Physiological characterization of motor unit properties in intact cats

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Single motor units were isolated in intact cats, by microstimulation through chronically implanted microwires in the L5 ventral roots. Motor unit axonal and mechanical properties were obtained by stimulus-triggered averaging the signals from an implanted femoral nerve recording cuff and patellar tendon force transducer. All unit types were sampled with this technique, and it was also possible to stimulate in isolation an axon whose ventral root spike was recorded during treadmill locomotion. A new technique was described, spike-triggered microstimulation, for verifying the identity of a stimulated and a recorded axon.

Introduction

The motor units of a number of cat hindlimb muscles can be classified into 3 major categories on the basis of their physiological properties. Each unit class is solely composed of 1 of the 3 histochemically identifiable muscle fiber types (for review see Burke, 1981). Recently, it has become possible to record the discharge and axonal conduction velocity of single hindlimb motor units in freely walking cats (Hoffer et al., 1979, 1980, 1981a, b). The present work was performed to determine whether the contractile characteristics of the innervated unit could be measured also, by extending to the intact animal those techniques developed to characterize units in anesthetized preparations. In addition, we describe a new technique, spike-triggered microstimulation, for verifying the identity of a stimulated and recorded axon.

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Materials and Methods

The methods for characterizing single motor units in the intact cat are based on those developed by Burke and his collaborators in the anesthetized cat (Burke et al., 1973). According to this scheme, units can be segregated into types by comparing their isometric myograms in response to controlled electrical stimulation. Specifically, units are distinguished into slow twitch (type S) or fast twitch (type F) depending on whether they exhibit ‘sag’ in an unfused tetanus at a stimulation frequency with an interpulse period approximately 1.25 × the unit’s contraction time. Type F units display sag, type S do not. The F category can be further subdivided into 2 classes by employing a fatigue test, in which units are tetanized repetitively at 40 Hz for 330 ms, once/s, for 2 min. The fatigue index is defined as the ratio of the tetanic tension of the hundred-and-twentieth contraction to the first. Units with fatigue indices > 0.75 are designated FR, (fatigue resistant). Those with fatigue indices < 0.25 are designated FF (fatigable). A small number of intermediate units exist and are designated F (int). All type S units have a fatigue index > 0.75. For further details see Burke et al. (1973).

To achieve a similar characterization in the intact animal we implanted a tendon force gauge (Walmsley et al., 1978) in cats that had also been implanted with EMG electrodes, and ventral root microelectrodes to record single motor unit discharges (Hoffer et al., 1981b). Single motor units were stimulated through the implanted ventral root wires and their mechanical responses recorded with the implanted gauge, as described below.

Device implantation and single unit recording

The ventral roots (L5VR) of adult cats were implanted with up to 12 microwires, under aseptic conditions during Nembutal anaesthesia, as described previously (Hoffer et al., 1981b). The electrodes consisted of 50 μM platinum 90%-iridium 10% wire insulated with 12 μM of Pyre-TML (Polymide, California Fine Wire) and 15 μM of Parylene-C (Loeb et al., 1977), and cut off obliquely. These were pushed into the ventral root which had been exposed by a small laminotomy. In some animals the ventral root electrodes were of a modified ‘hatpin’ design (Salcman and Bak, 1976). These consisted of a short length of obliquely cut iridium wire (37.5–50 μM diameter) welded to a flexible gold wire (diameter 37.5 μM) and insulated (see Fig. 1C). A silastic recording cuff (Hoffer et al., 1981a) was implanted around the femoral nerve, which contains all the motor axons that supply the 5 anterior thigh muscles. This group of muscles includes the vastus intermedius (VI), vastus lateralis (VL), vastus medialis (VM), rectus femoris (RF) and sartorius (SA). Each of these muscles was implanted with a bipolar EMG electrode. These electrodes were constructed by twisting two platinum–iridium wires (multistrand, Teflon-coated, from which the insulation had been removed by flaming at multiple alternating sites) around a Silastic tube (0.5 mm o.d.) as illustrated in Fig. 1. This design was chosen to maximize sampling within the muscle to enhance detection of single unit EMG potentials.
Fig. 1. A: diagrammatic representation of the chronically implanted devices used for the recording and stimulation single motor units in intact cats. For simplicity only 3 ventral root 'hatpin' electrodes are shown inserted into the ventral roots. The neural cuff consisted of 5 circumferential electrodes mounted inside a Silastic tube. The central and outer electrodes shorted together acted as the indifferent (FI) for two tripolar differential sets centered around the proximal (FP) and distal (FD) electrodes. (Separation D = 11.5–15 mm). Also illustrated is one bipolar EMG electrode and the strain gauge (see text for further details). B: photograph of the implanted strain gauge and retaining bar. C: schematic view of a 'hatpin' electrode implanted in the ventral roots.

