

## THE CLASSIFICATION OF AFFERENTS FROM MUSCLE SPINDLES OF THE JAW-CLOSING MUSCLES OF THE CAT

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### SUMMARY

1. The effects of the muscle-depolarizing drug succinylcholine (SCh) on the stretch responses of jaw-closer muscle spindle afferents were studied in the anaesthetized cat. Using ramp and hold stretches repeated every 6 s the basic measurements made were: initial frequency (IF), peak frequency (PF) and static index (SI), the frequency 0.5 s after the end of the ramp of stretch. Derived from these were: dynamic difference (DD) = PF – IF, dynamic index (DI) = PF – SI and static difference (SD) = SI – IF. Increases in these measures caused by a single i.v. dose of SCh ( $200 \mu\text{g kg}^{-1}$ ) are symbolized by the prefix  $\Delta$ .

2. In a population of 234 units,  $\Delta\text{DD}$  and  $\Delta\text{IF}$  were each distributed bimodally, but were uncorrelated, thus defining four subgroups.

3.  $\Delta\text{DD}$  was argued to be an index of the effect of bag<sub>1</sub> intrafusal fibre contraction and  $\Delta\text{IF}$  to be an index of the effect of bag<sub>2</sub> fibre contraction. On this basis it is proposed that units can be divided into four groups according to the predominant influences of the bag<sub>1</sub>, bag<sub>2</sub> and chain fibres as b<sub>1</sub>c (6.8%), b<sub>1</sub>b<sub>2</sub>c (22.2%), b<sub>2</sub>c (54.3%) or c (16.7%).

4. Testing with sine wave stretches at 1 Hz showed that changes in mean frequency and amplitude of response caused by SCh correlated with  $\Delta\text{IF}$  and  $\Delta\text{DD}$  respectively, but separated groups of units much less effectively than did ramp and hold testing.

5. Evidence is presented to indicate that the control value of DD in passive spindles does not relate to the potential strength of bag<sub>1</sub> fibre effects in fully activated spindles. The bag<sub>1</sub> fibre appears to contribute little to responses of spindle afferents in the passive state. DD is superior to DI as a measure of bag<sub>1</sub> effects.

6. Conduction velocity was unimodally distributed in masseter spindle afferents and was not correlated with  $\Delta\text{DD}$  or  $\Delta\text{IF}$  and was therefore of no value in classifying them.

7. Neither the threshold of afferents to quick transient stretch nor the coefficient of variation of interspike intervals provided any significant additional help in classification.

8. The unexpectedly high proportion of units of b<sub>2</sub>c type is thought to include primaries lacking appreciable bag<sub>1</sub> fibre contacts and secondaries with more or less substantial bag<sub>2</sub> contacts.

## INTRODUCTION

The classification of muscle spindle afferent axons has been considered repeatedly since Ruffini's description of primary and secondary sensory endings nearly 100 years ago, yet it is still not fully settled. Ruffini (1898) designated as primary those endings at the equator of the spindle with prominent spiral terminations and large diameter fibres and as secondary the less conspicuous juxta-equatorial endings with smaller diameter afferent fibres. The difference in fibre diameter is reflected in the existence of a bimodal distribution of conduction velocities, measured from the periphery to the dorsal roots (see review by Matthews, 1972). This observation is associated with the often confirmed correlation of conduction velocity with various measures of dynamic sensitivity to stretch (Cooper, 1961; Matthews, 1963; Rack & Westbury, 1966; Wei, Kripke & Burgess, 1986; Scott, 1990) and with the strength of the monosynaptic excitation of motoneurons. Taken together, these findings have led to a general assumption of the validity of classifying all spindle afferents as belonging to one or other of the morphologically defined types of sensory ending, primary or secondary.

Several problems arise from this approach. First, conduction velocity does not always separate two groups unambiguously, even in the hindlimb where the conduction velocity spectrum is best developed (Boyd & Davey, 1968). In other cases, such as the neck muscles (Richmond & Abrahams, 1979), intercostals (Sears, 1964), extraocular muscles (Bach-y-Rita & Ito, 1966; Browne, 1975), jaw muscles (Inoue, Morimoto & Kawamura, 1981) and primate forelimb (Cheney & Preston, 1976) conduction velocities are by no means clearly bimodal. Attempts have been made in such cases to distinguish two populations on the basis of dynamic stretch sensitivity or other properties such as high frequency vibration following, variability of discharge or the effects of succinylcholine (Cody, Lee & Taylor, 1972*b*; Cheney & Preston, 1976; Price & Dutia, 1987; Scott, 1990). However, in the absence of a clear correlation with conduction velocity or direct identification of endings by morphological studies, the resulting attributions as primary or secondary must remain to some extent uncertain. Another difficulty is that the patterns of innervation generally accepted as standard from studies of certain muscles of the cat hindlimb (notably soleus and tenuissimus), are often departed from in other muscles. There have been many reports of multiple-bag and single-bag spindles e.g. lumbrical muscles (Decorte, Emonet-Dénand, Harker & Laporte, 1990), neck (Richmond & Abrahams, 1975) and jaw (Lund, Richmond, Touloumis, Patry & Lamarre, 1978; Banks, Barker, Saed & Stacey, 1988). In particular tandem spindle capsules containing only bag<sub>2</sub> and chain fibres are not uncommon (Banks, Barker & Stacey, 1982; Price & Dutia, 1987, 1989) and the behaviour of their afferents may well differ from that of afferents with otherwise similar endings in spindles with the full intrafusal fibre complement.

