EFFERENT DISCHARGES RECORDED FROM SINGLE SKELETOMOTOR AND FUSIMOTOR FIBRES IN MAN

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SUMMARY

1. Experiments were performed on awake human subjects in which single nerve fibre activity was recorded in the lateral peroneal nerve using tungsten micro-electrodes as described by Hagbarth & Vallbo (1967, 1968*a*).

2. The discharge of twelve single efferent fibres innervating the tibialis anterior muscle (t.a.) or the extensor digitorum longus muscle (e.d.l.) was recorded. On the basis of their functional activity, six fibres were identified as skeletomotor and six as fusimotor fibres.

3. Skeletomotor fibres, which were completely silent in relaxed subjects, discharged when subjects performed voluntary isometric or isotonic contractions, they also fired during Jendrassik's manoeuvre and tonic vibration reflex (t.v.r.) induced by mechanical vibration applied to the distal muscle tendon.

4. Units considered as fusimotor fibres were generally spontaneously active with some fluctuation in the discharge frequency. Various tests used to identify afferent fibres elicited no response of these fibres (nor of the skeletomotor fibres). Efferent fibres were considered as fusimotor because their discharges were uncorrelated with any activation of extrafusal muscle fibres. Several means were used to detect activation of extrafusal fibres: surface electromyogram (e.m.g.) electrodes, tungsten electrodes deeply implanted in the muscle and especially the use of a high-sensitivity tension transducer (0·1 mN) placed on muscle tendons.

5. The activity in fusimotor fibres could be either elicited or modulated under the following conditions: clenching of the fists, pinna twisting, mental computation, voluntary isometric contraction, passive phasic stretch of the muscle, environmental disturbances, subject laughing, the sound of hand clapping, and subject listening to manoeuvre instructions. Moreover, during spontaneous fusimotor fibre activity the subject was able to voluntarily stop the unit discharge.

6. The results are compared to those obtained in animal studies and discussed with reference to the notion of α–γ linkage, static and dynamic γ-motoneurone activities,

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and to other available data concerning the effects of various stimulations on muscle spindle afferent activities in man.

INTRODUCTION

The structure and function of mammalian muscle spindles have been extensively studied, including the activity of fusimotor neurones in anaesthetized and awake animals (see Matthews, 1972, 1981a, b; Murthy, 1978; Laporte, 1979; Boyd, 1981a, b; Prochazka & Hulliger, 1983; Hulliger, 1984).

In humans, using the technique of recording single fibre activity with tungsten micro-electrodes introduced by Hagbarth & Vallbo (1967, 1968a), the sensory discharge from muscle spindles has been investigated during voluntary movement (see Szumski, Burg, Struppler & Velho, 1974; Vallbo, Hagbarth, Torebjork & Wallin, 1979; Burke, 1981; Vedel & Roll, 1983; Prochazka & Hulliger, 1983; Hulliger, 1984). From changes in the afferent spindle discharge as well as muscle tension and electromyography (e.m.g.) activity, the activity in fusimotor neurones has been indirectly assessed. Surprisingly, no information has been published on activity in γ-fusimotor neurones although the microneurographic technique has been used to study activity in sympathetic axons (Burke, Sundlof & Wallin, 1977; Hagbarth, 1979; Vallbo *et al.* 1979) which are considerably smaller.

Since spindle afferent discharge depends not only on muscle length changes and concurrent fusimotor and skeletomotor activity, but also on after-effects of prior fusimotor discharge and stretch (Emonet-Dénand, Hunt & Laporte, 1985a, b) a more direct measure of fusimotor activity would be highly desirable. In the present study, conducted on human subjects, efferent activity has been recorded from axons, some of which were skeletomotor and others of which appeared to be clearly fusimotor. A preliminary report of the results has appeared (Vedel, Roll & Ribot, 1985).

METHODS

Experiments were performed at both laboratories on sixteen healthy human subjects aged 19–30, all of whom had given informed consent to the experimental procedures as required by the Helsinki declaration (1964). The subjects were seated in a comfortable armchair. Their legs were placed in cushioned grooves permitting the maintenance of a stereotyped relaxed position without any muscular activity. The right foot was placed on a stationary plate and the left foot fixed to an electronically driven rotating pedal, the rotation axis of which was centred in front of the ankle joint (Roll & Vedel, 1982). Another mechanical device made it possible to move the toes. Ankle and toe passive and active movements were recorded using linear potentiometers.

Recording procedure

Activity from single nerve fibres was recorded from the lateral peroneal nerve (l.p.n.) of the leg at the level of the popliteal fossae. This superficial nerve was located by tactile exploration and sometimes by transcutaneous electrical stimulation. Single unit recording was performed using insulated tungsten micro-electrodes (Frederick Haer & Co. Brunswick, U.S.A., impedance 300–1000 kΩ at 1000 Hz, tip diameter around 1–8 μm) sterilized with formaldehyde and washed with absolute alcohol before use. The micro-electrode was inserted transcutaneously until the detection of physiological noise induced by various types of sensory stimulations on the pretibial and dorsal side of the foot (pressure on the skin, tendons and muscles, scratching of the skin, joint manipulation) which is innervated by the lateral peroneal nerve. The micro-electrode was then

guided to an appropriate site in the nerve where single unit activity was sought by moving the micro-electrode in minute steps. The electrode was always manipulated manually and left 'free-floating' with no rigid external fixation in order to avoid nerve injury if the subject moved his leg. Micro-electrode recording was continuously monitored on an oscilloscope and a loudspeaker. The band width of the recordings was usually maintained between 300 and 3000 Hz to obtain optimal signal-to-noise ratio.

Considering the microneurography procedure it was never possible to establish a relationship between the spike amplitude and the category of the nerve fibre recorded. Nerve signal voltage apparently strongly depended on the micro-electrode impedance and on its tip localization with regard to the recorded fibre. Moreover, during axonal unitary recording, spike amplitude often changed owing to minute displacement of the electrode consequent on involuntary movements of the subject. Under these conditions it was impossible to consider the nerve impulse amplitude as a criterion permitting us to identify the nature of the recorded fibre. No systematic difference was observed in peak to peak amplitude between skeletomotor and fusimotor impulses.

