CHAPTER 7

Roles of muscle activity and load on the relationship between muscle spindle length and whole muscle length in the freely walking cat

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The objective of this research was to compare the length of muscle spindles to the length of the whole muscle, during normal movements. Pairs of piezoelectric crystals were implanted near the origin and insertion of muscle fibres in the medial gastrocnemius (MG) muscle of cats. The distance between crystals was measured with pulsed ultrasound, the origin-to-insertion length of the MG muscle was measured with a transducer made of saline-filled silicone tubing, MG force was measured with a tendon force transducer and EMG activity was selectively recorded in the vicinity of implanted crystals. These signals were simultaneously recorded during posture or locomotion on a motorized treadmill. Three periods were identified in the step cycle, during which the relation between muscle length and spindle length changed dramatically. In period I (roughly corresponding to the late F and E1 phases of swing), the MG muscle and spindles followed similar length changes: both were stretched and then shortened by about 6 mm. In period II (corresponding to the stance phase, E2 – E1) the MG muscle yielded under the weight of the body and was stretched by 1 – 3 mm, whereas the MG spindles remained nearly isometric. In period III, the MG muscle shortened rapidly by 6 – 8 mm after the foot left the ground and then stretched again by about the same amount, whereas the spindles could remain nearly isometric. We attribute these large discrepancies in muscle and spindle length to the architecture of the MG muscle and the compliance of long tendinous elements in series with the spindles. We conclude that the length changes imposed on muscle spindles during voluntary movements are not simply related to the parent muscle length changes and cannot be estimated without taking into account the muscle architecture, the location of the spindle within the muscle, the level of muscle activation and the external load.

Key words: Muscle spindle; Muscle fiber; Muscle length; Cat locomotion; Fusimotor neuron

Introduction

Mammalian muscle spindles are stretch receptor organs whose afferent output is thought to reflect complex interactions between two kinds of time-dependent input: muscle length and fusimotor drive. In freely moving animals, the activity of identified fusimotoneurones has been impossible to record, due to their small size. Instead, fusimotor activity has been inferred by assuming it responsible for any features in spindle afferent activity that depart from the "passive" responses of de-efferented spindles to similar changes in muscle length (e.g., Prochazka et al., 1976, 1979, 1985; Loeb and Duyens, 1979; Loeb and Hoffer, 1981; 1985; Hulliger, 1984; Hulliger et al., 1987).

In analysing spindle afferent discharge patterns in normal movements, it has generally been assumed that the changes in muscle length are equally imposed onto the muscle spindles and that the spindle movements can be replicated in the passive muscle. Implicit in this assumption is the concept that ten-
tendons are series elements that are either so stiff that their length remains essentially constant, or that their length varies as a constant fraction of the total muscle length during normal movements. However, whereas this assumption may be largely valid for passive muscles, it is likely to be invalid for active muscles. The stiffness of activated extratendinous muscle fibres increases markedly (e.g., Hoffer and Andreason, 1981; Proske and Morgan, 1984), to the extent that it may meet or exceed the stiffness of the "entire tendinous component" (Rack and Westbury, 1984; see also Viddik, 1972; Morgan, 1977; Morgan et al., 1978; Griffiths, 1984). In pinnate muscles the angles of pinnation may change when the fibres are activated and a large, variable fraction of muscle stretch may be taken up by the aponeurotic sheets where the muscle fibres insert (v.i., Otten, 1988).

As a result, a distorted version of the muscle movement is likely to be registered by the muscle spindles. The complexity of the interplay between muscle and tendon stiffness is further compounded by the fact that muscle stiffness will vary in proportion to the number of fibres activated at any time, as well as their discharge rates (Proske and Morgan, 1984; Rack and Westbury, 1984).