All of the anterior thigh muscles, with the exception of the medial portion of sartorius, insert onto the patella. Force in the patellar ligament was recorded using an implanted strain gauge, which consisted of an E-shaped stainless-steel substrate (1–5 mm thick) with a semiconductor strain gauge element (BLH, SR-4 type SPB1-12-35) bonded to each side. The assembled device was insulated and moisture-proofed with a conformal coating of Parylene-C (15–30 μM) after lead attachment (Fig. 1B). The gauge was implanted so that the ligament lay over the central arm and under the 2 outer arms of the E (see Fig. 1A). A retaining bar was sewn onto the gauge through holes in the ends of its arms. Gauges were calibrated in
situ in a terminal experiment. The gauge elements formed part of a Wheatstone bridge whose output was differentially amplified. Further details of construction and performance of this type of gauge can be found elsewhere (Walmsley et al., 1978). The leads from the various devices and the microelectrodes were soldered to a connector on the animal's back. The microelectrode wires were connected to the inputs of 12 single-ended FET amplifiers (Bak Electronics MMRS-IP) mounted on the connector. Microelectrode signals were amplified with a 1–10 kHz bandwidth, EMG signals with a 0.05–5 kHz bandwidth.

Conduction velocity was measured by averaging the signal from a Silastic recording cuff around the femoral nerve, using either electrical stimulation or recorded spikes as the trigger. In early experiments the conduction velocity was obtained by dividing the estimated distance from the recording or stimulating electrode to the active cuff electrode, by the latency from the stimulus or the negative peak of the ventral root spike, to the peak negative phase of the averaged cuff spike. However, this method can be subject to errors in the estimation of conduction distance, and for stimulated units there is an undetermined stimulus utilization time prior to spike initiation in the axon. Therefore, in later animals we implanted a longer cuff with 2 active electrodes, separated by up to 15 mm (see Fig. 1). The enabled conduction velocity to be estimated by dividing the known electrode separation (D in Fig. 1) by the latency difference of the 2 averaged spikes at each electrode, with an estimated error of $\pm 5\%$ (Hoffer et al., 1981a).

Microstimulation of single motor axons

Microstimulation through the ventral root electrodes was generally performed under light Nembutal anesthesia. This was necessary to reduce the background level of EMG in the various muscles to allow identification of single unit potentials. The implanted limb was positioned with the knee and hip angles at 90°, with the animal lying on its side on a heated pad. Constant voltage monophasic or negative–positive biphasic pulses (50–100 $\mu$s) were delivered through the ventral root electrodes, either cathodally or anodally with reference to an indifferent electrode implanted in the animal's back. The stimulator triggered on oscilloscope that displayed the EMG signals from the 5 muscles together with patellar ligament force. The lowest threshold responses were usually obtained with stimulus strengths at $< 1$ V for 50 $\mu$s (typically into a 100–300 k$\Omega$ electrode as measured at 1 kHz). When constant current stimulation of similar duration was used, threshold responses were obtained with currents of 5–10 $\mu$A. Floating microelectrodes of either design (hatpin or microwires) appeared to drift very slowly through the tissue; frequently, microstimulation tended to recruit the same motor units in reproducible order for several consecutive days.