Control of muscle activity

The activities of the tibialis anterior (t.a.), extensor digitorum longus (e.d.l.) and soleus-gastrocnemius (s.g.) muscles were recorded by e.m.g. surface electrodes. Moreover, in view of the reinforcement manoeuvres used to elicit unitary fibre activation under our experimental conditions and the fact that Hagbarth, Wallin, Burke & Lofstedt (1975b) have demonstrated in connexion with Jendrassik's manoeuvre that 'the manoeuvre had no effect upon the afferent spindle discharge as long as there were no e.m.g. signs of unintentional contraction occurring in the receptor bearing muscle', muscular activity was initially carefully monitored in four experiments on subjects not subjected to microneurography recording (Fig. 1). E.d.l. muscle (two subjects) and t.a. muscle (two subjects) activity was therefore recorded using four insulated tungsten electrodes (diameter 200 μm, tip diameter 10 μm) deeply implanted transcutaneously and evenly spaced along the same muscle. Moreover, a highly sensitive transducer was used, equipped with a subminiature triode RCA 5734 whose plate was linked to an external pin through a flexible diaphragm. The triode was mounted in a mechanical device in which the pin was moved by position changes of a flexible stainless-steel blade, the extremity of which was placed on the t.a. and toe extensor muscle distal tendons at the level of the dorsal side of the ankle. Displacement of the pin which produces an anodic current change of 20 V for 0·5 degree of arc, permitted detection of small variations in torque, down to 0·1 mN, when the tendon tension increased and imposed a presure on the flexible blade. During the reinforcement manoeuvres, including Jendrassik's manoeuvre and fist contraction, the e.m.g. activities of the finger flexor and extensor muscles were also recorded using surface electrodes.

Fig. 1 shows an example of the effects observed in the e.d.l. muscle during various reinforcement manoeuvres; similar results were obtained on the t.a. muscle. As illustrated in Fig. 1, besides the voluntary isometric contraction of the e.d.l., it was observed that the well defined Jendrassik's manoeuvre ('locking the two hands in a firm grip and pulling each other in opposition', Jendrassik, 1883) induced, in three of the four subjects, a slight muscle activation that was detectable both by the deeply implanted electrodes and by the transducer. It should be noted that this muscle activation was not systematically detected by surface electrodes over the t.a. and e.d.l. muscles. Deep e.m.g. activity was never detected at times when the transducer was registering no force output. As can be seen in other recordings, the various reinforcement manoeuvres which were tested on unitary fibre activities, notably strong clenching of the fists, caused no pretibial muscle tension change except for passive plantar flexion of the toes which brought about an e.d.l. muscle stretch producing a brief increase in tension. Such a response also occurred in extensor hallucis longus (e.h.l.). In view of the synergistic function of e.d.l. and e.h.l. muscles, it cannot be excluded that some observations attributed to the e.d.l. in this paper may also concern the e.h.l. muscle.

Head movements in all directions, noise, fast respiratory movements and slight contralateral leg contraction were also tested under the same conditions, and no t.a. or e.d.l. muscle activation was observed. The main aim of these preliminary experiments was to demonstrate that the transducer system was sufficiently sensitive to detect minute muscle tension changes. In our microneurography experimentation, it was the main system adopted to control muscle activity (surface e.m.g. recording was insufficiently reliable), thus avoiding the deep implantation of several e.m.g. electrodes, which is often painful for the subject. Electrophysiological recordings, transducer recordings and signals indicating the onset and offset of the reinforcement manoeuvres were stored
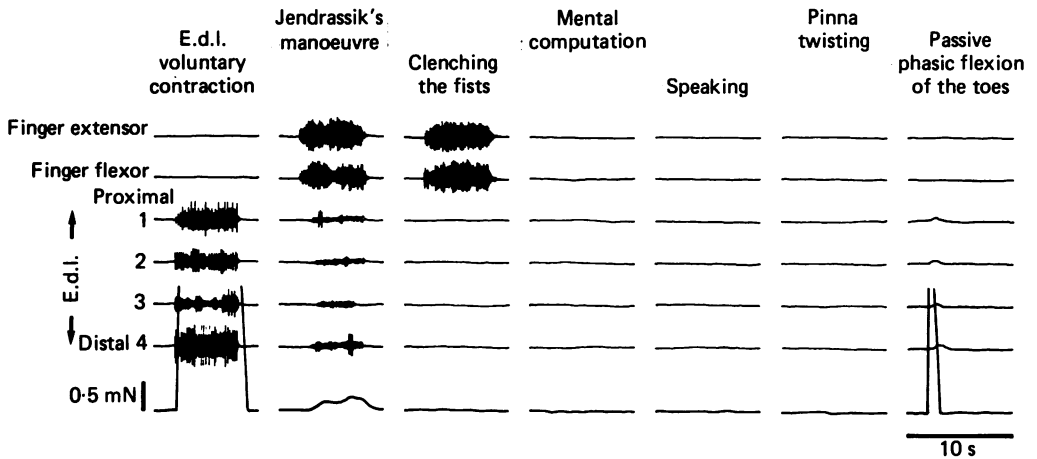
Fig. 1. Control of the possible activation of extensor digitorum longus (e.d.l.) muscle during various mechanical and mental manoeuvres imposed on or performed by a human subject (see text). Finger extensor and flexor muscle activity was recorded by e.m.g. surface electrodes in order to visualize motor reinforcement manoeuvres such as Jendrassik's manoeuvre and clenching of the fists. E.d.l. activity was recorded by four deeply implanted tungsten electrodes evenly spaced along the muscle (1, 2, 3, 4). The muscle tension changes were monitored by a mechanical device equipped with an electronic tube RCA 5734, the plate of which was mobile. This device was applied to the e.d.l. tendons at the level of the ankle or on the dorsal side of the foot. The minimal sensitivity of this transducer was 0·1 mN. Using identical tests, the same results were observed in the tibialis anterior (t.a.) muscle.

on tape during experiments and then filmed on a multibeam oscilloscope. Spike frequency discharge was analysed using an instantaneous frequency meter.

