

**FUSIMOTOR — INDUCED POST-CONTRACTION CHANGES IN MUSCLE SPINDLE
AFFERENT OUTFLOW AND RESPONSIVENESS IN MUSCLE FATIGUE IN DECEREBRATE
CATS. EFFECTS OF AFFERENT INFLOW FROM OUTSIDE THE CONTRACTING MUSCLE**

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Changes in discharge rate of muscle spindle afferents from triceps surae muscles were recorded and their responsiveness to muscle length changes tested during long-lasting fatiguing isometric contractions of either medial gastrocnemius or lateral gastrocnemius and soleus muscles in decerebrate cats. The whole hind limb was either denervated, except for the contracting muscle, or its innervation was preserved. The experiments were aimed to compare the effects on muscle spindles of the reflex increase in fusimotor activity developing in parallel with muscle fatigue when fusimotor neurones are deprived of afferent inflow originating from outside the contracting muscle with those exerted when fusimotor reflex responses are affected by this inflow.

In denervated preparations a long-lasting postcontraction increase in discharge rate occurred in the majority of muscle spindle primary endings and in all the secondary afferents studied. However, in innervated preparations it was replaced in the majority of the primary endings by a short-lasting burst, occurring immediately after the end of muscle contraction and in secondary afferents it was either absent or shorter-lasting than in denervated preparations.

In spite of these differences in changes in discharge rate, similar changes in responsiveness to muscle length changes of muscle spindle endings were found in both innervated and denervated preparations. They indicated influences of both static and dynamic fusimotor neurones.

Key words: muscle fatigue, muscle spindle afferents

INTRODUCTION

An increase in discharge rate of spindle afferents and in dynamic sensitivity of the primary endings developed (Nelson and Hutton, 1985; Hutton et al., 1992) when muscle fatiguing contractions were elicited by electrical stimulation above fusimotor threshold so that the fatigue was paralleled by artificially raised

fusimotor activity. If the increase in fusimotor activity, developing reflexly in both decerebrate and spinal cats during long-lasting fatiguing muscle contractions (Ljubisavljević et al., 1992a) is strong enough to elicit similar changes in afferent inflow from muscle spindles from the contracting muscle, it would result in an improvement in both support of skeletomotor activity and in information sent to nervous centres initiated automatically from the muscle when fatigued. While in cats an increase in gain of the afferent part of the reflex loop was indeed found to accompany its decrease in the efferent part in the fatigue of single muscle units (Christakos and Windhorst, 1986; Windhorst et al., 1986), data on spindle support in muscle fatigue in humans is controversial (Balestra et al., 1992; Macefield et al., 1991; Marsden et al., 1972; Ribot-Ciscar et al., 1991). Apart from possible species differences, these discrepancies might be due to reflex influences on fusimotor neurones of segmental afferent inflow of origin other than the contracting muscle (Appelberg et al., 1983a, b, c, d), provoking profound changes in their reflex responses to muscle fatigue (Anastasijević et al., 1993). In this work, therefore, changes in muscle spindle outflow as well as alterations in its responsiveness to muscle length changes, during fatiguing muscle contractions obtained while the hind limb was denervated, except for the contracting muscle, were compared to those found under more physiological conditions with the innervation of the hind limb preserved.

Preliminary results have been presented (Ljubisavljević and Anastasijević, 1993) and will be published in a short communication form.

MATERIALS AND METHODS

Surgical preparation. The experiments were performed on 29 adult decerebrate cats. The operative procedure till decerebration was carried out under halothane in oxygen anaesthesia. In 14 cats the right hind limb was completely denervated except for the triceps surae muscles while in the remaining 15 cats all the nerves were left intact. Lumbar laminectomy was performed and the dura cut to allow access to dorsal roots L7 and S1. Cats were fixed to the stand by clamps on the third lumbar spine and the iliac processes, and screws in the right tibia and femur. The exposed tissues were kept moist in paraffin pools. Blood pressure and the temperature of both the animal and the paraffin pools were monitored and maintained within physiologically desirable ranges.

Recoding techniques. Spike discharges of functionally single afferent fibres were recorded from transected fascicles dissected free from otherwise intact L7 and S1 dorsal roots. The afferents were identified as muscle spindle's if a pause appeared in their spontaneous firing during parent muscle twitch contraction and as belonging to group Ia or group II afferents on the basis of the conduction velocity. Muscle tension changes were recorded by a tension transducer attached to the tendon of the triceps surae muscles. The compliance of the transducer was 20 $\mu\text{m/N}$.