Criteria for single unit activation

In response to increasing stimulus voltage, the evoked EMG responses incremented in an all-or-none manner. Often the earliest response was confined to a
single muscle and was constant over a substantial range of stimulus voltage. Further increases in voltage resulted in stepwise increments of EMG in either the same or other muscles (see Fig. 2). Responses were regarded as unitary if they fulfilled conventional criteria as reported in previous studies of single unit microstimulation (Taylor and Stephens, 1976; Garnett et al., 1979). These included recruitment of the EMG potential in an all-or-none manner, constancy of waveform during high

1. EMG Responses to Ventral Root Microstimulation

A. (2.13 V)

B. (2.41 V)

2. Femoral Neurogram

3. Patellar Force

Fig. 2. 1A: EMG responses in the 5 anterior thigh muscles (see text for abbreviations) to ventral root microstimulation just (2.13 V) suhreshold stimulation for the rectus femoris (RF) unit whose all-or-none response to threshold stimulation (2.41 V) is shown in panel 1B. Records are the superimposition of several sweeps. The stimulus-triggered, averaged femoral neurogram (512 sweeps) with the stimulus set just above threshold for the RF unit is shown in 2B. With the stimulus reduced to just below threshold for the RF unit the neural average revealed the presence of two units with significantly different conduction velocities, (73.6 and 43.6 m/s), whose electrical thresholds were essentially indistinguishable. Computer subtraction of record A from B (shown in the lower trace of 2) reveals the femoral nerve spike associated with the newly recruited RF unit shown in B. In 3, the averaged patellar ligament force records (99 sweeps) are shown associated with the femoral neurograms in 2. Notice that the fastest conducting axon (CV = 84.9 m/s) was the last to be recruited electrically. Calibration bar for the EMG records in 1A is 100 μV for VI, 200 μV for VM, VL and RF and 400 μV for SA. In 1B each record gain has been halved with the exception of VM. The stimulus to the ventral roots coincides with trace onset in 1A, B and 3. In 2 it is shown by the initial artifact.
frequency (100 Hz) stimulation, and the absence of either averaged force or electrical activity to just sub-threshold stimulation. An additional criterion employed in the present study was the presence of a single triphasic action potential averaged from the femoral nerve cuff signal, and its absence to just sub-threshold stimulation.

These criteria applied to the lowest threshold unit. Later recruited units could often be investigated by subtracting averaged force and neural cuff records obtained with just sub-threshold stimulation, from those in which stimulation was suprathreshold for the axon of interest (Fig. 2). We assumed that motor unit tensions sum linearly but did not verify this in these experiments (but see Lewis et al., 1972). In principle, it should be possible to obtain mechanical and axonal characteristics of many sequentially stimulated units at a single electrode site, providing there is an adequate separation of individual thresholds. In practice only the first 2 or 3 units could be investigated in this way.

Since EMG electrodes were designed to maximize sampling at the probable expense of selectivity, in many cases stimulation of a single ventral root axon resulted in the appearance of electrical activity in the electrodes sampling two or more adjacent muscles (Fig. 2B). If the threshold behavior of each evoked potential was identical, so that all potentials were simultaneously recruited under all testing conditions, then such activity was considered to be generated by a single unit whose electrical field was detected by the electrodes in neighboring muscles. Indeed, such cross-talk was also seen when the EMG signal was spike-trigger averaged from a recorded ventral root spike during locomotion (see Fig. 1, Hoffer et al., 1981b).

Verification of the identity of a recorded and stimulated unit: spike-triggered microstimulation

On a few occasions (3/24) it was possible to stimulate in isolation the same axon whose discharge had been recorded during locomotion. We used several criteria to establish the identity of the recorded and stimulated unit. The most important of these employed a new technique, spike-triggered microstimulation, which is illustrated in Fig. 3. Initially the unit EMG and neurogram were obtained by spike-triggered averaging during walking. If a similar but not necessarily identical EMG and neural waveform could be elicited by microstimulation through the recording electrode, then the stimulating voltage was set at approximately 2 x threshold for that unit.

The stimulator was triggered by each naturally occurring motoneuron action potential, together with an ultra-fast relay that switched the recording electrode from the input of the amplifier to the output of the stimulator. This transition could be achieved within 200 μs. In addition, the ventral root spike triggered an averager which received the EMG and neural cuff signals.