An alternative basis for classification without presumption as to sensory ending morphology would be an assessment of the relative influence on each afferent of b<sub>1</sub>, b<sub>2</sub> or c intrafusal fibre contraction. This should be possible through the use of succinylcholine (SCh), which enhances dynamic sensitivity by b<sub>1</sub> fibre contraction and enhances bias by b<sub>2</sub> fibre contraction (Gladden, 1976; Boyd, 1985*a*). The work

of Dutia (1980) and of Price & Dutia (1987, 1989) on hindlimb and neck muscles has progressively emphasized this approach, but in applying it to the jaw-closing muscles the present work seeks to establish firmer statistically based criteria for such a classification. Some of this work has appeared in abstract form (Taylor & Durbaba, 1990), while the succeeding paper describes similar observations extended to hindlimb muscles.

#### METHODS

Observations were derived from twenty-one adult cats of either sex in the weight range 2.0–3.5 kg. They were initially anaesthetized with sodium pentobarbitone ( $40 \text{ mg kg}^{-1}$ ; i.p.) and given supplements i.v. as  $12 \text{ mg ml}^{-1}$  in saline as specified below. Both forearm veins were cannulated, one for anaesthetic and the other for SCh administration. The trachea and left femoral artery were also cannulated, the latter for monitoring arterial blood pressure. In some experiments, one or both lingual arteries were cannulated centrally to permit infusions of SCh into the carotid artery branches supplying the jaw muscles. For i.v. injection, SCh was diluted with saline to give  $200 \mu\text{g kg}^{-1}$  in 1.0 ml. i.a. infusions were given at  $0.5 \text{ ml min}^{-1}$  using dilutions of  $1 \text{ mg ml}^{-1}$  or  $100 \mu\text{g ml}^{-1}$  irrespective of body weight.

Body temperature was maintained by heating blanket and radiant heat so as to keep the pharyngeal temperature between 35 and 37 °C. The bladder was emptied as necessary by suprapubic puncture. Arterial blood gases were checked from time to time and ventilation adjusted accordingly, and metabolic acidosis corrected with i.v. sodium bicarbonate ( $1 \text{ mmol ml}^{-1}$ ). Animals remained in good condition regarding blood pressure, acid–base and plasma sodium and potassium levels even in the longest experiments lasting up to 33 h.

Masseter and temporalis nerves were exposed by incising the periosteum along the surface of the zygoma, which was cleared along its length and excised. The underlying muscle was split and the masseter nerve exposed in its vertical middle section. Two enamelled silver wires ( $125 \mu\text{m o.d.}$ ) with the final 3 mm bared were bent loosely round the nerve with a spacing of 2–3 mm. They were isolated by a slip of Polythene film and soft paraffin. In most cases an attempt was made to place additional stimulating electrodes around the combined temporalis and masseter nerve as it emerged from the mandibular notch. Usually only one wire (the cathode) could be so placed, the other being inserted into adjacent muscle. The individual wires were sutured to the muscle fascia, which was repaired to restore as far as possible the origin of the masseter detached from the zygoma. In a few experiments spindle properties were studied without placing stimulating electrodes so as to leave the muscles undisturbed. The preparation also usually involved placing stimulating electrodes on the inferior alveolar and digastric nerves as required by the experiments of a subsequent paper.

The animal was secured in a stereotaxic frame and the body supported prone by a clamp on a thoracic vertebra. Holes were made in the skull for inserting one electrode at 10 deg to the vertical (tip caudally) to reach the mesencephalic trigeminal nucleus (MeV) and another at 25 deg to the vertical (tip rostrally) to reach the motor trigeminal nucleus, as required for other observations. The dura was reflected under oil. It was necessary to detach part of the origin of the posterior temporalis muscle from the skull. Since this part apparently contains very few spindles, there was not expected to be any significant distortion of spindle behaviour. Jaw movements were imposed by a displacement servo attached to a pin screwed into the symphysis menti. The movement patterns used were trapezoids of 10 mm total displacement. The rise and fall each lasted 1.0 s, the plateau 1.5 s and the cycle repeated every 6.0 s. The resting position of the mandible was 10 deg from the fully closed position and the 10 mm ramp stretch corresponded to 8.5 deg further opening. Maximum natural opening possible is about 45 deg. Small transient stretches were also used. They were of approximately triangular form, lasting 5 ms at the base and of variable amplitude.