Muscle contraction and stretching. Isometric muscle contractions were elicited by electrical stimulation of either the medial gastrocnemius (MG) or

lateral gastrocnemius and soleus (LGS) nerves (the heteronymous nerve with respect to the afferent recorded). Electrical 0.2 ms stimuli at 1.3 times motor threshold (Ljubisavljević et al., 1992a) were applied at a rate of 40 Hz until the muscle tension fell to approximately one third of the initial value. Sinusoidal muscle stretches at a rate of 1 Hz and 1mm half-to-peak amplitude were produced by a servo-controlled electromagnetic puller and applied immediately before the beginning of the muscle contraction, immediately before and after its end as well as two minutes later.

Analysis of data. Afferent discharges were recorded before (100 s), during and after (300 s) muscle contraction, stored on magnetic tape and/or analysed on-line on a Hewlett-Packard 9817 computer. The number of impulses per 1 s interval as well as per 10 s interval was counted during the whole recording period. Mean value and the standard deviation of the spontaneous discharge rate were computed from the counts per 1 s interval during a 100 s period immediately preceding the onset of stimulation. The magnitude of changes in discharge rate was estimated at the beginning and the end of the muscle contraction as well as after its end at the moment of the largest departure of the line drawn through the counts per 10 s interval and the mean spontaneous firing rate.

The responses to ten cycles of sinusoidal stretching were averaged by constructing cycle histograms and analysed by fitting a simple sinusoid to the histogram using a least square algorithm which ignored periods of afferent silence (Hulliger et al., 1977b). The mean discharge rate, depth of modulation and phase of the response (relative to the phase of the stimulus) were estimated.

RESULTS

Changes in discharge rate of eighteen primary (eight MG and ten LGS units) and twenty secondary (thirteen MG and seven LGS units) afferents from fourteen cats with denervated hind limbs were studied during long-lasting muscle contraction. Spontaneous firing rates of the primary afferents ranged from 7-26 impulses/s and those of the secondary afferents from 8.5-37 impulses/s. The effects of preserved innervation of the whole hind limb on changes in discharge rate of muscle spindle afferents during long-lasting fatiguing contractions of either MG or LGS muscles were studied in an additional 22 primary (thirteen MG and nine LGS units) and 14 secondary (seven MG and seven LGS units) afferents from 15 cats. Spontaneous firing rates of the units ranged from 5-34 impulses/s and 7-28 impulses/s respectively.

Post-contraction changes in firing rate and responsiveness to sinusoidal muscle stretching of muscle spindle afferents are presented in Tables 1 and 2, respectively. While in denervated preparations a long-lasting gradual increase in discharge rate developed in the majority of the primary and all the secondary afferents studied, in innervated preparations it was either lacking, or else it was short-lasting in secondary afferents, and a sharp bursts, lasting for approximately 20 s, occurred immediately after the end of muscle contraction in the majority

of primary afferents. The changes in discharge rate of the afferents in denervated vs innervated hind limb were similar in magnitude, while their duration was markedly different (Table 1). The increase in discharge rate following muscle contraction lasted longer than one minute in two thirds of the primary afferents from denervated hind limb while a short-lasting burst (up to 20 s) prevailed in those from innervated hind limb. The increase in discharge rate following muscle contraction, occurring in 72 percent of secondary units from innervated hind limb was gradually developing, but nevertheless shorter-lasting than that found in secondary afferents from denervated hind limb, where it occurred in all the 20 units studied. It lasted longer than 150 s in 50 percent of secondary units from denervated hind limb and in seven percent of those from innervated hind limb.

Table 1. Postcontraction increase in discharge rate (impulses/s) of muscle spindle afferents in denervated and innervated hind limb

	denervated		innervated	
	Ia	II	Ia	II
(n)	(18)	(20)	(22)	(14)
increase (n)	(15)	(20)	(20)	(10)
mean (range)	5.1 (1-17)	4.3 (1-15)	6.6 (2-22)	5.4 (1-13)
duration (s)				
mean (range)	116 (20-270)	122 (10-200)	37 (4-160)	78 (15-170)

n = number of units

Changes in responsiveness to muscle length changes were estimated by comparing afferent responses to sinusoidal muscle stretching applied immediately before and after the end of muscle contraction, as well as two minutes later, to those obtained before its start. In primary afferents from denervated hind limb both increases and decreases in modulation depth, similar in magnitude and significant at a 0.05 level were equally encountered (Table 2). The decrease in modulation depth was accompanied by shortening or disappearance of the pause in firing during the releasing phase of the sinusoidal stretching. Changes in modulation, tested in four units, were smaller, but still present two minutes after the end of muscle contraction. The responsiveness of secondary afferents to sinusoidal muscle stretching applied during muscle contraction was practically unchanged, while after the contraction an increase, significant at the 0.01 level, occurred in seven out of eight units. It was still present in three out of four units tested two minutes after the end of muscle contraction. Changes in modulation of discharge rate of the primary afferents from innervated hind limb during sinusoidal muscle stretching applied both before and after the end of muscle contraction, did not differ significantly in either incidence or magnitude from those in denervated hind limb (Table 2). The changes were smaller on most occasions, but still present two minutes after the contraction ended. Changes in responsiveness of secondary endings were also similar to those in denervated hind limb. After denervation of the

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hind limb performed during some experiments the magnitude of changes in modulation of the three primary and one secondary afferents tested remained practically the same as before.