The stimulus to the ventral root electrode was delivered at 1 of 2 different intervals following the occurrence of the natural spike. One interval (generally 15 ms after the spike) was long enough to ensure adequate stimulation of the unit without temporal overlap of the evoked EMG potentials. The other interval was arranged to be short enough (usually 0.8 ms after spike onset) to fall within the refractory period
Fig. 3. Verification of the identity of a recorded and microstimulated rectus femoris unit using spike-triggered microstimulation. The same RF unit as illustrated in Fig. 2. Each record is the averaged rectus femoris EMG triggered on-line by the occurrence of a discriminated, ventral root spike during treadmill locomotion. The initial EMG response in each case is the unitary EMG recorded from the muscle fibers innervated by the axon whose spike was recorded. The averager was triggered by a pulse derived from the spike discriminator so each trace starts 0.5 ms after the onset of the ventral root spike. The spike-triggered average without subsequent stimulation is shown in A. In B and C: the spike additionally triggered an ultrafast relay which switched the recording electrode from the input of the VR amplifier to the output of a stimulator. The stimulator was triggered after 1 of 2 different delays following the natural spike, at a voltage set to be approximately 2× threshold for the unit whose identity with the recorded unit was suspected. C: the record with the longer stimulus delay (15 ms) is displayed and it can be seen that microstimulation recruits a unit that closely resembles the form and amplitude of the naturally evoked EMG. Proof of the identity of the microstimulated unit with that of the naturally occurring spike is shown in B in which the stimulus delay (0.3 ms; 0.8 ms after VR spike onset) was sufficiently short to fall within the refractory period of the unit and resulted in a failure to evoke the microstimulated electromyogram. All records are displayed at the same gain.

of either the axon or the muscle fibers of the recorded unit. If, and only if, the same axon was stimulated whose natural spike was the trigger then stimulation using the shorter interval resulted in a failure of the stimulus to evoke either the femoral nerve potential or the unitary EMG or both. In contrast, stimulation using the longer interval, under otherwise identical conditions, resulted in an evoked waveform (Fig. 3). Any other axons activated contributed EMG signals to both stimuli.

Because this test was technically demanding we relied in general on a comparison between the conduction velocities of the recorded and stimulated units, and the form and amplitude of their averaged neural and EMG potentials. In cases where these parameters did not differ significantly it seemed reasonable to assume the unit detected by each method was the same. Since the recording conditions for spike-triggered averaging and for microstimulation differed in ways which affected the form and amplitude of the evoked response, a lack of correspondence between the spike- and stimulus-triggered averaged waveforms did not necessarily imply that the two sets of evoked waveforms belonged to different units. Spike-triggered averaging was performed during walking, with accompanying variations in both muscle length and
EMG electrode location, as well as in the level of activity in both muscle and femoral nerve, all of which affected the form of the averaged unit potential. In contrast, microstimulation was performed in the lightly anesthetized animal in which unit EMG and neural responses were examined in the absence of ongoing EMG and minimal nerve traffic, and at a fixed muscle length.

It is probable therefore that we have underestimated the occasions when the same unit was both stimulated and recorded rather than the reverse, since we rejected those units in which correspondence between the two sets of evoked waveforms was uncertain.

Characterization of single motor unit contractile and axonal properties

We have characterized single motor units by examining their contractile and axonal properties and classified them into types according to the criteria of Burke (see Burke, 1981 for review). The contractile properties of single motor units were recorded using an implanted force gauge on the patellar ligament, whose amplified output fed a signal averager triggered by the stimulus. In general, between 32 and 256 sweeps were necessary to resolve isometric twitches and tetani, although with some large units averaging was only necessary because of the mechanical noise resulting from the ballistocardiogram and respiration. Generally, the limb was not rigidly immobilized, since its inertia was sufficient to ensure quasi-isometric conditions for most unit contractions. Although no external limb movements were evident, some internal muscle shortening could have occurred. As illustrated in Fig. 4, a number of contractile properties, including single twitch, unfused and fused tetani, and fatigue resistance, could be investigated for the lowest threshold unit. In addition the presence or absence of sag in an unfused tetanus, and fatigue index could be computed for many units allowing a presumptive classification into motor unit type.