RESULTS

Twelve unitary fibre activities were recorded in the lateral peroneal nerve, all of which were characterized by impulses with a satisfactory signal-to-noise ratio. The usual forms of natural stimulation used to identify afferent fibres: i.e. pressure applied to the skin, tendon, joint and muscle, muscle stretch at low velocity, passive joint movements, response to mechanical vibrations applied to the skin and to the distal tendon of the muscles involved produced no activation or modulation of the discharge of these fibres. The fibres tested were thus identified as efferent units and on the basis of their response to the various reinforcement manoeuvres they were divided into two categories (Table 1) named skeletomotor fibres and fusimotor fibres. Table 1 summarizes the various effects obtained on these two kinds of efferent fibres under the various experimental conditions tested.

Skeletomotor fibres

In relaxed subjects, all six of these fibres were spontaneously silent and none of the peripheral sensory stimulations ever induced their discharge. During electrode manipulation, some of them momentarily (0·5–3 s) discharged at 20–40 impulses s^{-1}. These induced discharges were sometimes related to a painful sensation, probably due to a local spasm of the motor unit, in a small part of the muscle, and local muscle

contractions were visible in some cases on the muscle surface. The sensation generally disappeared when the fibre stopped firing. These observations suggest that this kind of unit was a skeletomotor fibre: this possibility was further investigated by asking the subject periodically to perform slight isometric contractions of the e.d.l. or t.a. muscles. This manoeuvre also made it possible to identify the muscle innervated by the recorded fibre. Five of these units (three e.d.l., two t.a.) fired during the entire

TABLE 1. Responses of twelve efferent fibres recorded to various reinforcement manoeuvres

	Skeletomotor fibres						Fusimotor fibres					
	1	2	3	4	5	6	1	2	3	4	5	6
Spontaneous activity	−	−	−	−	−	−	+	+	+	+	+	+
Jendrassik's manoeuvre	+	0	+	+	−	0	0	0	0	0	0	0
Clenching of the fists	−	−	−	−	0	0	+	+	+	+	0	+
Mental computation	−	0	0	−	−	0	+	+	0	+	0	+
Pinna twisting	0	−	0	0	−	−	+	+	0	0	+	0
Sound of hand clapping	−	0	−	0	0	−	+	+	0	0	0	+
Phasic muscle stretch	0	−	−	0	0	0	+	+	+	+	0	0
Tonic vibration reflex	0	+	+	+	−	0	−	−	0	0	+	−
Isometric muscle contraction (e.d.l.)	+	+	+	0	−	0	+	+	+	−	−	0
Isometric muscle contraction (t.a.)	−	−	−	+	−	+	−	0	−	−	+	+
Isotonic muscle contraction (e.d.l.)	0	+	+	0	0	0	+	0	0	+	0	0
Isotonic muscle contraction (t.a.)	−	0	−	0	+	+	0	0	0	0	0	0
Subject laughing	0	−	0	−	0	−	+	0	0	+	0	+
Subject speaking	−	−	0	−	0	0	+	0	+	+	0	0
Environment changes	−	−	0	0	−	0	+	+	0	0	+	+
Voluntary stopping of fibre activity	0	0	0	0	0	0	+	+	0	0	0	0
Muscle innervated	e.d.l.	e.d.l.	e.d.l.	t.a.	t.a.	t.a.	e.d.l.	e.d.l.	e.d.l.	e.d.l.	t.a.	t.a.

+ = positive response, − = no response, 0 = manoeuvre not tested.
E.d.l., extensor digitorum longus muscle; t.a., tibialis anterior muscle.

duration of the voluntary isometric contraction recorded by surface electrodes and transducer (three of them, two e.d.l., one t.a., also being activated during isotonic contraction). This activity began after a variable latency in relation to the onset of the overall e.m.g. burst, and generally stopped immediately when the subject was requested to relax (Fig. 2A). The discharge frequency increased with the degree of contraction but never exceeded 5–10 impulses s^{-1}. One of the units was never activated by isometric contraction. It should be noted that the torque involved in the contractions performed by the subject was always limited to avoid recording disturbance resulting from micro-electrode displacement. In this connexion it might be suggested that the unit remaining silent under slight isometric contraction had a higher threshold of activation, since it was observed to discharge only during isotonic contraction of the t.a. muscle, which caused loss of the units when repeating the manoeuvre. Three of the units (two e.d.l., one t.a.) firing during isometric

contraction were also activated by mechanical vibrations of small amplitude (0·2–0·5 mm peak-to-peak, 70–80 Hz) applied to the distal tendon of their muscles. This type of activation occurred only when tendon stimulation induced the tonic vibration reflex (t.v.r.) through a sustained discharge of the Ia muscle spindle afferents (Hagbarth & Eklund, 1966; Eklund, 1972; Roll, Gilhodes & Tardy-Gervet, 1980) (Fig. 2B).
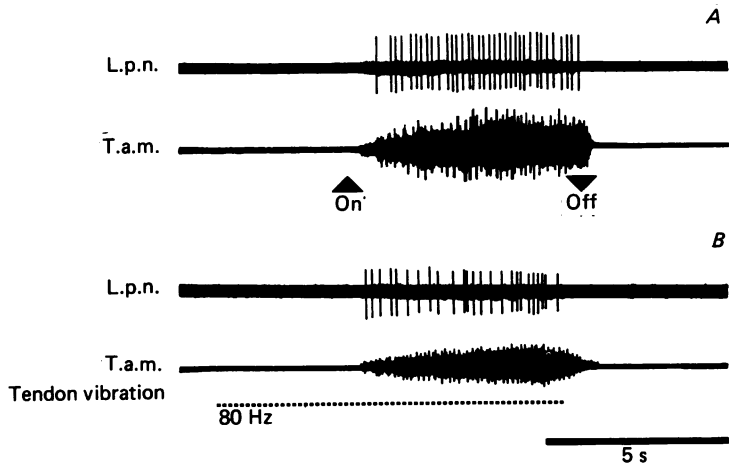