The role of tendinous components is likely to be even more important in biarticular muscles, where muscle fibres and spindles typically span a small fraction of the length of a limb muscle. In wallabies hopping at high speed, Griffiths (1984) concluded from the mechanical properties of the median gastronemius (MG) muscle and tendon that the MG fibres shortened in the early stages of muscle stretch. In cats, the rest-length of MG muscle fibres is of the order of 15–25 mm (Wallmesley and Proske, 1981), whereas the origin-to-insertion length of a large cat's MG muscle varies from some 115 to 125 mm (Goslow et al., 1973).

Although complex arrangements like, for example, "tandem" spindles have also been described (e.g., Banks et al., 1982), the typical MG spindles are arranged in parallel with extratendinous muscle fibres in the central region of the muscle (Swett and Eldred, 1960). Thus, a typical MG spindle is 15–25 mm long and is in series with some 100 mm of tendinous elements and in parallel with extratendinous fibres that have low stiffness when inactive and high stiffness when active.

In this study we tested the hypothesis that the length input to muscle spindles is not strictly related to the length of the parent muscle during voluntary movements. We used the ultrasound transit-time technique to measure muscle fibre and spindle length in central regions of the MG muscle. This technique has been widely used in cardiovascular research (v.i., Rushmer et al., 1956) and in the study of diaphragm movements (reviewed by Newman et al., 1984). A method for using ultrasound to study muscle fibre length in the contracting MG muscle of anaesthetized cats was recently developed by Griffiths (1987). This approach gave preliminary data from one chronically implanted cat (Griffiths and Hoffer, 1987), prior to the present study.

Our results confirm the hypothesis that muscle spindles are not subjected to the same length changes as the parent muscle during normal locomotion, and suggest that the length of a muscle spindle is a complexly varying fraction of total muscle length that depends on the muscle architecture, the location of the spindle within the muscle, the extent of muscle activation and the external load.

Methods

Experimental design

Three large male cats (3.6–4.4 kg) were trained to walk or trot on a motorized treadmill enclosed within a Plexiglas box, set at level, uphill (+10% grade) or downhill (−10% grade) positions, at a range of speeds from about 0.2 to over 2.0 m/s. After 4–6 weeks of daily training, each cat was deeply anaesthetized with halothane in oxygen/nitrous oxide mixture. The left hindlimb was prepared for surgical implantation of electrodes and transducers (described below). The leads from the implanted devices coursed subcutaneously and emerged in small bundles around a 40-pin conne-
tor (see Hoffer et al., 1987) attached to the cat's back with four size-2 subfascial Mersilene sutures. After surgery, the cats were administered a sedative (Atravet) and an analgesic (morphine sulfate, 0.1 mg/kg, subcutaneously every 8 h) for at least 24 h. Two or three days after surgery, the cats could be exercised on the treadmill for several minutes at slow speeds. Recordings were carried out starting on the sixth postsurgical day. The cats showed little or no sign of impairment and by the second week after implant they could walk for 30 min or more with periodic rest periods, and run at up to 2.2 m/s.

Measurement of MG muscle spindle length

The essence of our estimation of spindle length lies on the careful implantation of pairs of piezoelectric crystals near the origin and insertion of identified groups of muscle fibres (as in Griffths, 1987) in central regions of the MG muscle (Fig. 1). Implicit in the measurement of transit time of pulsed ultrasound bursts that are emitted by one crystal and received by the other, are two important assumptions: (1) that the velocity of ultrasound does not change much with the state of activation of the muscle (Hatta et al., 1988) and (2) that muscle fibres and spindles run straight between their origin and insertion. Fibres near the surface of a muscle can curve markedly during active shortening, but fibres in the central region of the MG muscle, where most spindles are located (Swett and Eldred, 1960), are likely to remain nearly straight (e.g., Otten, 1988, Fig. 15).