The background to recording from spindle first order afferent units in the MeV has been described fully elsewhere (Cody, Lee & Taylor, 1972*a*; Taylor, 1990). The stimulus used while searching for units was a 1 Hz sine wave of 1.0 mm amplitude. The following sequence of tests was applied as far as possible to each unit. (a) Attempt to identify the muscle of origin by local pressure on the masseter, on the anterior temporalis directly and by pressing the eye through the upper

eyelid, intraorally on the medial pterygoid, and by lateral and medial deviation of the jaw. (b) Record ramp stretch response (control 1). (c) Record interspike interval histogram. (d) Repeat (b) and (c) 1 min after i.v. supplement of sodium pentobarbitone of 6–12 mg to suppress fusimotor activity (control 2). (e) Measure threshold for transient minute stretch. (f) Repeat (b) and (c) 1 min after i.v. dose of 200  $\mu\text{g kg}^{-1}$  SCh. (g) Record response to nerve stimulation while paralysis still prevented interference from the EMG response. (h) In a proportion of experiments, responses to the 1 Hz, 1.0 mm amplitude sine wave stretch were also recorded after (b), (d) and (f) above.

#### *Data analysis*

Trapezoidal responses were estimated as the means of five repeated cycles from cycle histograms with 50 bins of 100 ms each. They were constructed either on-line or from FM tape recordings with a CED 502 computer and subsequently plotted with measures of the responses as detailed below. Cycle histograms were used rather than the more usual instantaneous frequency plots in order to give more statistically stable estimates of measures such as dynamic index, which otherwise depend critically on individual interspike intervals, with consequent marked variability. The peak frequencies estimated from histograms will be expected to be lower than those from instantaneous frequency plots. The latter were additionally available in many cases from tape recordings, in order to follow the time course of changes in detail. The basic measurements made on the ramp stretch responses were as follows. Initial frequency (IF) was averaged from the 0.5 s preceding the stretch onset. Peak frequency (PF) was taken as the maximum value at the end of the dynamic stretch (i.e. ignoring any initial burst). Static index (SI) was the frequency 0.5 s after the end of the dynamic stretch. From these were derived dynamic difference (DD) as  $\text{PF} - \text{IF}$ , dynamic index (DI) as  $\text{PF} - \text{SI}$  and static difference (SD) as  $\text{SI} - \text{IF}$ .

Variability of interspike intervals was computed as coefficient of variation (c.v.) and the interval histogram plotted from 1000 intervals recorded with the jaw in the maximum stretch position of the ramp. Sinusoidal cycle histograms were recorded with twenty-five bins per cycle, taking twenty cycles. Sinusoidal fitting was performed using a least sum of squared errors routine, which ignores zero counts (Matthews & Stein, 1969).

## RESULTS

The data are based on recordings from 234 spindle afferent units. On the basis of responses to masseter or temporalis nerve stimulation or to local muscle pressure 186 of them could be attributed to their muscle of origin as follows: masseter 44 (23.7%), temporalis 115 (61.8%) and pterygoid 27 (14.5%).

#### *Evidence for elimination of natural fusimotor drive*

In assessing the properties of the spindles and their response to SCh it is desirable to start from a basis of no intrafusal contraction. This is easily achieved in hindlimb preparations by ventral root section, but not in the trigeminal system in which the motor and proprioceptive sensory fibres are mixed together in the so-called motor root. The alternative is to depress central motor outflow by deep anaesthesia and to this end stretch responses were recorded before and after a supplement of sodium pentobarbitone of 6–12 mg i.v. If there was an appreciable change, the dose was repeated till no further change occurred, in which case fusimotor output was assumed to have been eliminated.

#### *Time course of the effect of SCh and repeatability*

In order to choose the most appropriate time at which to assess the SCh effect the latter was studied in continuous records of instantaneous frequency for 62 units. In each case IF, PF and SI were measured for each ramp stretch (i.e. every 6.0 s) before,

during and after the i.v. injection, which was in 1 ml saline given in 5 s. Four representative examples of the range of changes induced are shown in Fig. 1. It is evident that all three measures reached a reasonably steady state in the period 60–90 s. Although this does not always include the period of maximum increase in