Table 2. Changes in responsiveness of muscle spindle sensory endings to sinusoidal muscle stretching applied before and after the end of fatiguing muscle contraction (differences, mean and range, in modulation depth from the control responses, impulses/s)

	denervated		innervated	
	Ia	II	Ia	II
number of units tested				
(n)	(11)	(8)	(11)	(3)
before the end of contraction				
decrease	—15.7 (7–37)		—16.1 (8–23)	
(n)	(5)		(7)	
increase	+8.5 (2–17)		+5.7 (2–12)	
(n)	(5)		(3)	
after the end of contraction				
decrease	—11.4 (2–27)		—4.3 (2–9)	
(n)	(5)	(0)	(7)	(0)
increase	+9.8 (3–27)	+4.8 (2–10)	+9.3 (5–14)	+6.6 (5–9)
(n)	(5)	(7)	(3)	(3)
two minutes later				
(n)	(5)	(4)	(11)	(3)
decrease	—4.8 (1–10)		—5.2 (2–6)	
(n)	(4)	(0)	(7)	(0)
increase	+9.0	+5.0 (4–7)	+3.2 (1–7)	+3.0 (1–6)
(n)	(1)	(3)	(3)	(3)

DISCUSSION

The experiments performed were aimed to show the effects of a reflex increase in fusimotor activity, due to muscle fatigue (Ljubisavljević et al., 1992a), on muscle spindle afferent inflow and responsiveness when deprived of segmental influences shown to exert profound changes in these fusimotor reflex responses (Anastasijević et al., 1993), as well as in their presence. The postcontraction increase in discharge rate of muscle spindle afferents, developing in denervated preparations, corresponded in its time course and duration to the late increase in discharge rate of fusimotor neurones in long-lasting fatiguing muscle contraction (Ljubisavljević et al., 1992a). Its disappearance when the transmission in either the small-diameter afferents of nerve impulses from the contracting muscles or in fusimotor axons to the muscle of origin of the spindle afferent is blocked by procaine (Ljubisavljević and Anastasijević, 1993), strongly indicates that it appears primarily due to this reflex increase in fusimotor activity. The increase in both mean firing rate and responses to muscle stretching (Brown et al., 1969; Crowe and Matthews, 1964) of group II afferents after muscle contraction as well as the decrease in modulation and disap-

pearance of pause in some primary afferents both during and after the contraction, speak in favour of the increase in static fusimotor activity with enough certainty. The increase in modulation of discharge rate during sinusoidal muscle stretching encountered equally in the primary afferents (Appelberg et al., 1982; Hulliger et al., 1977a, b) indicates, however, that dynamic fusimotor neurones are also active albeit to a lesser degree.

The postcontraction long-lasting increase in discharge rate occurring in ten out of 14 secondary afferents and in six out of 22 primary units in innervated hind limb, smaller in incidence and duration than that in denervated hind limb, might also appear due to the reflex increase in discharge rate of fusimotor neurones developing with muscle fatigue, which was also smaller in both incidence and duration in innervated hind limb (Anastasijević et al., 1993). The short-lasting sharp burst, however, appearing in the majority of primary afferents, and replaced by a prolonged increase in discharge rate after hind limb denervation (Ljubisavljević and Anastasijević, 1993), might rather represent a true after-effect (Hutton et al., 1973) of the prolonged enhancement in fusimotor activity starting at the onset of muscle contraction while lacking after its end, as encountered in the majority of these neurones in innervated hind limb (Anastasijević et al., 1993). Changes in responsiveness to sinusoidal muscle stretching of muscle spindle sensory endings in innervated hind limb, surprisingly similar in both incidence and magnitude to those found when the hind limb was denervated in spite of the differences in changes in the mean discharge rate, might be provoked, at least partly in this same way.