We used cylindrical crystals, 1.5 mm in diameter and 1.5 mm in length, having a natural frequency of 5 MHz (CY5-2; Triton Technology), fitted with Teflon-coated, multistrand, stainless steel leads (Cooner AS 631). Cylindrical crystals performed far better than disc crystals used in earlier experiments (Griffiths, 1987; Griffiths and Hoffer, 1987), mainly because disc crystals must be critically aligned when implanted and must remain well aligned through movement to obtain a usable signal, whereas the strength of the signal detected with cylindrical crystals is largely independent of rotational changes. In addition, the ultrasound-absorbing air gap that tended to be formed between disc crystals and muscle surface (viz., Griffiths, 1987, Fig. 1) was reduced or eliminated using cylindrical crystals. Since silicone rubber also absorbs ultrasound, we further improved the strength of the transmitted signal by adhering with epoxy a small piece of Dacron cloth to the top surface of each crystal, rather than using a silicone rubber block (viz., Griffiths, 1987).

Implantation of piezoelectric crystals

After both the deep and medial surfaces of the MG muscle belly were surgically exposed, the intended placement of one crystal of each pair was selected along the midline of the deep surface of the muscle and marked with a grain of Methylene blue (as in Griffiths, 1987). The orientation of tendinous fibres was used as a reference for orientation and placement of the crystals. The corresponding placement of the superficial crystal in each

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Fig. 1. A: schematic diagram of the left MG muscle, dorsal view, with implanted devices. B: diagram of the MG muscle, longitudinal cross-section, shows typical dimensions and orientation of its muscle and tendon fibres (adapted from Wahlensley and Proskie, 1981). The crystals recorded the length of muscle spindles in the highlighted region.
pair was determined by electrical microstimulation at the marked point (modified from Griffiths, 1987), using a concentric needle electrode (o.d. = 0.5 mm) and stimulating at 2 Hz using 40 – 70 μA \times 0.2 \text{ ms} \text{ pulses}. Upon each stimulus, a tiny dimple was observed on the medial surface, indicating the origin of the extrafusal fibres that were being stimulated near their distal end. A second grain of Methylene blue was placed at the dimple. A piezoelectric crystal was then positioned directly over each marked spot, such that the cylinder axis was perpendicular to the plane determined by the long axis of the MG muscle and the axis of the fibres to be measured (Fig. 1), and its Dacron cloth piece was sutured to the fascia using size 5-0 sutures. Either 12 or 13 piezoelectric crystals were implanted in each of the three cats, strategically placed to measure the length of fibres and spindles in three regions of the MG muscle, as well as the length changes of segments of aponeurotic sheets in series with the muscle fibres and spindles of interest.

The amplitude of the recorded signals often improved markedly during the second week post-implant, suggesting that the crystals were being encapsulated by proliferating connective tissue and any remaining air was being absorbed. In post-mortem verification, each crystal left a precise imprint in the connective tissue on the muscle surface. This confirmed the position of the crystals and suggested that they were not displaced during movement.

**Estimation of accuracy of muscle spindle length measurement with piezoelectric crystals**

The measurement of distance between pairs of crystals was made with a Sonomicrometer 120 (Triton Technology) as described by Griffiths (1987). Our estimation of absolute muscle fibre and spindle length may have included a systematic error of the order of 1 mm, due to uncertainty in the placement of the crystals and the thickness of the aponeurotic sheets. A further source of occasional measurement uncertainty was a false trigger on other than the first waveform in the received burst. This tended to happen when signal strength declined for relatively long lengths, or when signal strength increased markedly for short lengths. A false trigger that skipped by one wavelength would cause an error in length measurement of 0.33 mm. A few examples of false triggers can be seen in the data in Figs. 2A and 3A, typically around the shortest and longest spindle length values recorded during walking. These false triggers were rare enough that they did not seriously distort the shape of the recorded signal. Assuming 1 – 2% variations in the conduction velocity of ultrasound in active muscle (Hatta et al., 1988), the total uncertainty in the measurement of spindle length changes was generally less than \pm 0.5 mm.