In addition to unit contractile properties, it was possible to determine certain axonal properties, the most important of which was conduction velocity. This was achieved by stimulus-triggered averaging of the femoral nerve cuff signal, and could also be obtained for recorded units by spike-triggered averaging (Hoffer et al., 1981a), as described in the Methods section. In addition, the axonal and muscle fiber relative and absolute refractory period could be determined using double pulse stimulation (Fig. 5).

Comparison of the conduction velocities of recorded and stimulated units

One of the purposes of the present study was to determine whether a particular recorded unit could also be stimulated in functional isolation and characterized physiologically. Thus it was of interest to determine whether the units sampled by microstimulation were drawn from the same population as those we recorded. Therefore, we compared the conduction velocities of stimulated and recorded units. We chose this parameter for comparison because it was the one most frequently and easily recorded for both stimulated and recorded units and because it was likely to
be a sensitive and relevant indicator of any bias in the sampling; the electrical
thresholds of axons are known to be proportional to their conduction velocity
(Erlanger and Gasser, 1973) and during locomotion units tend to be recruited in
order of increasing conduction velocity (J.A. Hoffer, M.J. O'Donovan, C.A. Pratt
and G.E. Loeb, unpublished observations).

The pooled data (all experiments in which conduction velocity was determined
using a single or double cuff) reveal recorded units to have a mean conduction
velocity of 91.8 m/s (range 56.6–121 m/s, S.D. 16.6, n = 29) compared to 82.9 m/s
(range 43.6–115 m/s, S.D. 17.5, n = 21) for microstimulated units. However, as
mentioned in the Methods section and reported previously (Hoffer et al., 1981a),
recording of conduction velocity using a single cuff is subject to errors which
introduce variability into the measurement. Further variability arises because data
from different animals were pooled. A more satisfactory comparison between the
conduction velocities of recorded and stimulated units can be made by comparing
data obtained within the same animal using the double cuff technique. To further
reduce variability, comparisons were made between stimulated and recorded units at
Characterization of the axonal and muscle fiber refractory period of a microstimulated type S, vastus intermedius unit whose contractile characteristics are illustrated in Fig. 4. In A, determination of the axonal refractory period is illustrated. Each trace is the averaged femoral neurogram (1028 sweeps) in response to double pulse stimulation of the ventral roots with a varying delay between pulses. The averager was triggered by the first pulse and each sweep commences approximately 200 μs after the stimulus onset. The intervals between the pulses are displayed in front of each trace. The refractory period of the axon is reached at 1.2 ms in the lowest trace. Notice that at 1.3 ms there is no obvious attenuation of the second evoked neural spike indicating this interval does not fall within the relative refractory period of the axon, which presumably was between 1.3 and 1.2 ms. The arrows indicate the neural waveforms to distinguish them from the stimulus artifact, and the line connects the onset of the second stimulus in the different traces. In B the averaged (8 sweeps) unitary EMG responses to double pulse stimulation are shown. In the upper trace the EMG waveform to a double stimulus within the refractory period of the axon (1.2 ms) is illustrated, followed below by double pulse stimulation outside the refractory period of the muscle fibers or neuromuscular junction. Compare these traces with those in C in which the stimulus interval was reduced as indicated. Notice that even at 1.8 ms there is obvious alteration of the second EMG waveform (arrowed) indicating that this interval falls within the relatively refractory period of either the muscle fiber or the neuromuscular junction. The refractory period is reached at 1.5 ms, revealing the longer refractory period of the muscle fibers or NMJ compared to the axon. Note that there is a difference in time scales between B and C.

