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SINGLE UNIT CONDUCTION VELOCITIES FROM AVERAGED NERVE CUFF ELECTRODE RECORDS IN FREELY MOVING CATS

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The conduction velocity of peripheral neurons recorded by wire microelectrodes implanted in intact, freely moving cats was determined on-line using the technique of spike-triggered averaging of nerve cuff electrode records described here. Axonal velocity was estimated from the conduction latency between two adjacent sets of tripolar recording electrodes inside a cuff, thereby avoiding uncertainties that could arise from differences in spike shape, variable conduction distance, or unknown stimulus utilization time. This method rendered conduction velocity values for individual afferent and efferent myelinated fibers ranging from 27 to 120 m/sec, estimated with an uncertainty of ±5%.

In addition, predictions from theoretical models relating extracellular potential amplitude, wavelength, and conduction velocity were confirmed experimentally for en passant records obtained from intact myelinated fibers.

INTRODUCTION

In recent years it became possible to record single-unit activity from cat hindlimb afferents using fine flexible wire electrodes inserted chronically in dorsal roots (Prochazka et al., 1976), or in dorsal root ganglia (Loeb and Duysens, 1979). Efferent fiber activity can be similarly recorded with electrodes implanted in ventral roots or spinal nerves (Hoffer et al., 1979). However, conclusive identification of cell type and muscle of destination has proven quite difficult in intact, normally behaving animal preparations. Since all hindlimb muscles remain innervated, the range and specificity of manipulations available for receptor characterization is more limited than in acute preparations involving isolated muscles. In addition, the unit under study often cannot be electrically stimulated in isolation, as would be required to determine conduction velocity from latency measurements.

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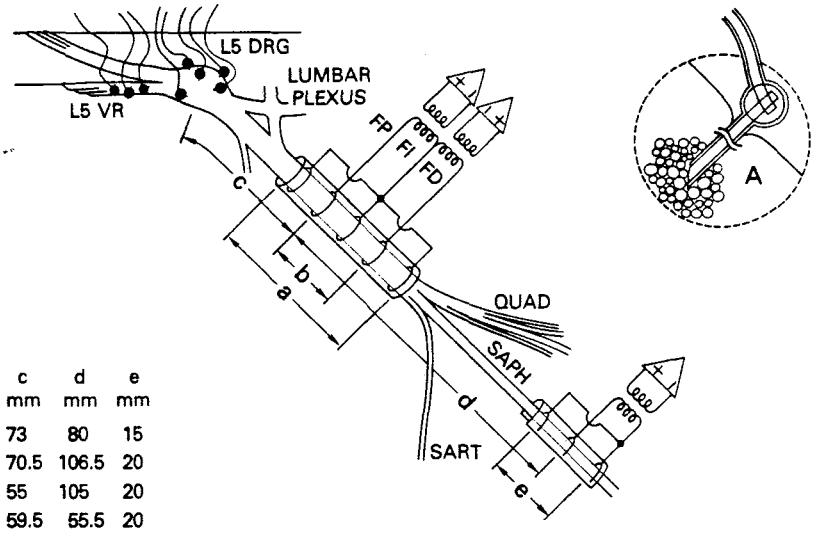
Axonal conduction velocity has classically been used as a criterion for classifying peripheral neurons. In particular, cat hindlimb muscle spindle afferents characterized physiologically as group Ia usually have conduction velocities above 72 m/sec, while group II fibers conduct at below 72 m/sec (Matthews, 1972). Guard hair afferents and cutaneous pressure receptor afferents have also been classified by conduction velocity (Burgess et al., 1968). Distinction between α- and γ-motoneurons may be made on the basis of conduction velocity since the efferent fiber diameter histogram is bimodal and non-overlapping (Boyd and Davey, 1968).

In order to determine the direction and velocity of conduction of recorded units and the muscle group of destination, we have applied the technique of spike-triggered averaging (Mendell and Henneman, 1971; Kirkwood and Sears, 1975) to extract correlated unitary potentials from the aggregate peripheral nerve activity recorded by implanted nerve cuff electrodes (Hoffer, 1975; Stein et al., 1975; Gordon et al., 1980). The conduction latency between two adjacent sets of recording electrodes inside a cuff was used to estimate axonal velocity, thus avoiding uncertainties arising from differences in spike shape, variable conduction distance, or unknown stimulus utilization time. This method rendered conduction velocity values for individual afferent and efferent myelinated fibers ranging from 27 to 120 m/sec, with a measurement uncertainty of ±5%.