Fig. 2. Modulation of the activity of two skeletomotor fibres recorded in different subjects during voluntary (A) and reflex (B) t.a. muscle isometric contraction. Skeletomotor unit discharge and t.a. muscle activity (surface e.m.g. electrodes) were recorded simultaneously. A, skeletomotor fibre activation (mean firing rate: 7 impulses s⁻¹) during voluntary isometric contraction of t.a. muscle. B, skeletomotor unit activation (mean firing rate: 5 impulses s⁻¹) during tendon vibration (80 Hz) of the t.a. muscle. Under this condition, t.a. contraction was induced when the vibrations triggered the tonic vibration reflex (t.v.r.). L.p.n.: lateral peroneal nerve; t.a.m.: tibialis anterior muscle. The dotted line symbolizes the occurrence of tendon vibration (spikes were retouched). L.p.n. signal calibration (vertical bars): 100 μV.

Skeletomotor fibres were also subjected to various reinforcement manoeuvres chosen to test the activation modalities of the efferent units. Three units (two e.d.l., one t.a.) were slightly activated by the classical Jendrassik's manoeuvre (discharge frequency 2–6 impulses s⁻¹. All other stimulations such as clenching of the fists, mental computation, pinna twisting, head movements, noise, stimulation of the skin covering the muscle, and hand clapping had no effect on any of the skeletomotor fibres recorded.

Fusimotor fibres

The other six fibres recorded were assigned to a different category from the previous one because they all showed a conspicuous spontaneous discharge (5–20 impulses s⁻¹) in completely relaxed subjects. Here the spontaneous discharge fluctuated from time to time, sometimes stopping momentarily and then firing again for a long period although the subject was still relaxed and the environment relatively quiet and steady in terms of mental stimulation (Fig. 3A). This spontaneous discharge was never related to the e.d.l. or t.a. muscle activity monitored by e.m.g. surface electrodes and particularly by the high-sensitivity transducer described in the Methods. None of the

peripheral sensory manipulations used to identify cutaneous, tendon and muscle afferents ever caused a change in their discharge pattern, suggesting that they were also efferent units.

Various manoeuvres were then made in order to test this assumption. On the six fibres tested, four yielded only partial information about their modalities of activation because their recording time was short (10–20 min). The two others were recorded during more than one hour, so that it was possible to test several times all the various reinforcement manoeuvres likely to activate the fusimotor system.

When the subject was asked to perform a particular task although he was required to rest and remain relaxed, the verbal description of the task usually caused a variable enhancement of the discharge frequency of the unit recorded which was probably related to change of the subject's attention (Fig. 3*C*). The starting signal was given only when the unit activity was stable (or nil). No difference in the fibre discharge modulation was observed whether or not the subject received feedback information about the unitary activity provided by a loudspeaker and an oscilloscope.

(1) Excluding the Jendrassik's manoeuvre, which frequently triggered muscle activity (Fig. 1), a motor reinforcement manoeuvre was performed in which the subject, whose forearms were lying comfortably on the arms of the armchair, was asked to strongly clench both fists. When the starting signal was given, fist clenching elicited a tonic activation of the fusimotor fibres after a short latency (Fig. 3*B*) without any t.a. or e.d.l. muscle tension change. This activation persisted throughout the duration of the manoeuvre and generally continued for several seconds after the instruction to stop was given and forearm e.m.g. activity disappeared. This kind of manoeuvre had very conspicuous effects on all the units tested. Under these conditions, the discharge frequency of the units increased to 15–25 impluses s^{-1} at the beginning of the stimulation and then decreased progressively, ceasing only after the signal to stop.

(2) Mental computation (for example: addition of all the odd numbers from 34 to 72) was also a very efficient means to modulate fusimotor activity. This manoeuvre was tested on four of the six units recorded. In this case, providing verbal instructions to the subject always produced an increase of the unit discharge. After the starting signal, the latency of the unit discharge facilitation was very variable (sometimes several seconds). Both inter-trial and inter-subject variability were observed. Discharge frequency under these conditions often reached a lower value than during other manoeuvres and was found to be somewhat variable but never stopped during the mental computation. At the stopping signal, the activity progressively decreased, but increased again when the experimenter asked the subject to give the result. Fig. 3*C* and *D* illustrate on one e.d.l. unit activity the effect of mental computation.

(3) As previously demonstrated by Granit, Job & Kaada (1952) in animals, pinna twisting was also able vigorously to excite the fusimotor neurones (Fig. 3*E*). This effect, called 'pinna reflex' by Granit *et al.* (1952), was obtained without any muscle activation. The increase in fusimotor discharge frequency began either immediately or after a short latency, continued as long as stimulation was maintained and generally persisted several seconds after pinna twisting stopped.

