supply primary endings, while secondary endings receive fibres from the Group II range. The absence of a bimodal spindle afferent distribution in the duck could mean that the spindle possesses only one kind of afferent ending. However, D. Barker (personal communication) has found endings in the chick which he presumes to be secondary and which are supplied by fibres whose diameters (3–4·5 μ) are only slightly less than those to the primary endings (6–8 μ). A narrow diameter range like this would not allow an easy separation of spindle units into two groups on conduction velocity alone. Further experiments on the behaviour of spindle units during muscle stretch are necessary in order to reveal functional differences in the behaviour of avian spindle units similar to those found in mammals (Cooper, 1961; Harvey & Matthews, 1961*b*; Matthews, 1963).

Tendon organs

The responses of tendon organs to muscle contractions were consistent with their 'in series' anatomical situation and resembled those found in the mammals. The low mechanical thresholds found in many tendon organs from FPP3 were unexpected, as workers on mammalian muscle receptors (Matthews, 1933; Hunt & McIntyre, 1960) considered high tension thresholds to be characteristic of tendon organs. However, Alnaes (1967) reported passive extension thresholds between 0 and 180 g in

the anterior tibial muscle of the cat, with four units firing spontaneously at no measurable muscle load. Furthermore, Houk & Henneman (1967) have shown that the absolute threshold of tendon organs in cat muscles may be very low under conditions in which appropriate subdivisions of the muscle were selectively activated. Thresholds of tendon organs to passive stretch appear therefore to be reflecting properties of the surrounding muscle tissue rather than the actual threshold of the receptor itself. Hence the low thresholds observed for some tendon organs in the duck need not be regarded as showing a fundamental difference between these receptors and their mammalian counterpart.

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