MATERIALS AND METHODS

Design of implanted electrodes

Data presented in this paper were obtained from 4 adult cats fully instrumented for the study of afferent and efferent units during locomotion. Electrodes were surgically implanted under deep Nembutal anesthesia and aseptic conditions. Cats were allowed to recover for several days before recording sessions began. As shown diagrammatically in Fig. 1, 12 fine flexible wires were inserted in either the L5 dorsal root ganglion (DRG) or the L5 ventral root (VR), through a small laminotomy. The DRG electrodes were initially made of 50 μm 90% Pt—10% Ir wire, coated with 12 μm of tri-ML polyimide (California Fine Wire) and 15 μm of Parylene-C (Loeb et al., 1977). Each wire was cut off obliquely before insertion, as described by Loeb and Duysens (1979) for the L7 DRG preparation. Since electrodes of similar design proved difficult to insert in ventral roots, a modified hatpin electrode (Salcman and Bak, 1973) was adopted, consisting of a stiff, short (2—3 mm) untapered iridium shaft (37.5 μm) welded to a flexible gold lead of the same diameter (see Fig. 1, inset A). The weld was covered with a drop of epoxy, the entire assembly was insulated with 15 μm of Parylene, and a recording surface (60—200 kΩ impedance at 1 kHz) was exposed by cutting the iridium wire with scissors prior to insertion. Cats I, J and K received conventional DRG electrodes and hatpin VR electrodes. Cat L received hatpin electrodes in both DRG and VR, with shafts made from 50



CAT	a mm	b mm	c mm	d mm	e mm
I	26	12	73	80	15
J	30	15	70.5	106.5	20
K	29	14.5	55	105	20
L	30	15	59.5	55.5	20

Fig. 1. Schematic diagram indicating placement and dimensions of implanted electrodes. Up to 12 flexible lead microelectrodes were inserted in the L5 dorsal root ganglion (DRG) or ventral root (VR). Inset A shows dimensions of hatpin electrode (37—50 μm shaft) relative to ganglion cells. A cuff with 5 circumferential electrodes was implanted around the femoral nerve, distal to the lumbar plexus. The middle- and two end-electrodes, shorted together, served as indifferent (FI) in two tripolar differential sets centered about the proximal (FP) and distal (FD) recording electrodes. A U-shaped patch containing a tripolar electrode set was wrapped around the cutaneous saphenous nerve (SAPH). The separations between recording sites, b, c and d, established the conduction distances over which axonal velocity was measured. The other femoral nerve branches (QUAD and SART) supply the anterior thigh muscles.

μm Pt—Ir wire coated with tri-ML and Parylene.

Thirty-six leads from the various implanted devices emerged percutaneously and were soldered to individual posts of a saddle connector which was attached to the cat's back by two Mersilene size 5 sutures threaded through holes drilled through the dorsal spines of the L4 and L7 vertebrae. Single-unit records were amplified close to the source by 12 single-ended hybrid FET amplifiers (Bak Electronics MMRS-1P) in order to drive a long flexible cable. Signals were further amplified 1000—10,000-fold and filtered between 1 and 10 kHz prior to recording on FM tape (10 kHz bandpass).

A nerve cuff with recording electrodes was implanted around the femoral nerve, which in adult cats can be isolated from surrounding tissue for 30—35 mm in a reasonably movement-free region, proximal to the inguinal canal. Cuff construction followed the description by Hoffer (1975) and Davis et al. (1978) for other hindlimb nerves. Femoral nerve cuffs were made of 2.5 mm (i.d.) silicone rubber tubing (Extracorporeal), and were 26—30 mm long. Five electrodes (75 μm stranded Pt—Ir wire, Teflon-coated; Medwire) were sewn circumferentially at uniform intervals along the inside wall of the cuff

(Fig. 1). The central and end electrodes, shorted together, served as indifferent for the two tripolar recording configurations. The nerve was introduced through a longitudinal slit, and the cuff was sealed shut with Mersilene sutures positioned circumferentially every 4—5 mm, to ensure maximal rejection of unwanted EMG signals arising from neighboring muscles (Hoffer, 1975; Stein et al., 1977). Impedances were in the 1—3 kΩ range when measured at 1 kHz (Stein et al., 1978).