**Measurement of whole muscle length**

The origin-to-insertion length of the MG muscle was recorded with a length transducer made of saline-filled silicone tubing (Loeb and Hoffer, 1981, 1985). Heavy sutures tied to the ends of the transducer were passed through holes drilled in a sesamoid bone within the tendon of origin of MG, and the calcaneum. The transducer was connected to an AC bridge amplifier (Bak Electronics) driven at a constant frequency (25, 30 or 35 kHz). The DC output signal was low-pass filtered (5 ms time constant). In limited recordings, the length of the MG muscle was simultaneously measured with a pair of piezoelectric crystals attached to the sesamoid bone and to the proximal end of the force transducer (described below), although this measurement excluded the distal 30 mm of MG tendon. The length transducer records were calibrated for specific steps of interest, using joint angle measurements made from videotaped records (30 frames/s) and measurements of bone lengths. The cosine law was used to calculate MG length (viz., Goslow et al., 1973).

**Measurement of muscle force and EMG**

Force was recorded from the MG tendon by an implanted spring steel “E” transducer (Waismley et al., 1978; Loeb and Hoffer, 1981, 1985). Force records were low-pass filtered at 100 Hz. The elec-
tromyogram was selectively recorded by bipolar electrodes consisting of a pair of Teflon-coated, multistrand, stainless steel wires (Cooner AS 631) with exposed ends. The two electrodes were sewn into the muscle at the sides of each of the superficial crystals, about 5 mm apart, such that one electrode was about 2 mm deep and the other was superficial. EMG records were amplified 1000-fold and filtered in the 50 – 5000 Hz range prior to tape-recording. To remove noise generated by the crystals, EMG records were further low-pass filtered at 250 Hz (18 dB/octave).

All signals were recorded on FM tape (10 kHz bandpass), along with a master time code (Datum) that was used for synchronization of videotaped images during data analysis. Data shown in Figs. 2 and 3 were played back into an electrostatic recorder with 25 kHz peak capture (Gould S1000).

Results

Relation between muscle length and muscle spindle length during locomotion

A consistent finding that emerged from our records was that the relationship between MG

![Fig. 2. A: example of records obtained during a typical step. From top, traces are: force recorded from the MG tendon by an implanted spring steel transducer; electromyogram recorded by bipolar electrodes sewn near the crystals; origin-to-insertion length of the MG muscle, recorded with a saline-filled silicone tubing transducer spanning from the sesamoid bone in the tendon of origin, to the calcaneum; length of muscle spindles in the central portion of MG, recorded by piezoelectric crystals. Horizontal bar indicates weight-bearing period for the implanted hindlimb. Arrows indicate paw touchdown and liftoff. B: traces corresponding to the length of the MG muscle and the length of muscle spindles are superimposed to reveal three periods (I, II, III) of dissimilar relationship. The phases of the Phillipson step cycle (F, flexion; E1, E2, E3, extension) are also shown. Note that muscle and spindle length are very similar in period I, but the spindles are not stretched with the muscle in period II, and the spindles are not shortened with the muscle in period III.](image-url)
muscle length and MG spindle length changed systematically and dramatically during locomotion. We identified three distinct periods in the step cycle, that overlapped roughly, though not exactly, with the four classic phases of the step cycle (F = flexion; E₁, E₂, E₃ = extension phases) described by Philippson (1905) from joint angle transitions. During period I, while the limb was unloaded during late swing, the muscle length and spindle length excursions had similar direction and shape, and comparable amplitude. During period II, while the limb was loaded during stance, the muscle was stretched while the spindles were not. During period III, in early swing, the muscle was first shortened considerably and then lengthened by about the same amount, while the spindles showed only modest changes in length.

Fig. 2A shows the MG force, EMG, muscle length and spindle length signals recorded from a cat taking one representative step at about 0.5 m/s on a level treadmill. Fig 2B shows again the muscle length and spindle length traces from the same step, now superimposed to highlight the principal similarities and differences. The weight-bearing phase (stance) for the instrumented hindlimb is shown by a horizontal bar. Arrows mark transitions between loaded and unloaded phases. It is apparent that the muscle and spindle length traces obey very different relations during the three periods, indicated in Fig. 2B as I, II and III.