(4) In addition to these three reinforcement manoeuvres, fusimotor fibre activation was also observed in various situations such as hand clapping behind the subject's
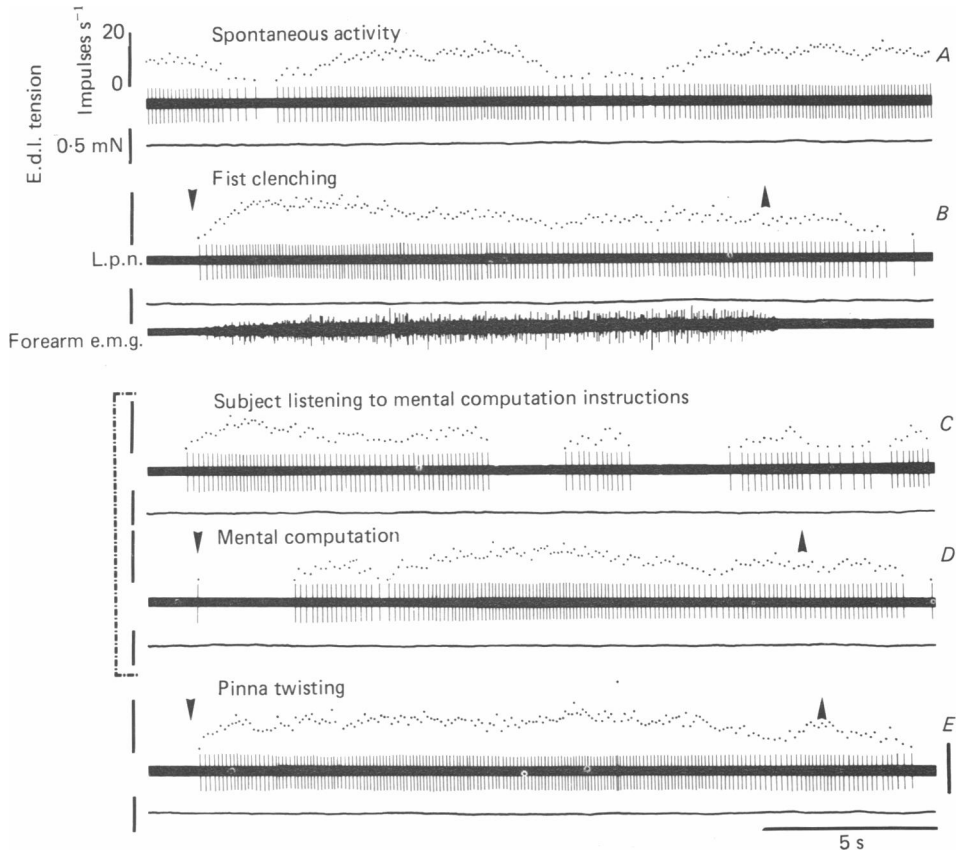
Fig. 3. Modulation of the discharge of a fusimotor fibre innervating the e.d.l. muscle, caused by various reinforcement manoeuvres. Instantaneous frequency curve (upper recording), unitary discharge (l.p.n.; medial recording), muscle tension transducer (lower recording) and occasionally e.m.g. activity were simultaneously recorded. Modulation of the unit discharge frequency was successively observed during spontaneous discharge (A), clenching of the fists (B), subject listening to the mental computation instructions (C), mental computation (D) and pinna twisting (E). The maximal discharge frequency observed during spontaneous activity and the various manoeuvres fluctuated from 10 to 18 impulses s^{-1}. (Spikes were retouched.) L.p.n. signal calibration (vertical bar in E): 150 μV.

head (Fig. 5A), subject laughing (Fig. 5D), subject speaking and changes in environmental conditions, such as a person entering the experimental room. Discharge frequency of the fusimotor fibres in these situations was very variable but never exceeded the values obtained in the previous reinforcement manoeuvres. In fact, none of the activating processes ever elicited a firing rate higher than the maximum spontaneous discharge of these fusimotor fibres.

(5) With regard to motor and reflex effects, five of the six fusimotor units studied were activated during slight isometric muscle contraction. It was thus possible to identify the location of the muscle spindle supplied by each fibre: three were found to supply the e.d.l. muscle responding to its selective isometric contraction, and the other two were attributed to the t.a. muscle. The sixth unit recorded was also related to the e.d.l. muscle but only responded to isotonic contraction (Fig. 4D).

The activity of only one fusimotor fibre began regularly to increase before muscle contraction (e.d.l., Fig. 4*A*), one fired poorly under the same condition (Fig. 5*B*), and the discharge of three other fibres (two e.d.l., one t.a.) (Fig. 4*C–D*) increased after the skeletomotor fibre activation, sometimes with a latency of several seconds. At the end of the contraction, fusimotor discharge stopped immediately or persisted for only a short time.
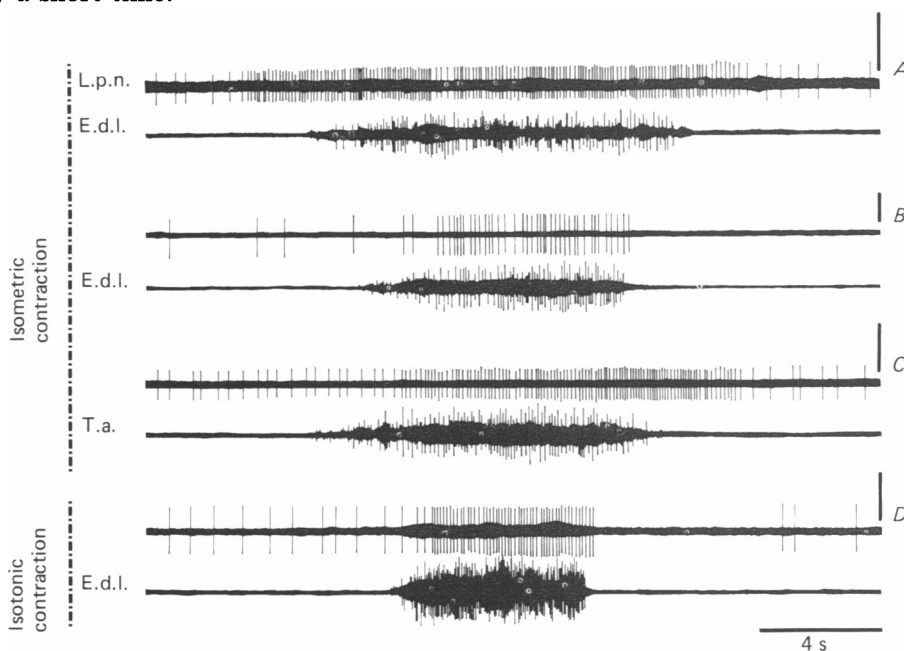

Fig. 4. Temporal relation between the γ-fibre and α-fibre discharge during isometric (*A*, *B*, *C*) and isotonic (*D*) muscle contractions. The four examples were obtained in different subjects. Only the first recording shows a γ-fibre activity clearly preceding the occurrence of the e.m.g. burst. (Spikes were retouched.) L.p.n. signal calibration (vertical bars): 100 μV.