Neural potentials were recorded from the saphenous nerve by similar Pt—Ir stranded wire electrodes sewn inside a U-shaped Silastic sheet patch (0.25 mm thick, 10 mm wide, and 15—20 mm long; Dow Corning). The flexible patch was folded around the nerve and sewn to overlying fascia (Fig. 1). Using this design, the smaller, more fragile saphenous nerve remained attached to locally feeding blood vessels and some connective tissue. This approach reduced surgical trauma and prevented conduction failure that can be caused by ill-fitting cuff electrodes (viz. Stein et al., 1980). The poor EMG rejection afforded by such non-sealing patch electrodes was unimportant in this case because cutaneous and joint afferents could be easily activated for averaging in relaxed or lightly anesthetized cats, using manipulations that caused little or no activity in neighboring muscles. Saphenous tripolar interelectrode distances approximated those in the femoral nerve cuff. Impedance were in the 1—5 kΩ range. High-gain (× 20,000—× 50,000) differential amplifiers with 1—10 kHz bandpass were coupled to femoral and saphenous nerve electrodes through impedance-matching transformers (JAF-1; Triad) equivalent to those described by Stein et al. (1977).

Each of the muscles supplied by the femoral nerve (the 4 heads of quadriceps, plus sartorius) received an implanted bipolar EMG electrode. Associated muscle unit potentials were routinely searched by spike-triggered averaging as part of the identification protocol of recorded motoneurons (Hoffer et al., 1979, 1980, 1981).

Isolation of unitary potentials

Afferent units were characterized on-line during limb manipulations and while the cat was walking on a treadmill. Efferent unit identification was done either on-line or by averaging cuff and EMG data recorded previously on FM tape. Unitary spikes recorded by microelectrodes were isolated using a threshold and window discriminator (Bak Electronic DIS-1). Each occurrence of a discriminated spike triggered the sweep of a signal averager (Nicolet 1 070). Concurrent records of peripheral nerve activity, delayed 3—10 msec using an analog time delay (Bak Electronics AD-5), were sampled by the averager every 20 μsec. As sweeps accumulated, if the unit projected through the femoral nerve cuff electrodes, a correlated neural potential was resolved at a fixed latency from the occurrence of the discriminated potential at the spinal root level. Owing to their respective directions of conduction, afferent units showed femoral nerve cuff spikes that preceded the occurrence of the discriminated DRG potential, while motor units gave femoral nerve

cuff potentials occurring after the discriminated VR potential. Since cutaneous units and proprioceptive joint afferents projecting through the femoral nerve also projected through the saphenous nerve branch, they yielded an additional correlated saphenous neural potential at an appropriate latency from the femoral nerve potentials.

Examples of unitary potentials obtained from spike-triggered, averaged records are shown in Fig. 2. All records were delayed 5 msec prior to averaging. The top trace in Fig. 2A shows the delayed, averaged record from a unit microelectrode implanted in the L5 DRG. Each occurrence of a discriminated unitary potential triggered the sweep of the averager. The traces labeled FP (proximal femoral) and FD (distal femoral) were obtained from the two recording electrodes built into the femoral nerve cuff, separated by an interelectrode distance of 14.5 mm. The correlated potential obtained from the saphenous nerve electrodes is shown in the bottom trace of Fig. 2A. The femoral cuff potentials are shown again in expanded scale in Fig. 2B.