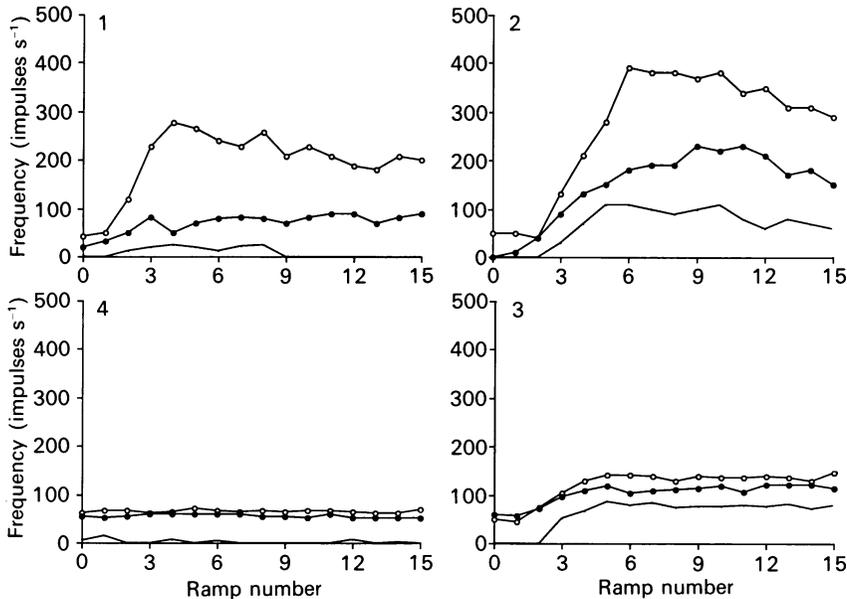


Fig. 1. Representative examples of the time course of changes in IF (—), PF (—○—) and SI (—●—) caused by single i.v. injections of  $200 \mu\text{g kg}^{-1}$  SCH in four different spindle afferents. The time scale is labelled in terms of ramp stretch number from the time of injection, each cycle lasting 6 s. The four units are numbered 1–4 according to their responses as later described in relation to Fig. 6 below.

PF, it was nevertheless taken as the most appropriate time during which to compare the SCH effects on the different units. Rack & Westbury (1966) also noted maximum PF to be reached in less than 60 s in hindlimb spindles with the same i.v. dosage.

The validity of the following analysis of SCH effects requires that the responses should be repeatable and that sensitivity of spindles to SCH should not diminish with repeated doses during the course of prolonged experiments. At least 35 min was allowed between doses and this permitted full recovery as indicated by three units studied with repeated doses. Their mean values of increase in IF with first and second tests were  $26.4$  and  $26.3$  impulses  $\text{s}^{-1}$  respectively and of increase in DD were  $71.0$  and  $71.1$  impulses  $\text{s}^{-1}$  respectively.

#### *Population properties*

The main body of data consists of measurements of ramp stretch responses without and with SCH for 234 spindle units. In the absence of any accepted criterion such as conduction velocity, other possible measures by which subgroups might be distinguished should be identifiable in the population statistics. To this end Fig. 2

presents histograms of the distributions of the basic measures IF, PF and SI and the derived measures DD, DI and SD. The controls show no clear evidence of bimodality of distribution, with the possible exception of SI in which there seems to be a small excess group at very low values. It is notable that the IF plot shows the great