From the functional point of view the data obtained shows that the increase in fusimotor activity developing during muscle fatiguing contraction in both denervated and innervated hind limb (Ljubisavljević et al., 1992a), only exceptionally strong enough to raise the discharge rate of the muscle spindle afferents beyond the spontaneous firing level until the muscle stops contracting (Ljubisavljević and Anastasijević, 1993), is sufficient, however, to counteract the effects of unloading on their responsiveness during muscle contraction as well as to provoke both an increase in their discharge rate and changes in responsiveness to stretch after muscle contraction. Since during muscle contraction a gradual decrease in skeletomotor discharge rate is required to match the changes due to fatigue in muscle contractile properties (Bigland-Ritchie et al., 1986), the increase in support from muscle spindles might be aimed to oppose inhibitory segmental influences from the fatigued muscle on skeletomotor neurones (Bigland-Ritchie et al., 1986; Hayward et al., 1988) without provoking a net increase in skeletomotor discharge rate. On the other hand changes in their responsiveness could help in providing fine moment-to-moment control of matching of skeletomotor discharges, as proposed by Windhorst and Kokkoroyiannis (1991), to changes in demand imposed by slowing of contractile muscle machinery. The increase in ability to detect small changes in muscle length as well as in responses of muscle spindle primary endings would result also in an earlier start and increase in information to be transmitted to higher nervous centres. Thus improved information of higher nervous centres involved in motor control without an overt increase in gain and a consecutive instability of the stretch reflex as proposed by Llewellyn et al. (1991) for another kind demanding motor task will be achieved. The increase in afferent inflow from

muscle spindles, those in group II afferents in particular, might also contribute to spreading of activity to other muscle groups when the contracting one gets fatigued (Dimitrijević et al., 1992; Lippold et al., 1960; Ljubicavljević et al., 1992b). On the other hand, both the long-lasting increase and the sharp post-contraction burst of discharges in some primary afferents might be expected to affect the responses to subsequent changes in muscle length as proposed by Gregory et al. (1986) and as most likely happens with responses of these afferents to sinusoidal muscle stretching applied after muscle contraction in these experiments. The information sent to the motor centres might serve as a warning signal to prevent initiation of the next movement until the muscle is wholly recovered.

Thus the final outcome of changes in fusimotor activity initiated by muscle fatigue itself and influenced by background afferent activity of other origin, would be a modest sustained level increase in afferent discharges from muscle spindle sensory, mainly the secondary, endings and marked changes in their responsiveness, making them ready to signal any disturbances to both skeletomotor neurones and higher nervous centres involved in motor control. Changes provoked in the intact animal, where both descending and afferent discharges are different from those in our experiments, and may vary depending on both the internal and external environment, cannot be guessed with certainty. The reflex pathways leading to the increase in fusimotor activity during muscle fatigue may be open or shut, attenuated or enhanced depending, possibly, on the current task and priority.

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**POSTKONTRAKCIJONE PROMENE AFERENTNOG PRAŽNJENJA I OSETLJIVOSTI
SENZITIVNIH ZAVRŠETAKA NEUROMIŠIČNIH VRETENA DECEREBRISANE MAČKE U
ZAMORU MIŠIĆA. UTICAJ AFERENTNIH IMPULSA KOJI NE POTICU IZ ZAMORENOG
MIŠIĆA**

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SADRŽAJ

Promene učestanosti pražnjenja nervnih impulsa u aferentnim vlaknima iz neuromišićnih vretena m. triceps surae decerebrisane mačke, kao i promene osetljivosti ovih senzitivnih završetaka na promene dužine mišića, registrovane su za vreme zamora m. gastrocnemius medialis ili m. gastrocnemius lateralis i soleus, izazvanog dugotrajnom izometrijskom kontrakcijom, dok je zadnji ekstremitet bio ili potpuno denervisan, izuzev mišića koji se kontrahuje, ili mu je inervacija bila očuvana. Cilj eksperimenata je bio da se uporedi dejstvo refleksnog povećanja aktivnosti fuzimotornih neurona koje se razvija u toku zamaranja mišića kada na ove ćelije deluju samo aferentni impulsi iz mišića koji se kontrahuje, sa dejstvom fuzimotornih neurona kada je njihov refleksni odgovor na zamor mišića izložen uticaju aferentnih impulsa drugog porekla.

Kada je ekstremitet bio denervisan, kod većine ispitivanih primarnih završetaka i kod svih sekundarnih završetaka neuromišićnog vretena javljalo se dugotrajno postkontrakciono povećanje učestanosti pražnjenja. Kada je inervacija ekstremiteta bila očuvana, kod sekundarnih završetaka ono se nije javljalo ili je trajalo kraće, dok je kod većine primarnih završetaka dolazilo do pojave naglog kratkotrajnog praska pražnjenja nervnih impulsa odmah po prestanku mišićne kontrakcije.

Uprkos ovim razlikama u promenama učestanosti pražnjenja, promene osetljivosti senzitivnih završetaka neuromišićnog vretena inervisanog i denervisanog ekstremiteta na promene dužine mišića bile su slične i ukazivale su na uticaj kako statičkih, tako i dinamičnih fuzimotornih neurona.