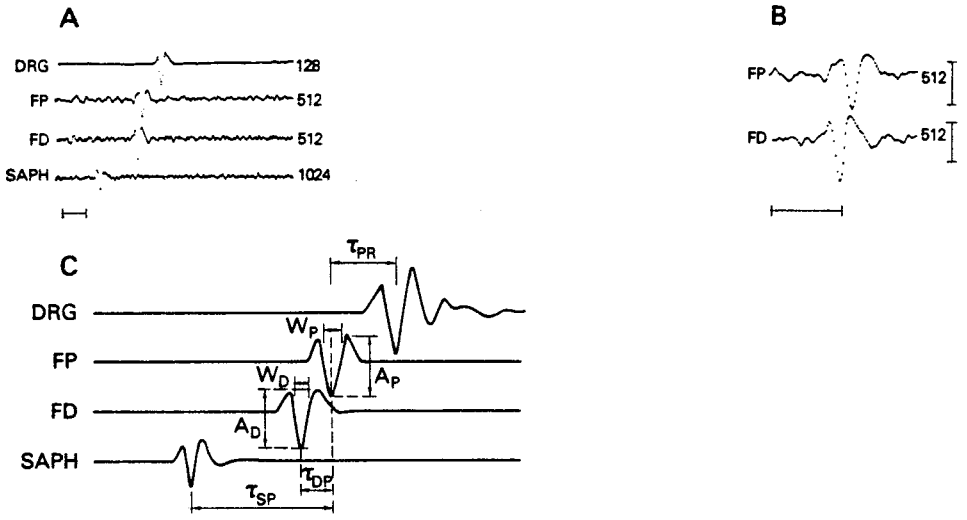


Fig. 2. A: spike-triggered, averaged records obtained from a guard hair afferent fiber (unit K3A19) supplying the medial portion of the foot dorsum. The 4 traces correspond to the single-unit electrode (DRG), the proximal femoral (FP), distal femoral (FD) and saphenous nerve electrodes. All records were delayed 5 msec prior to averaging. Number of sweeps accumulated in each average are shown at right. B: the proximal and distal femoral nerve records are reproduced in expanded scales. Consecutive points occurred every 20 μsec.Vertical calibration bars indicate 1 nA, horizontal bars indicate 1 msec. C: parameters measured from averaged records, shown diagrammatically, were the amplitude of the proximal and distal femoral cuff potentials (A_P, A_D), their duration (W_P, W_D), and the latency from the occurrence of the negative peak in each record with respect to the proximal femoral record (τ_{SP}, τ_{DP}, τ_{PR}). Conduction distances shown in Fig. 1 were divided by these latencies to obtain the various estimates of conduction velocity.

The characteristic set of triphasic neural potentials obtained from a given unit was quite reproducible with repeated averaging. Conduction velocity between recording sites was determined from the time interval of occurrence of the negative peaks in the corresponding potentials. Since these were the times of fastest change in slope, they could be determined most precisely. Other features measured from the proximal femoral and distal femoral triphasic potentials, shown schematically in Fig. 2C, were the peak-to-peak amplitude, and the duration or width of the negative peak, measured from the zero crossing of the falling and the rising phases.

An absolute calibration of potential amplitude, in units of current, was obtained by injecting a known signal (a single-cycle sinusoidal wave, 3kHz, generated by a Wavetek model 112 B; 10 nA peak-to-peak) in parallel with the cuff electrodes, and averaging the recorded signal. Readers who prefer to visualize extracellular events in terms of potential differences may assume that a nerve fiber generating 1 nA across a 2 kΩ cuff electrode produces a 2 μV signal. Calibration of unitary potentials in units of current, however, permitted the comparison of amplitudes of units recorded in different cats and on different days for the same cat, independent of differences in individual cuff design, or variations in cuff impedance that are known to take place over a period of several weeks (Stein et al., 1978).

Unitary potential shapes recorded from the ganglion or roots were highly variable, and therefore the only parameter that was monitored was the latency to the main negative peak. Single-unit potential amplitudes were generally not well correlated to cell size (as inferred from cuff conduction velocity); they depended primarily on the relative position of the microelectrode tip. Amplitudes from averaged saphenous records, though reproducible for individual units, proved to be poorly correlated to presumed fiber size (based on conduction velocity). Transverse shunting of current due to the irregular geometry of the non-circumferential patch probably made fiber location within the nerve a more important and random determinant of recorded potential amplitude.

In a terminal acute experiment in each cat, the conduction distances between the different recording electrodes were measured in situ in order to calculate the conduction velocities between the different recording sites. Conduction distance between the proximal and distal femoral cuff recording electrodes was invariant and could be measured within ±0.3 mm (±2%), since the recording wires were built onto the cuff wall. In contrast, the distance between the saphenous and femoral recording electrodes depended on knee joint angle and could only be estimated within ±5 mm (±5—10%). Furthermore, their average separation could have been altered by migration of either electrode during the 4—7 weeks that each experiment lasted. Likewise, the distance between the femoral cuff and the individual dorsal root or ventral root recording wires could be estimated only roughly, since the microelectrode wires were placed over several millimeters and axons can course tortuously through the lumbar plexus. Conduction distances between femoral

nerve and root or ganglion recording points were estimated within ±5 mm, or about ±10%.

The matched electrode characteristics and the fixed separation between the two femoral cuff electrodes gave the most reliable estimates of conduction velocity in these studies. The signal averager resolution of 20 μsec allowed estimation of the occurrence of neural spike minima with ±5 μsec uncertainty from interpolation. Taking into account the measurement error in electrode separation, conduction velocity could be estimated within ±5% for the fastest conducting fibers (approximately 120 m/sec). Precision was considerably higher for slower conducting fibers.