The same electrode sites on the same days. These data are presented in Table 1. There are 12 stimulated units in one animal for which this comparison can be made. At 5 of the electrode locations, units were also recorded during locomotion. In the remaining cases, units could be stimulated in isolation at that electrode but no units were detected or adequately resolved during treadmill locomotion on that day. At these 5 electrodes 7 units were stimulated and 6 recorded. The conduction velocities of the 7 stimulated units ranged from 82.1 to 115 m/s (mean 95.4, S.D. 10.4)
TABLE 1

COMPARISONS OF THE CONDUCTION VELOCITIES FOR RECORDED AND STIMULATED UNITS AT THE SAME ELECTRODE SITE, ON THE SAME DAY IN THE SAME ANIMAL.

Twelve stimulated units are displayed from one animal. The stimulation order column indicates the ranking of electrical thresholds (1 = lowest). The spike column refers to the amplitude of the extracellular ventral root spike recorded during locomotion (A = largest). Blanks in the recorded unit columns indicate that no units could be recorded or adequately resolved on that day during walking. Muscles indicated as pairs (e.g. VL/VI) indicate that the recording electrode was sampling both muscles as detected at postmortem examination.

<table>
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compared to a range of 71.9–92.7 m/s (mean 82.3, S.D. 8.7) for the recorded units.

We also examined the influence of conduction velocity on the electrical threshold of a unit to microstimulation by comparing the conduction velocities of units serially stimulated at the same electrode site. In 2 out of 4 such cases the lowest threshold unit had a lower conduction velocity than a subsequently recruited unit and this difference could be significant, as in the case where 2 units (CV 73.6 and 43.6 m/s) were recruited prior to one with a higher conduction velocity (84.9 m/s) than both.

**General Conclusions**

We have demonstrated that single motor units can be stimulated in functional isolation in the intact animal, using implanted ventral root microelectrodes, and their axonal and contractile properties determined by stimulus-triggered averaging the signals from an implanted neural cuff and force transducer. The comparative ease with which units can be isolated using this technique suggests that it may also be useful for unit studies in the acute anesthetized preparation.

The conduction velocities of microstimulated units did not differ significantly from a similar population of recorded units, although in one experiment there was
some tendency to microstimulate faster conducting axons than were recorded at a particular electrode.

These observations suggest that the method is not strongly biased toward the large diameter axons, and that the intrinsic axonal excitability, which is directly proportional to conduction velocity, was not the only determinant of an axon's electrical threshold to ventral root microstimulation. Rather, it seems likely that the proximity of a particular axon to the stimulating electrode (perhaps more specifically its nearest node of Ranvier), also influences its electrical threshold. This presumably also accounts for our ability on some occasions to stimulate the axon whose discharge we had also recorded.

We successfully stimulated a recorded axon in isolation on 3 out of 24 attempts. In the remaining cases, other axons were stimulated earlier than the recorded axon which could not be isolated adequately, as the stimulus strength was increased. However, this relatively low rate was not unexpected. We recorded the majority of units during slow treadmill walking, when a significant fraction of ventral root axons are unrecruited and hence electrically silent. Therefore, an active axon may be surrounded by many silent ones that could be stimulated first. If, as seems likely in the present experiments, these unrecruited axons are being stimulated with a lower threshold than a discharging axon, then recruiting and recording such axons in more vigorous movements (running, galloping, jumping) should yield a significant increase in the frequency of stimulating a recorded axon.

In addition, it should be emphasized that there may be discharging axons in the vicinity of the recording electrode whose ventral root spikes cannot be recorded or adequately resolved, but which are capable of being stimulated with a lower electrical threshold than an axon whose spike is recorded. Whether this occurs or not will depend upon the factors governing the size of the recorded extracellular action potential and whether they are equally important in determining the threshold of an axon to ventral root microstimulation.

The demonstration that an axon whose discharge was recorded during locomotion can also be stimulated in isolation and characterized physiologically, offers promise for the analysis of motor unit recruitment in natural movements, particularly with regard to unit type. At present, the participation of the various unit types in natural movements can only be inferred from glycogen depletion studies which are subject to problems of interpretation (see Burke, 1981), or from measurements of whole muscle force using an implanted tendon gauge (Walmsley et al., 1978). The application of the techniques described in this paper to a wide sample of units should enable the participation of different unit types in normal movements to be directly determined.

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