Period I

This period comprises half of the swing phase, since it starts in the middle of the F phase and includes the E₁ phase. Initially the MG muscle is passively stretched by the action of antagonists. No EMG is present. The MG spindles are also stretched, and follow a very similar timecourse to the MG muscle length. At the F to E₁ transition, almost coincident with the onset of EMG, the MG fibres proceed to rapidly shorten against minimal load. The MG muscle also shortens, following an almost identical time course and extent as the spindles. The rapid muscle shortening phase comes to an abrupt end at the moment of foot contact, as

the limb is loaded (downward arrow in Fig. 2A, 2B), and here also ends period I.

Period II

This period consists of the E₂ and E₃ phases, the periods of load-bearing of the instrumented limb. As the weight is transferred, the MG muscle “yields” and stretches by a variable amount. In contrast, the muscle fibres typically do not yield during the E₂ phase. Rather, the fibres usually continue shortening during E₂ (viz., Griffiths, 1984), albeit at a considerably slower rate than during E₁. Thus, the MG spindles are typically not stretched during the E₂ phase, even though the MG muscle is. During the E₃ phase, the MG length record can show multiple inflexions. Active shortening usually follows the peak of yield. Toward the end of E₃ the muscle can be passively lengthened as its EMG activation declines and the knee extends maximally. In contrast, spindles in the central region of the MG muscle tend to remain fairly isometric, or experience only an attenuated version of the changes seen in the whole muscle length.

Period III

This period consists of the early F phase. Initially, the MG muscle is rapidly and passively shortened following the release of foot contact at the end of the stance phase (upward arrow in Fig. 2). The spindles do not follow the abrupt shortening of the MG muscle, probably because the pushoff is mediated by muscles other than MG (e.g. posterior tibial muscle; viz. Abraham and Loeb, 1985). As the ankle extends further but the knee starts to flex, the previously stretched MG tendon appears to take up the shortening, sparing the MG fibres and spindles from participating. Eventually, the MG length reaches a minimum and the MG muscle starts to be passively stretched by the action of ankle flexors. The fibres and spindles follow the stretch at an initially much reduced rate but, eventually (presumably once the tendon is sufficiently stretched), the rate of stretch of the spindles catches up with the whole muscle and a new Period I begins.
Comparison of length and velocity of MG muscle and spindles during the step cycle

From a 4.4 kg cat walking on a level belt at 0.5 m/s, the following observations were made from the data in Fig. 2.

Periods III and I, F phase

The origin-to-insertion length of the MG muscle changed by 10 to 12 mm, from about 110 to 120 mm (10% of MG rest-length). The length of the muscle spindles in the central portion of MG increased by about 7.5 mm, from 15.5 to 23 mm (35% of rest-length). During the final 100 ms of the F phase, the velocity of stretch of the MG muscle was 550 mm/s, or about 5 rest-lengths per second (RL/s; viz., Prochazka and Hulliger, 1983). At the beginning of stretch, still in period III, the spindles were slow to follow the stretching muscle, probably because the distal tendon started out slack. Mid-way through the F phase the spindles caught up with the muscle and their peak velocity of stretch was about 550 mm/s, or about 25 RL/s, during period I.

Period I, E₁ phase

The amount of shortening during E₁ depends on the timing between the onset of EMG and the contact with the ground, and is in fact kept fairly constant, both for level walking and for uphill or downhill walking (see further examples in Fig. 3). In the example of Fig. 2, the MG muscle shortened by 5 mm and the spindles by almost the same amount. The velocity of shortening of both the MG muscle and spindles during E₁ was about 800 mm/s, corresponding to about 8 RL/s for the muscle and 40 RL/s for the muscle spindles.