RESULTS AND DISCUSSION

Data presented in this paper were obtained from 75 units, of which 69 were afferent and 6 were efferent. The following axonal properties were measured and compared: (1) the conduction velocity derived from proximal to distal femoral cuff latency, and from femoral cuff to saphenous nerve or cuff to single unit electrode latency; (2) the amplitudes of individual unitary potentials recorded by proximal and distal femoral cuff electrodes; (3) the relation between amplitude of potentials recorded by femoral cuff electrodes and conduction velocity; (4) the relation between duration of potentials recorded by femoral cuff electrodes and conduction velocity; and (5) the effect of tripolar interelectrode separation on the amplitude and duration of potentials recorded by femoral cuff electrodes.

Variability in measurements of conduction velocity obtained over different segments of the nerve

Fig. 3A shows conduction velocity measurements obtained from latency between proximal and distal femoral cuff electrodes (FD → FP; abscissa) and between saphenous and proximal femoral cuff electrodes (S → FP; ordinate) for 38 cutaneous and joint afferent units which projected through the saphenous nerve. Statistical analysis showed that these data distributed normally ($P < 0.05$) about a line of slope 1 (dashed in Fig. 3A). Much of the scatter is attributed to uncertainty in the conduction distance between saphenous and femoral electrodes. Since cutaneous nerve fibers normally do not taper this far away from receptors (Iggo, 1974), the occurrence of any systematic deviations from the line of slope 1 in Fig. 3A would have suggested that one or both of the chronically implanted electrodes had caused chronic compression of the nerve. Mechanical compression is known to affect the diameter of large myelinated fibers (Sunderland, 1968; Aguayo et al., 1971).

Conduction velocities between proximal and distal femoral cuff electrodes (FD → FP; abscissa) and from proximal femoral cuff to single unit electrodes in the ganglion or roots (ordinate) are shown in Fig. 3B for 69 sensory and

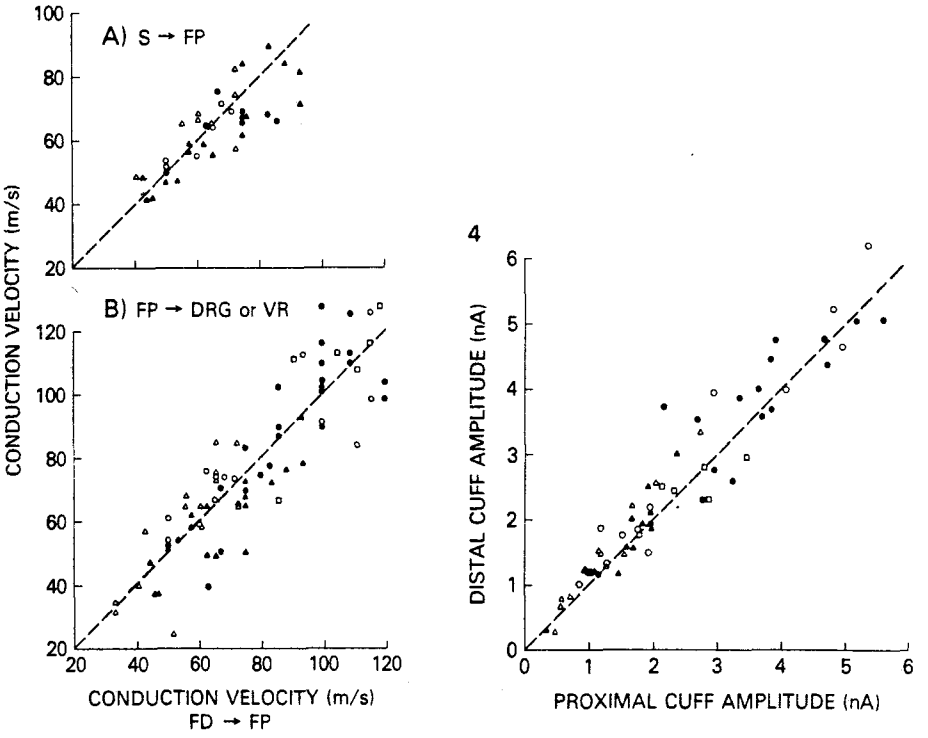


Fig. 3. A: comparison of conduction velocity measurements obtained between distal and proximal femoral cuff electrodes (FD → FP; abscissa) plotted against values obtained for the span from saphenous nerve to proximal femoral nerve (S → FP; ordinate). B: same abscissa; ordinate shows conduction velocity for the span from proximal femoral to single unit electrodes in the dorsal root ganglion (DRG) or ventral root (VR). Lines of unit slope are shown dashed. In these and following figures, symbols represent: ○, cat I (sensory); ●, cat J (sensory); △, cat K (sensory); ▲, cat L (sensory); □, cat L (motor).

Fig. 4. Comparison between single-unit potential amplitudes determined from proximal and from distal femoral cuff records. Line of unit slope is shown dashed.