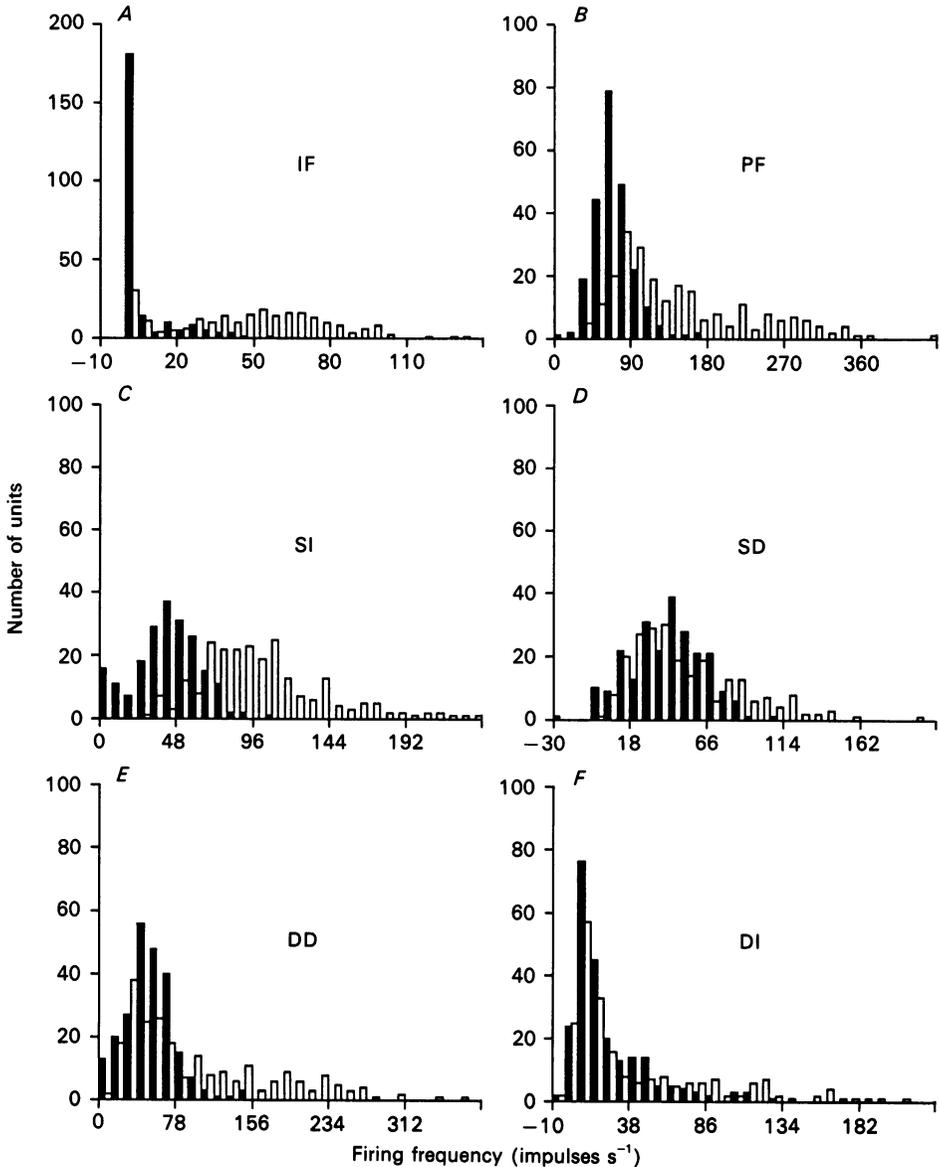


Fig. 2. Frequency histograms of the observed values of the measures of spindle afferent responses to ramp stretches for 234 units. *A*, *B* and *C* indicate the basic measures IF, PF and SI respectively, while *D*, *E* and *F* show the derived measures SD, DD and DI respectively. Filled columns are control values and open columns 1 min after  $200 \mu\text{g kg}^{-1}$  SCh.

majority of units under these conditions to have very low or absent discharge before stretch. Many of these units, however, were observed to regain a resting discharge when held at the shortened state for longer than allowed in the cyclical stretch pattern used here. The control DI distribution is skewed towards an excess of low values, while the other measures were approximately normally distributed.

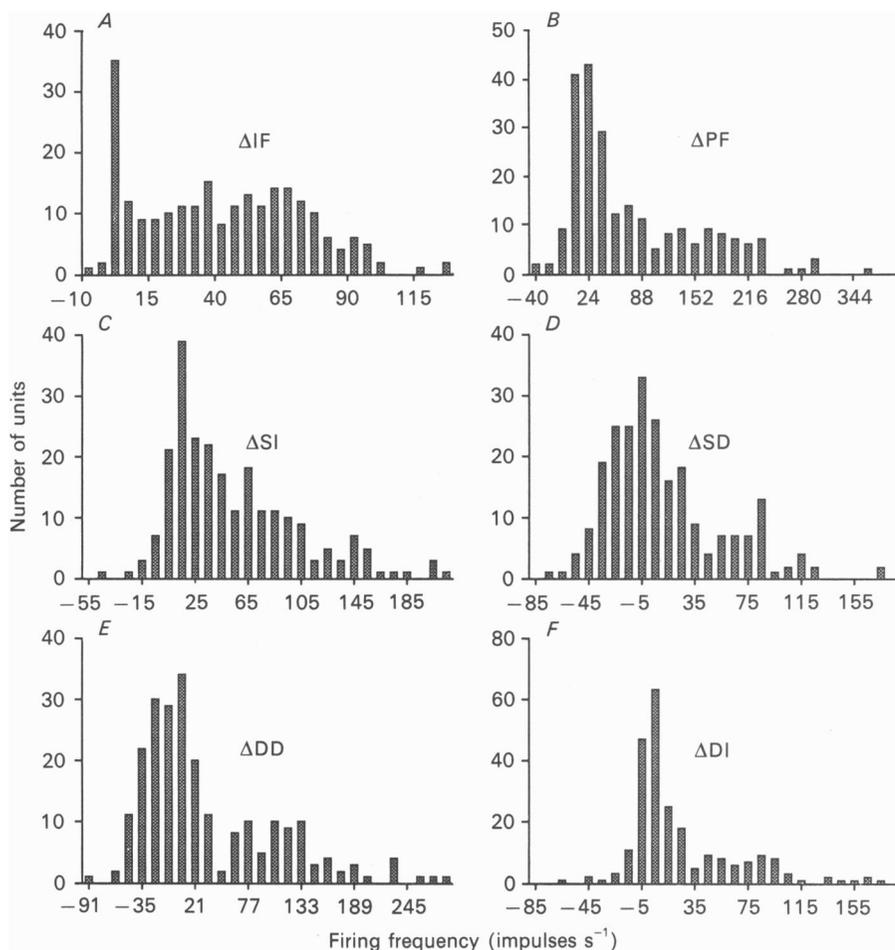


Fig. 3. Distributions of the increments in the measures of the ramp stretch responses caused by SCH.