Period II, E₂ phase

In the example for Fig. 2, the MG muscle yielded by 2.0 mm during the first 100 ms after foot contact, whereas the MG spindles, pulled by fully activated extrafusal fibres, were shortened by an additional 0.25 mm during the same time. The rate of stretch of the MG muscle during E₂ was 20 mm/s (0.2 RL/s), while the spindles shortened at a rate of 2.5 mm/s (−0.1 RL/s). The extent of muscle yield could be quite variable. In some steps the spindles could also experience some yield, although in such cases the extent of spindle yield was a small fraction of muscle yield (examples in Fig. 3). No systematic observations could be made on the extent and rate of length changes in the MG muscle during period II, E₃ phase, because of the high variability from step to step.

Period III, early F phase

A consistent observation was that the inactive MG muscle could shorten by as much as 8 mm following footlift and then stretch again by about the same amount, but the muscle fibres and spindles in the central region of MG experienced only a small amount of movement (<1 mm).

Variations in the relation between muscle length and muscle spindle length during level, uphill and downhill locomotion

Fig. 3A shows raw records obtained from the same cat as in Fig. 2, during seven consecutive steps on a level treadmill belt set at 0.47 m/s. There was considerable variation in the MG tendon force amplitude and EMG (upper traces) as well as in the cycle durations of the steps shown, because the belt speed had been reduced from 0.77 m/s moments before, and the cat was adjusting to the new speed. Note that the excursions in MG muscle and spindle length during the unloaded phases (late F and E₁; period I) were strikingly similar from step to step. We will concentrate here on the differences between muscle and spindle length that occurred during the load-bearing phases (E₂ and E₃; period II).

The first six steps in Fig. 3A were all different from each other. In the first step, the MG muscle length “yielded” prominently upon touchdown and then decreased through mid-stance, whereas the MG fibres and spindles were held briefly isometric and then shortened all through E₂ and into E₃. In the second step, there was only a small yield and the muscle remained fairly isometric
through $E_2$ and $E_3$. The spindle length record shows an almost imperceptible yield, but then the spindles shortened steadily throughout the rest of the stance phase. The amount of muscle yield in the third step was again small, but note that the spindles followed a similar time course to the first step during $E_4$ and early $E_5$. The force in the third step was considerably larger. In the fourth step, the muscle showed little or no yield; muscle length and spindle length declined similarly. The fifth step showed larger yield and also larger force than the previous steps; still, the MG spindles continued to shorten during $E_2$ and $E_3$. The sixth step showed the largest yield of all and an intermediate

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**Fig. 3.** A: examples of records obtained from a cat walking on a level treadmill at about 0.5 m/s, during seven consecutive steps. B: records obtained during uphill walking on a 10% grade at 0.4 m/s. C: same, for downhill walking on a 10% grade at 0.4 m/s. Traces as in Fig. 2.
force, but even here the spindles continued shortening. The last step shown in Fig. 3A, taken as the cat resumed a constant speed, looks fairly similar to the first step.

Fig. 3B shows records obtained from the same cat during uphill walking at 0.4 m/s. The same traces as in Fig. 3A are shown, and the calibrations are all the same. During uphill walking, the general shape of all the traces was roughly similar to level walking, but the amplitude of MG force, EMG and length changes were all larger. In contrast, the muscle spindle length records were almost identical to the level walking steps shown in Fig. 3A, except that the average length had shifted toward a somewhat longer value. The MG muscle yielded more prominently during uphill than level walking, but the muscle fibres and spindles did not yield any more than they did during level walking. Similarly, spindle length did not reflect the marked decline in MG muscle length at the end of stance. Thus, the characteristic dissociation between muscle and spindle length already observed during the E₂ and late E₃ phases of level walking (period II), was further exaggerated during uphill walking.

Fig. 3C shows records obtained from the same cat during downhill walking at 0.4 m/s. During downhill walking, the amplitude and duration of MG force and EMG were smaller than during level walking. The MG muscle yielded by varying amounts during E₂, and shortened less at the end of E₃. The muscle fibres and spindles did not yield, but they also did not shorten further at foot contact; rather, the spindles remained fairly isometric in two of the three steps shown and, in the third step, shortened markedly during E₂ and then lengthened during E₃, even while the muscle was shortening. Again, spindle length did not reflect muscle length during downhill walking, and the overall patterns were not quite the same as in level walking.