6 motor units. The scatter of points about the line of slope 1 is attributed to at least 3 effects: the relatively large uncertainty in the conduction distance between the femoral cuff and the different single unit electrodes, the convolutions that sensory fibers take in their course through the ganglion (Pannese, 1960), and the occurrence of multiple peaks in single unit records with complex shapes. Note that in spite of the scatter, the data in Fig. 3B are distributed normally about the line of slope 1, suggesting that unitary conduction velocities inside the femoral nerve cuff were on average similar to conduction velocities measured proximal to the cuff. The presence of units with conduction velocities in the upper ranges described for cat hindlimb peripheral nerves (Hursh, 1939) further indicates that little or no damage was produced by the chronically implanted nerve cuff.

Comparison between the amplitude of potentials recorded by the proximal femoral electrode and the distal femoral electrode

Data from 60 units are shown in Fig. 4. The reasonably good agreement between single unit amplitudes recorded by the proximal and distal cuff electrodes is attributed to their matched recording properties. Since the tripolar cuff electrode separations used (12—15 mm) were at least 6 times greater than internodal distances for the largest fibers, the relative longitudinal position between recording electrodes and nodes can be ruled out as a source of variability of either the amplitude of recorded potentials, or their timing (see Figs. 5 and 6 of Marks and Loeb, 1976). Rather, the few fibers that show significant deviation from the line of slope 1 may express local variations in their radial depth as they course through the nerve. Frequent fascicular exchanges are known to take place within peripheral nerve trunks (Sunderland, 1968). To compensate for this effect, potential amplitudes and durations measured from proximal and distal femoral cuff electrode records were averaged arithmetically prior to plotting in the remaining figures.

Dependency between amplitude of neural potential and fiber conduction velocity

Conduction velocity measured between proximal and distal femoral cuff recording sites is shown along the abscissa in Fig. 5. The arithmetic mean of

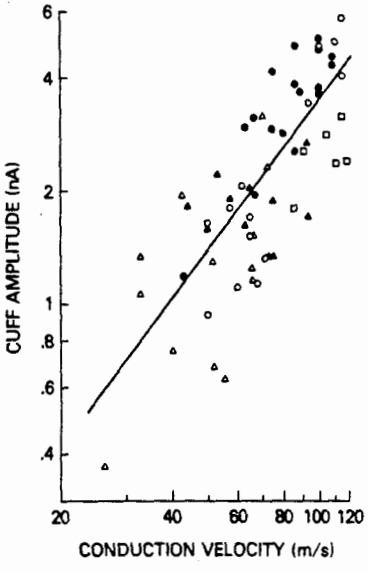


Fig. 5. Relation between fiber conduction velocity (measured between proximal and distal femoral cuff electrodes) and neural potential amplitude, shown in double-logarithmic plot. Parameters of least-squares fit were: slope = 1.3 ± 0.2, intercept = −2.1 ± 0.3; n = 61.

the amplitudes recorded by the proximal and distal femoral cuff electrodes for each of 61 units is shown along the ordinate. A straight-line fit in this double-logarithmic plot rendered a slope of 1.3 ± 0.2. A slope value of 1.7 ± 0.1 was obtained in acute experiments by Stein et al. (1977), who used 20 mm long tripolar electrodes on the tibial nerve and stimulated teased dorsal root filaments. Fractional power relationships indicate a dependency somewhere between linear and square, relating the extracellular triphasic potential amplitude and conduction velocity of individual fibers. A square dependency is predicted from recording theory (Stein et al., 1975; Marks and Loeb, 1976) whenever interelectrode separations approach the order of magnitude of potential wavelength (about 30 mm for 64 m/sec fibers; see Fig. 7A), whereas shorter tripolar configurations (of the order of one or a few internodes) would show a linear dependency (Marks and Loeb, 1976).

The 2- to 3-fold range of extracellular amplitudes observed for fibers of comparable conduction velocities is interpreted to reflect the depth of individual fibers within the peripheral nerve trunk, although some of the scatter may also be due to systematic differences in the current-to-voltage calibration determined for individual cats.

Relationship between fiber conduction velocity and duration of potential

The duration (or width) of the negative phase of the potential recorded by femoral cuff electrodes is shown in Fig. 6 for 71 units. The convention followed to measure duration is detailed schematically in Fig. 2C. Duration values from proximal and distal femoral cuff records (W_P and W_D in Fig. 2C) were averaged and plotted along the ordinate in Fig. 6.