Since the existence of an autogenetic excitation of the motoneurones by the Ia sensory fibres of its own muscle has been confirmed by various authors (Ellaway & Trott, 1976, 1978; Ellaway, Pascoe & Trott, 1976; Appelberg, Hulliger, Johansson & Sojka, 1983), reflex activation of the recorded human fusimotor fibres was tested using muscle tendon vibration. No activation was obtained under these conditions, only in one unit did activity (t.a.) increase slightly when vibration induced a tonic vibration reflex. Nevertheless, noticeable selective activation of four fusimotor fibres was observed (three identified as e.d.l. units, and one responding only to the e.d.l. isotonic contraction) when a brief e.d.l. muscle stretch was induced by phasic plantar flexion of the toes (Fig. 5*C*). In all four cases the increase in the discharge frequency persisted for a long time after the end of phasic stimulation (5–20 s). The two units innervating the t.a. muscle could not be submitted to the phasic reflex test. This failure resulted from the displacement of the electrode during this manoeuvre causing the loss of the fibre. Trials involving t.a. tendon percussion did not produce any activation of these two units.

(6) In two experiments, subjects were asked during spontaneous firing of e.d.l. fusimotor fibres to try to stop the unit discharge by entering a state of deep mental and somatic relaxation. During this test, subjects received feed-back information concerning their own fibre activity, which was provided by an oscilloscope and a
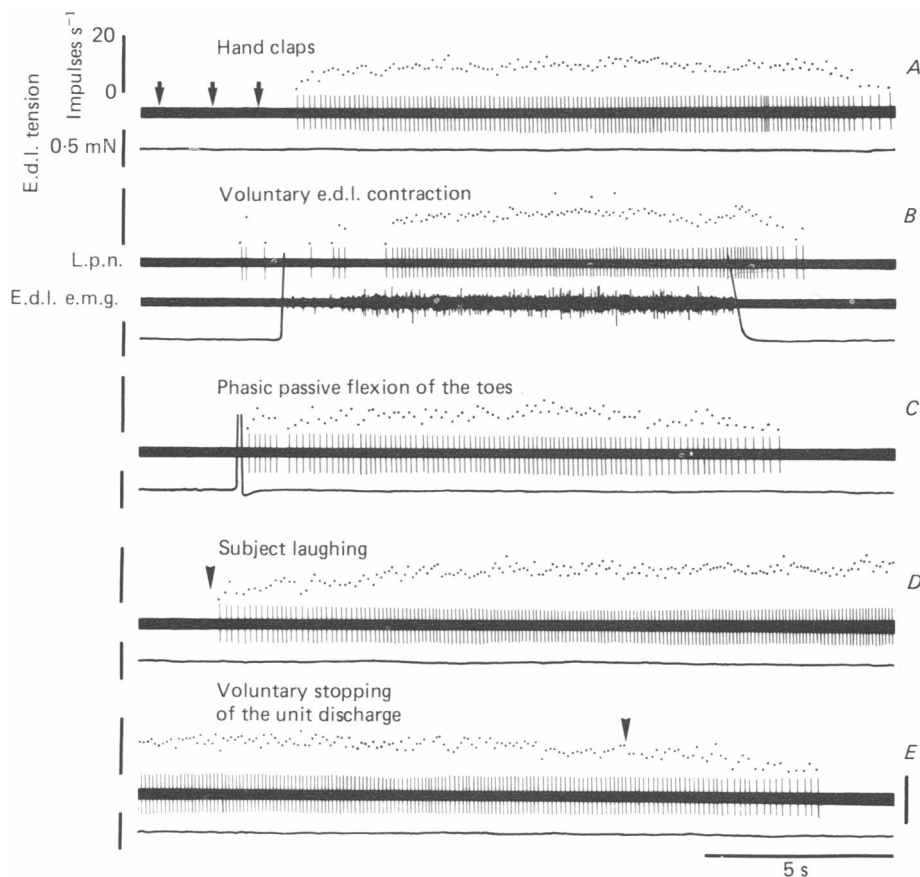

Fig. 5. Modulation of the same fusimotor fibre activity as in Fig. 3 but under different experimental conditions. Activation of unit discharge frequency (maximal discharge frequency: 8–18 impulses s^{-1}) by hand clapping (*A*), during voluntary isometric e.d.l. muscle contraction (*B*), passive plantar flexion of the toes (*C*), subject laughing (*D*), and during voluntary control by the subject of the fibre discharge causing its activity to stop (*E*). (Spikes were retouched.) L.p.n. signal calibration (vertical bar in *E*): 150 μV.

loudspeaker. After several trials, one subject consistently succeeded in achieving this state, completely silencing fusimotor activity with a relatively short latency (Fig. 5*E*). The other subject succeeded only in decreasing the firing rate.

(7) Finally, various other reinforcement manoeuvres known to activate γ-motoneurones in animals (see Hagbarth, 1952; Granit *et al.* 1952; Hulliger, 1984) never modified the human fusimotor fibre activity (pressure on the eye bulb, pinching or scratching of the skin covering the e.d.l. and t.a. muscles, moving the head and slightly contracting the contralateral leg).

Methodological considerations

The present study deals with the recorded activity from twelve efferent units. This may appear to be a limited pool of neurones although five years has passed since we first recorded efferent activity. The reason why the activity of these fibres was so difficult to record in man with the microneurography method could be either that the muscular efferent fibre bundles are difficult to reach with a micro-electrode (e.g. they may be located on the posterior side of the nerve), or that the efferent fibres are not arranged in bundles as are the sensory units and so they mingle with the afferent fibres. It should be noted that the recordings of efferent activities reported here have mainly been made by chance and we are still unable to describe any systematic method for locating such fibres.