In summary, a comparison of level, uphill and downhill walking confirmed the finding that the relationship between the length of the MG muscle and its spindles changed systematically during three periods of the step cycle.

Discussion

Relation between spindle length and muscle length during active movements

The main conclusion from this study is that the length changes imposed on the MG muscle spindles do not directly reflect the length changes undergone by the parent muscle during most of the step cycle. Three periods in the step cycle were identified, during which the spindle length and muscle length were differently related. Only during one period, when the limb was unloaded, were the length changes in the muscle and its spindles well correlated. During the loaded period of the step cycle the muscle was stretched much more than its spindles, while at the early swing phase, the muscle shortened much more than its spindles.

The simplest interpretation of these observations is that the MG spindles are in series with long, compliant tendinous fibres that take care, during most of the step cycle, of a large fraction of the length changes seen from the origin to the insertion of the muscle. Early during period I, with the tendinous fibres relatively stiffer than the inactive muscle fibres, the spindles closely follow the length changes that are imposed on the muscle. As the MG muscle is activated in E₁ and starts to shorten in the absence of external load, the ends of the muscle are pulled in by the shortening fibres, and now it is the spindle that closely follows the length changes of the spindles. After foot contact, during early period II, the MG muscle is active and the limb is loaded, so the tendon is pulled from both ends. The action of external loads causes the muscle to yield during E₂, but the tendinous components undergo the stretching, not the muscle fibres and spindles. The muscle fibres continue to actively shorten, at further expense of the tendinous components, and so the spindles shorten, even though the muscle "yields". During E₃ the MG muscle and tendon shorten somewhat, and the tendon force declines. At the end of E₃, the MG muscle is often lengthened again by the action of the extending knee. During period III, the MG muscle is released as the foot gives up contact with
the ground. This provides the opportunity for the still stretched tendinous elements to shorten. The now-inactive fibres, and spindles in parallel with them, do not participate in this shortening, and can in fact lengthen modestly as the muscle belly regains its shape.

Our data support prior suggestions by others, in particular by Rack and Westbury (1984), that spindles do not fully partake in the movements of their parent muscles, due to the compliance of tendinous series components. In addition, we have obtained preliminary recordings using piezoelectric crystals mounted along portions of the aponeurotic sheets of the MG muscle (Caputi, Hoffer and Pose, unpublished data) that further confirm this view. It should be noted that a recently published general muscle model by Otten (1988) includes several architectural features that are supported by our observations.

**Need for re-interpretation of prior observations on spindle activity patterns during normal movements**

Prior studies often assumed that fusimotor activity was responsible for any features in spindle afferent activity that departed from the "passive" responses of de-efferented spindles to similar changes in muscle length (e.g., Prochazka et al., 1976, 1979, 1985; Loeb and Duyens, 1979; Loeb and Hoffer, 1981, 1985; Hasan, 1983; Hulliger, 1984; Hulliger et al., 1987). As a consequence of this study, we now know that an estimation of muscle spindle length based on the length of the parent muscle is incorrect for most of the step cycle. For example, the amount of fusimotor activity during the "yield phase" of extensor muscles is likely to have been greatly underestimated in simulation studies that assumed that spindle length changes in active muscles could be reproduced in passive muscles if whole muscle length was reproduced (e.g., Prochazka et al., 1985; Hulliger et al., 1987). Also, models of spindle response to stretch that were based on passive muscle properties (e.g., Hasan, 1983) must be modified if they are to be applicable to active muscles. Clearly, future studies of natural spindle activity patterns will have to simultaneously include either the technique of pulsed ultrasound transit-time or some other, equivalent method of detection of actual spindle movement.

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