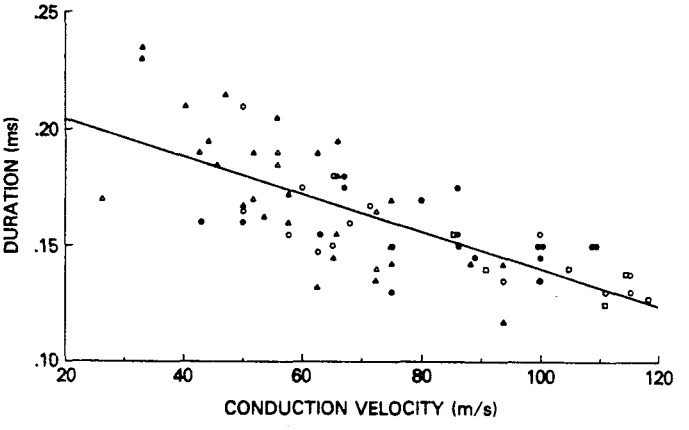


Fig. 6. Relation between fiber conduction velocity and duration of negative phase of potential recorded by femoral tripolar electrode sets. Parameters of line fit: slope = $(-8.0 \pm 0.9) \times 10^{-4}$, intercept = 0.220 ± 0.007; n = 71.

The original observations on monophasic potentials recorded from cut filaments (Paintal, 1966) lead to the prediction that the duration of triphasic action potentials recorded en passant from intact fibers should decrease for fibers with faster conduction velocity when recorded by tripolar electrodes of these dimensions (12—15 mm interelectrode separation). The data in Fig. 6 confirm this prediction and provide additional experimental evidence on the dependency of duration of the extracellular action potential as a function of fiber diameter.

Effect of tripolar interelectrode separation on the amplitude and duration of recorded potentials

Data shown in Fig. 7 were collected from one cat (I) where the central femoral cuff electrode (FM) had a separate lead from the end electrodes (I). FM could therefore be used as the recording electrode of a full-length tripolar set or, alternatively, could be shorted to the end electrodes to serve as indifferent of two adjacent tripolar sets, as shown in Fig. 7A. The ordi-

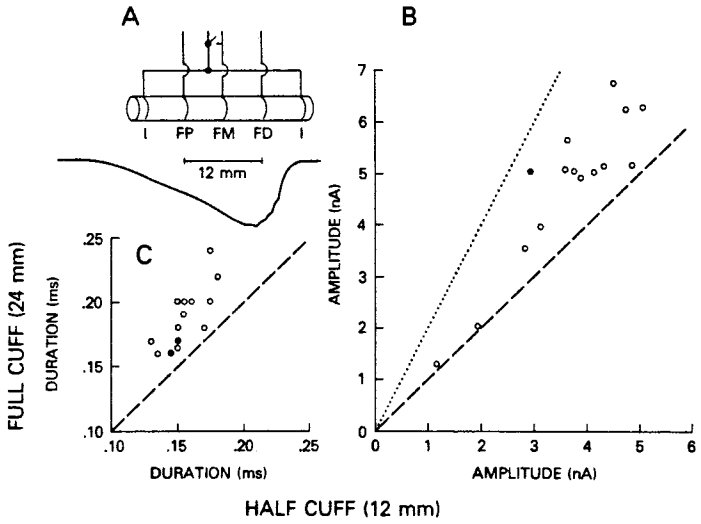


Fig. 7. Effect of interelectrode distance on amplitude and duration of fiber potentials. A: diagram of femoral cuff electrode configuration in cat I. Middle contact (FM) could be used either as recording electrode (with the end electrodes (I) as indifferent, spanning 24 mm; FULL CUFF) or alternatively, by shorting FM to the end electrodes, FP and FD could be used as recording electrodes (forming two tripolar sets each spanning 12 mm; HALF CUFF). An extracellular waveform calculated for a 64 m/sec fiber (from Marks and Loeb, 1976) is shown to scale. Note that cuff dimensions are roughly comparable to fiber wavelength. B: unitary amplitudes recorded by the long tripolar set (FULL CUFF; ordinate) plotted against averaged values recorded by FP and FD (HALF CUFF; abscissa). Full cuff amplitudes are larger, plotting somewhere between the 1 : 1 relation (dashed line) and 2 : 1 (dotted line). C: unitary durations for full cuff vs half cuff electrode configurations. Greater interelectrode separations rendered longer triphasic spike durations.