The activities recorded from the twelve single axons are considered to be efferent discharges because of the total lack of response to natural sensory stimulation. In particular the possibility that some of them, mainly activated by muscle contraction, could be Golgi tendon organ afferents was excluded because of the lack of response to stimuli which normally excite these receptors such as large amplitude muscle stretch and strong pressure applied on muscle and tendon (Burke, Hagbarth, Lofstedt & Wallin, 1976*a*, *b*; Vallbo *et al.* 1979; Vedel & Roll, 1983).

Six of the recorded unitary discharges were considered to be skeletomotor fibres mainly because of the increased activity recorded during voluntary and reflex isometric contraction (t.v.r.) and the lack of spontaneous discharge in relaxed subjects. It is possible that among the skeletomotor fibres we have observed, some were β-fibres, i.e. skeleto-fusimotor fibres, but our experimental conditions provide no evidence on this point.

The main purpose of this study was to demonstrate that the six other unitary activities recorded could be ascribed to fusimotor fibres. Their distinction from the skeletomotor fibres was mainly based on the existence of spontaneous activity and on the increase in discharge produced by various reinforcement manoeuvres, both observed without any concomitant muscle contraction. Another important point was to distinguish the fusimotor activity from that of sympathetic fibres which were the only efferents previously recorded and which were often activated by similar reinforcement manoeuvres (Delius, Hagbarth, Hongell & Wallin, 1972*a*; Normell & Wallin, 1974). The first argument in favour of identifying these units as fusimotor fibres is the relatively large size of the unitary nerve impulses recorded. Indeed, Vallbo *et al.* (1979) have reported that in most of their experiments the C fibre firing was characterized by mass activity and only occasionally by discharge of single small-amplitude units (Hallin & Torebjork, 1970, 1974). Moreover, the authors specify that 'in muscle nerve fascicles the resting activity of the sympathetic fibres is characterized in man by fairly regular pulse-synchronous bursts of impulses, sometimes occurring in short sequences separated by periods of neural silence, sometimes in more staccato patterns' (Hagbarth & Vallbo, 1968*b*; Delius, Hagbarth, Hongell & Wallin, 1972*b*; Sundlof & Wallin, 1977). The spontaneous efferent activities recorded in our experiments never manifested such patterns of discharge. Confusion with β-fibres might be possible during isometric contraction, but the fact that the same unitary

discharge was elicited by other manoeuvres, even when there was no concomitant muscular activity, rules out this possibility.

Functional considerations

In the light of the present results, it is interesting to consider certain data and hypotheses relating to fusimotor fibre properties and functions in man.

In our experiments, it was impossible to determine whether the skeletomotor axons were from α- or β-motoneurones. Since the isometric contraction associated with a discharge was weak, it can be suggested that tonic α-motoneurones and some β-motoneurones, the dynamic ones, may have been detected. This would be consistent with the 'size principle' put forward by Henneman and his collaborators (Henneman, Somjen & Carpenter, 1965 a, b) and the studies on animals demonstrating that the 'slow' spinal motoneurones are recruited first when muscles contract (Eccles, Phillips & Wu, 1968; Burke & Edgerton, 1975).

With regard to the γ-motoneurone activity, its occurrence and the modulation of its discharge were only inferred indirectly in previous studies on man where variations in muscle spindle sensory discharge were recorded. Recording of the activity of fusimotor fibres gives more direct answers to several questions.

(a) *Are skeletomotor fibres and fusimotor fibres coactivated or independent?* It has recently been demonstrated (Taylor & Appenteg, 1981; Prochazka & Wand, 1981; Appenteng, Hulliger, Prochazka & Zangger, 1983) that in anaesthetized as well as in freely moving cats, strict α–γ linkage does not necessarily occur during all motor activities. In man, the possibility of α–γ independence has also been suggested (Vallbo & Hulliger, 1979, 1981; Burke, McKeon & Westerman, 1980 a; Burke, McKeon, Skuse & Westerman, 1980 b). Our observations do not provide any evidence on the possibility that such α–γ independence occurs during movement, but show that in the relaxed and awake subject, selective activation of fusimotor fibres occurs spontaneously or can be induced. This observation supports the view that α–γ independence can occur under some behavioural conditions.

(b) *Skeletomotor fibre–fusimotor fibre coactivation: difference in onset time.* With regard to the difference in onset time between skeletomotor and fusimotor activation, Vallbo (1971) observed at the onset of a voluntary isometric contraction, 'that, at best, the fusimotor neurones were activated at the same time, but not before α-motoneurones were'. This suggestion, extrapolated from observations of spindle afferent activity, has also been put forward by other authors (Hagbarth, Wallin & Lofstedt, 1975 a; Hagbarth, Wallin, Burke & Lofstedt, 1975 b; Burke & Eklund, 1977; Burke, Hagbarth & Lofstedt, 1978 a, b), and is confirmed by our more direct results, since under similar experimental conditions, only one of six fusimotor fibres fired before the onset of the e.m.g. burst. In this case our observations on the temporal relations between α and γ discharge do not seem to comply with the motor fibre recruitment law (the size principle) established by Henneman and his collaborators (Henneman *et al.* 1965 a, b; Henneman & Mendel, 1981).

(c) *Does muscle-spindle primary-ending activation during contraction involve skeleto-fusimotor fibres or γ-fusimotor fibres?* The consistent increase in the spindle afferent activity which occurs during isometric contraction has been extensively studied by numerous authors (Vallbo, 1970, 1971, 1973, 1974; Hagbarth *et al.* 1975 a; Burg,

Szumski, Struppler & Velho, 1976; Burke *et al.* 1976*b*, 1978*b*, *c*, 1979, 1980*a*, *b*; Vedel & Roll, 1983). Although this effect demonstrates the occurrence of fusimotor action, it does not indicate whether this spindle sensory activation is attributable to slow-conducting dynamic β-skeleto-fusimotor neurones or to γ-motoneurones. Although our results demonstrate the occurrence of γ-activation during weak isometric contraction, showing that γ-motoneurones can produce spindle afferent activation in this condition, it is nevertheless possible that this effect may also be due to dynamic β-motoneurone activity. Coactivation of dynamic γ-motoneurones and dynamic β-motoneurones during voluntary contraction, responsible for the I a discharge increase, is in agreement with the observations of Buke *et al.* (1979; see Prochazka & Hulliger, 1983) during experiments of nerve pressure-block in awake human subjects.