Figure 2 also shows the values of these measures in the period 60–90 s after i.v. SCH. Of the 198 units with control IF < 10 impulses s<sup>-1</sup>, 41 were unaffected or fell slightly. In the remainder IF was increased to produce a broad, approximately normal distribution centred on 60 impulses s<sup>-1</sup>. Most units showed some increase in PF and the distribution was changed to show a tail to the right of units with a strong SCH effect. The SI was rather similarly affected. The derived measures DD, DI and SD

showed corresponding changes with a general tendency to increased skewing of distributions with excess high values, but leaving a substantial number of units either little affected (DI) or appreciably reduced (DD and DI) as becomes clearer in Fig. 3.

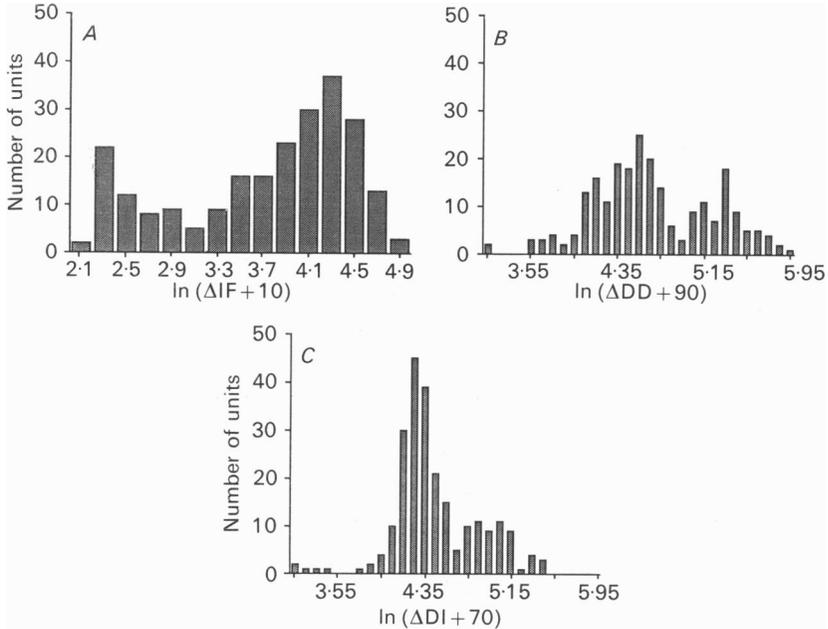


Fig. 4. Distributions of logarithmically transformed values of  $\Delta IF$ ,  $\Delta DD$  and  $\Delta DI$ . In each case a constant has been added as indicated before transformation, to avoid negative values.

It appears from previous studies (Boyd, 1985a) that Sch-induced contraction of  $b_1$  fibres will be expected to enhance dynamic sensitivity (DD and DI) and that of  $b_2$  fibres the bias (IF). It follows that it is the *increases* in these measures which will be expected to indicate the strength of the influence of  $b_1$  and  $b_2$  fibres respectively rather than their absolute values. These differences will be indicated by prefixing the variable name by  $\Delta$ , thus e.g.  $\Delta DI$  is Sch DI – control DI. The difference value distributions are shown in Fig. 3. In all cases there is some visual indication of bimodality in the distributions and this is particularly marked in the cases of  $\Delta IF$ ,  $\Delta DD$  and  $\Delta DI$ .

The question arises as to whether the distributions might be decomposed into subpopulations according to the presence or absence of an influence from  $b_1$  or  $b_2$  fibres. First it is clear that the total distributions of differences are asymmetrical, being positively skewed. When the data are logarithmically transformed the distributions each take on an appearance much more suggestive of the result of summation of two normal distributions, as shown in Fig. 4 for  $\Delta IF$ ,  $\Delta DD$  and  $\Delta DI$ . An objective method of separating subpopulations has been taken from Hald (1952) and is based on the fact that logarithmic transformation of the ordinates of a normal