nates in Fig. 7B and C correspond to the full cuff tripolar set with the recording electrode in the center, and a separation between the indifferent electrodes of 24 mm. The abscissae correspond to the averaged values of the potentials obtained from the proximal and the distal femoral electrodes, each of which had an interindifferent electrode separation of 12 mm. As expected, the longer interelectrode separation provided larger amplitude extracellular potentials, indicated by the data of Fig. 7B plotting above the dashed 45° line. However, the amplification provided by using a tripolar set twice as long was not a factor of 2 (which would have plotted as the 2 : 1 dotted line) but was somewhere between a factor of 1 and 2. This is predicted from the effects of interelectrode separation and wavelength (Marks and Loeb, 1976). In Fig. 7A the electrode is shown to scale with the traveling extracellular wave calculated for a 64 m/sec fiber. Since the cuffs used in these experiments were already nearly comparable to the wavelength of fast conducting fibers, the magnification attained by doubling the interelectrode separation was less than would have been expected for shorter cuffs. The data shown in Fig. 7B are also consistent with the differential effects predicted for fibers of different conduction velocities. Smaller potential amplitudes, corresponding to fibers with shorter wavelengths (slower conduction velocities), were less influenced by changing the interelectrode separation than was observed for fibers with longer wavelengths.

Changing the length of the tripolar electrode sets also affected the duration of the potentials recorded. This is shown in Fig. 7C for the same units as Fig. 7B. Tripolar interelectrode separations of 12—15 mm were chosen for these experiments as the best compromise to render large signal amplitudes and adequate temporal separation between two adjacent tripolar sets, within the anatomical limitations of the site.

CONCLUSIONS

The technique of spike-triggered averaging of nerve cuff electrode records described here can render a precise on-line determination of conduction velocity of peripheral neurons recorded in intact, freely moving animals. In addition, two fundamental properties of saltatory conduction, the inverse relationship between extracellular potential duration and conduction velocity, and the direct relationship between conduction velocity and action current, have been confirmed using an independent method.

The application of this technique warrants some comments of a practical nature regarding its advantages, limitations, and possible pitfalls.

Relying on the occurrence of natural spikes to trigger a signal averager circumvents the potential problem of stimulating electrically more than one unit in a small root filament (cf. Kirkwood and Sears, 1975; Stein et al., 1977). Measuring conduction velocity from the latency between two adjacent sets of recording electrodes eliminates uncertainties attributable to unknown stimulus utilization time (Ranck, 1975) and complex individual fiber

paths through the lumbar plexus, roots and ganglia (Pannese, 1960). However, the method requires accurate and secure discrimination of single-unit potential shapes in order to avoid contamination and degradation of cuff averages by false acceptance of other spontaneously active units recorded simultaneously by the same microelectrode. In practice, only one or a couple of units with the largest potentials recorded by a given microelectrode may be discriminated reliably, although occasionally up to 5 cutaneous units with non-overlapping skin fields recorded simultaneously by a single L5 DRG electrode have been discriminated and individually averaged.

In extracting spike-triggered single-unit averages it is often important to keep the unit firing at approximately constant rates. Driving a cutaneous unit at intermittently high and low rates may cause shifts in the propagation time at the soma, with consequent latency shifts which appear as distortions and partial cancellation of the signal averaged from the peripheral cuff electrode records (see also Boylls, 1980).

Resolution of averaged potentials is limited by the background 'noise' level, which is determined largely by the number of concurrently active fibers in the nerve trunk that contribute uncorrelated spike activity. In general, resolution can be improved by averaging over more sweeps, since signal-to-noise amplitude ratio increases as the square root of the number of averages. In theory, potentials of much slower conducting fibers than those presented here could be resolved by this method. However, the power function relating action current to conduction velocity, plus this square root enhancement limit, suggest that it will be impractical to average signals from fibers below 25 m/sec in nerve trunks several millimeters thick.

Implantation of nerve cuffs can sometimes cause chronic mechanical damage due to local compression (Aguayo et al., 1971). Indeed, histological follow-up in earlier preparations (Hoffer, 1975; Stein et al., 1977) revealed some shrinkage in large-diameter fibers. However, conduction velocity values within normal ranges and postmortem examination of nerves in 12 cats (unpublished observations) has indicated that these cuffs implanted on cat femoral nerves caused little or no damage. Important factors in minimizing damage to peripheral nerve fibers are: (1) selecting a site with little movement, away from joints, and requiring negligible disruption of local blood supply; and (2) designing a loosely fitting cuff with flexible lead wires, to avoid compression associated with postoperative swelling (Ducker and Hayes, 1968; Davis et al., 1978) and torques that could cause kinking, stretching, or entrapment.

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