(*d*) *Are static or dynamic fusimotor axons activated in relaxed human subjects?* The similarity of fusimotor firing patterns observed during various manoeuvres in the present study suggests that the recorded activity resulted from the same kind of unit, probably dynamic γ-motoneurones. In support of this argument is the fact that when the same tests were applied to twenty fibres identified as I a afferent fibres, none of these exhibited an increase of firing rate (J. P. Vedel & J. P. Roll, unpublished data). Since I a fibre tonic discharge is increased to a greater extent by γ-static neurones than by the γ-dynamic neurones (Crowe & Matthews, 1964; Brown & Matthews, 1966) one would have expected tonic activation of spindle afferents if the reinforcement manoeuvres activated static fusimotor fibres. The lack of spindle afferent static activation in our experiments might be attributable to the fact that dynamic γ-motoneurones selectively innervate the bag$_1$ intrafusal muscle fibre (Boyd, Gladden, McWilliam & Ward, 1977; Laporte, 1978) which contracts almost without shortening, unlike the bag$_2$ and chain intrafusal muscle fibres which shorten considerably during static γ-stimulation (Boyd, 1980, 1981*a*, *b*; Boyd, Gladden & Ward, 1981). Hence, it may be suggested that this quasi-isometric intrafusal contraction acting only on the bag$_1$ spiral ending of the I a fibre may not suffice, under our experimental conditions, to increase the primary ending static discharge since the latter seems to be mainly attributable to the I a spiral endings located on the bag$_2$ and chain fibres.

Although the above considerations provide support for our hypothesis concerning the selective activity of dynamic γ-motoneurones in relaxed human subjects, they do not provide final confirmation. A strong argument would be provided if a significant increase could be observed in primary ending dynamic sensitivity using the same reinforcement manoeuvres as for the fusimotor fibres in our experiments. Unfortunately, only negative results on dynamic sensitivity modulation in relaxed human subjects have been reported. For example, complete block of the peroneal nerve produced by anaesthesia (Burke *et al.* 1976*b*) or pressure (Burke *et al.* 1979; Burke, 1981) has no effect on the response of the primary endings to muscle stretch, tendon percussion and vibration (Vallbo, 1974; Burke *et al.* 1979).

Indirect confirmation of our findings and deductions may be found in previous studies on the human monosynaptic spinal reflex (Paillard, 1955, 1959) comparing its amplitude variation when it is elicited by electrical nerve stimulation (Hoffmann's 'H' reflex, Hoffmann, 1952) or by tendon percussion (tendon jerk reflex, 'T' reflex).

With this method it has been clearly demonstrated that T reflex amplitude can be selectively increased, without H reflex change, by reinforcement manoeuvres similar to those used in our microneurography experiments: e.g. loud sounds, fist clenching and mental computation. Since T reflex amplitude is determined by the level of the dynamic sensitivity of spindle primary endings, it can now be suggested that its increase might result from specific activation of the dynamic γ-motoneurones. From these observations, Paillard (1955, 1959) had already deduced that in relaxed human subjects, modification of the spindle dynamic reactivity could result from changes in the 'intrafusal myofibril stiffness' without increase in the receptor spontaneous discharge.

(e) *The possible role of static fusimotor fibres.* All the above functional interpretations imply the assumption that under our experimental conditions no activation of the static fusimotor fibres occurred. This seems difficult to justify at first sight, since the manoeuvres performed by the subjects involved both voluntary muscle activity and mental and physiological processes that are known to produce a general activation of motor systems. Absence of spontaneous firing of static fusimotor fibres in the absence of muscle activity could however explain why muscle spindle primary endings are often silent at short or intermediate muscle lengths in relaxed human subjects (Vallbo, 1981; Hulliger, 1984).

Similarly, a failure of reinforcement manoeuvres to cause static fusimotor fibre facilitation could also explain the lack of static activation of muscle spindle primary and secondary endings that we have consistently observed in unpublished experiments. It can therefore be suggested that static γ-fusimotor fibre activation may mainly occur during muscle activity. Concomitant activation of static γ-motoneurones and β-skeleto-fusimotor fibres would explain the clear-cut enhancement of the primary ending tonic discharge (30 impulses s^{-1}, Vallbo, 1974) during voluntary isometric contraction. So it cannot be excluded that among the skeletomotor fibres recorded some were in fact static γ-motoneurones.

(f) *Fusimotor fibre reflex activation.* Phasic plantar flexion of the toes was the only peripheral manoeuvre investigated which caused activation of the e.d.l. fusimotor fibres. This effect might be due to the autogenetic reflex of γ-motoneurones which has now been firmly established (Fromm & Noth, 1974, 1976; Fromm, Haase & Noth, 1974; Trott, 1976; Ellaway *et al.* 1976; Bessou, Joffroy, Montoya & Pagès, 1984). Phasic flexion of the toes indeed elicits a brief e.d.l. muscle stretch, mainly activating the I a fibres in a phasic burst, which is a prerequisite for γ-motoneurone autogenetic reflex activation (Lundberg & Winsbury, 1960; Stuart, Mosher, Gerlach & Reinking, 1970). Furthermore, the long duration of the increase in the fusimotor discharge characterizing this reflex effect in our experiments could suggest a reflex action occurring through polysynaptic pathways as demonstrated by animal experiments (Murthy, 1978).

In conclusion, although we successfully recorded from twelve efferent fibres in man, our investigation has yielded mainly qualitative data. We are now attempting to develop a method for locating efferent nerve bundles which consists in applying electrical pulses through the micro-electrodes. Presumably, greater experimental efficiency would allow a more quantitative study of the functional properties of the

fusimotor fibres in man. It would also allow investigation of their role in a wider variety of voluntary motor tasks in order to disclose the involvement of these fibres in the preparation for movement and its regulation.

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