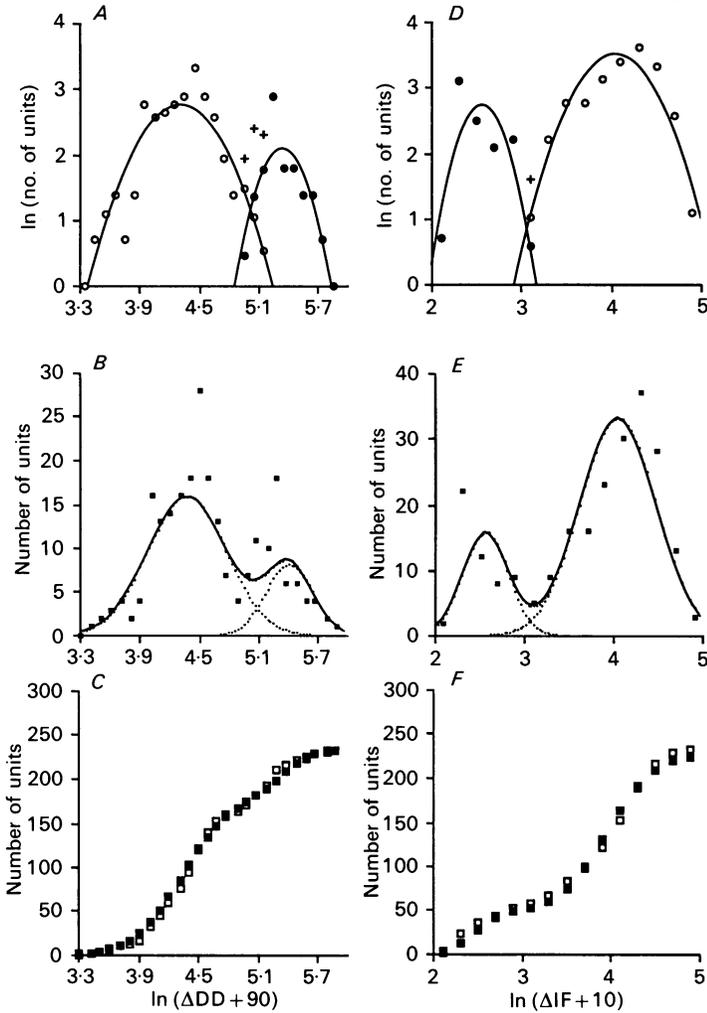


Fig. 5. Steps in the process of dividing the distributions of  $\Delta DD$  (A, B and C) and of  $\Delta IF$  (D, E and F) each into two normal subpopulations. In A the ordinates of the distribution (see Fig. 5B) have been logarithmically transformed and fitted with a parabola for abscissa values from 3.3 to 4.8 (○). This was extrapolated to the right and subtracted from the original data leaving points fitted by a second parabola (●). Original data in the region of overlap are shown by crosses. In B the ordinates of the parabolas have been transformed back into linear values and plotted separately (dotted) and summed (continuous line); ■, original data values. In C the cumulative sums of the observed distributions (□) are compared with those of the normalized fitted distributions (■). The process is repeated for  $\Delta IF$  in D, E and F, except that the first parabola was fitted for abscissa values from 3.4 to 4.9.

distribution yields a parabola, provided the class intervals are small. The process is illustrated in Fig. 5 for  $\Delta DD$ . In A, the logarithmically transformed ordinates have been plotted and fitted with a parabola using values to the left of the minimum in the distribution. Ordinates of the parabola extrapolated to the right were then

subtracted to leave a residual distribution which was then fitted with a second parabola. Converting the parabolas back by taking antilogarithms in *B* reveals two normal distributions, the sum of which is a reasonable fit to the original data. The cumulative plots in *C* are particularly convincing in this regard. The same process

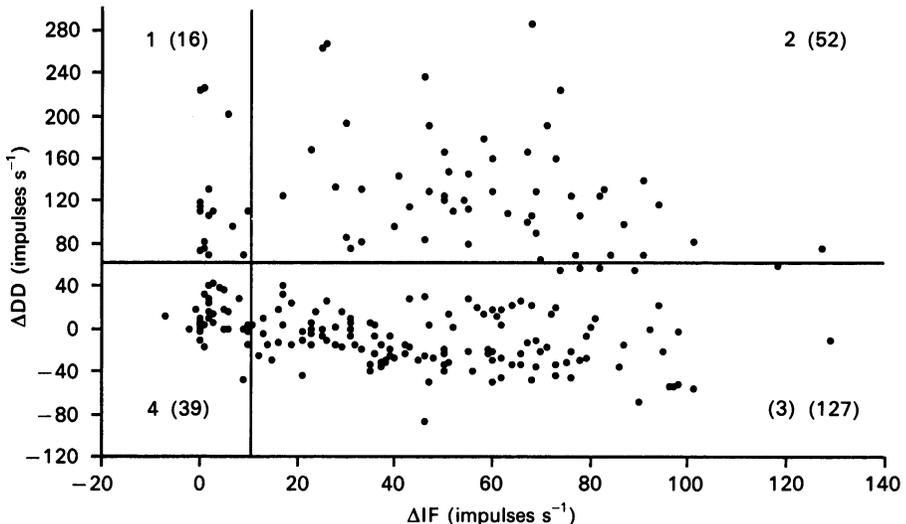


Fig. 6. Scatter diagram of values of  $\Delta DD$  against  $\Delta IF$  for all 234 spindle afferent units. The positions of the vertical line divides  $\Delta IF$  values at 11 impulses  $s^{-1}$  and the horizontal line divides  $\Delta DD$  values at 61 impulses  $s^{-1}$  as indicated by Fig. 5. The four quadrants so defined are designated 1-4 as shown, and the size of each population is shown in parentheses.

applied to the distribution of  $\Delta IF$  in Fig. 5*D-F* again leads to a strong impression that the data can be well described by two log-normal distributions. Since *DI* has long been accepted as a useful working measure of dynamic sensitivity, the distribution of values of  $\Delta DI$  has also been studied. This also indicates separation of units into two groups, one with small effects of *SCh* and the other with large effects, much as with  $\Delta DD$ . The separation according to  $\Delta DI$  is however less clear than that by  $\Delta DD$  and this may be expected because *DI* is the difference between *PF* (itself the sum of *IF* and *DD*), and *SI*, which is probably additionally influenced by  $b_2$  fibre effects.

An overview of the complete data on  $\Delta IF$  and  $\Delta DD$  is shown by the scatter plot of Fig. 6. It is immediately apparent that there is no correlation between these two measures. This is consistent with the view that they result from completely separate effects of *SCh* on the spindles. These two effects must presumably be contraction of  $b_1$  fibres leading to an increase in *DD* and a contraction of  $b_2$  fibres leading to an increase in *IF*. Although there is no overall correlation between  $\Delta IF$  and  $\Delta DD$ , the appearance of Fig. 6 and the bimodal distributions shown in Fig. 5 clearly suggest a tendency for the unit data to fall into four subgroups. These are highlighted by the lines superimposed on Fig. 6 to indicate the best values of  $\Delta IF$  and  $\Delta DD$  for the separations as derived from Fig. 5.

The interpretation which suggests itself therefore is that units in the upper part of the plot of Fig. 6 are more or less strongly influenced by  $b_1$  intrafusal fibres, while those in the right-hand side are more or less strongly influenced by  $b_2$  intrafusal fibres. As some c fibre influence is to be expected on all spindle afferents, it follows

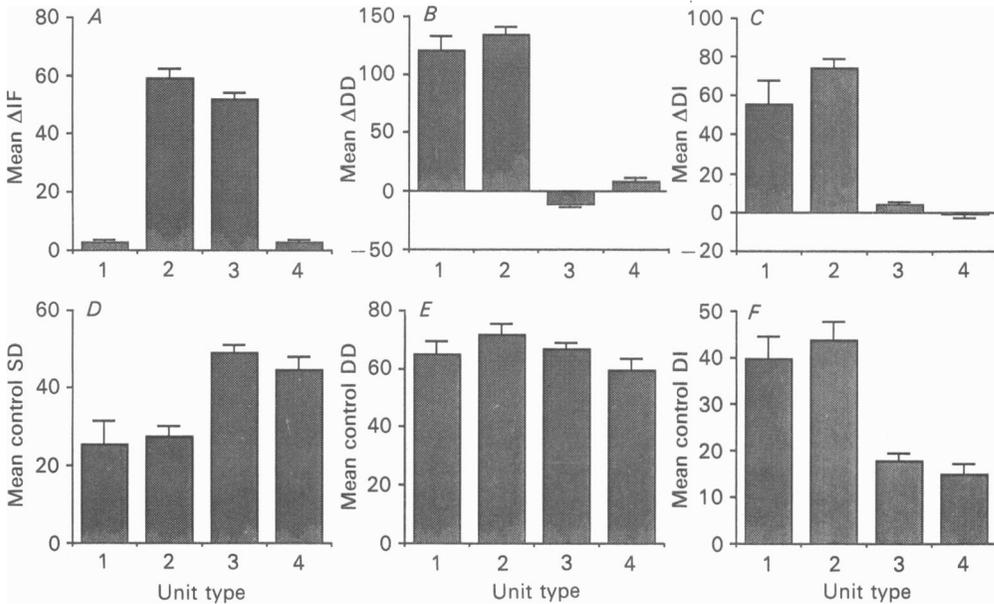


Fig. 7. Mean values (impulses  $s^{-1}$ ) of measured properties for each of the four types of unit as defined by Fig. 6. *A*, *B* and *C* show the relative effects of SCh on IF, DD and DI respectively. *D*, *E* and *F* show the control values for SD, DD and DI respectively. Bars indicate s.e.m.

that afferent units may be identified according to the combination of intrafusal muscle fibre influences by the quadrant of the plot in which they lie. Thus numbering clockwise from the top left as shown, quadrant 1 probably indicates  $b_1$  c influence, 2 indicates  $b_1$   $b_2$  c influence, 3 indicates  $b_2$  c and 4 with no evidence of  $b_1$  or  $b_2$  effects must represent units with c fibre influence only. In terms of the long-established classification of spindle afferents as primary or secondary, the above quadrants 1 and 2 would be attributed as primary and quadrant 4 as secondary. Units in quadrant 3 can be referred to as  $b_2$  c, for the present without any certainty as to whether they should be classed as primary or secondary. Further consideration of the validity of these interpretations will be left to the Discussion below. In the meantime we shall use the unprejudiced nomenclature of types 1–4 according to the quadrants in Fig. 6. There was no evidence of differences between the three muscles with respect to the sensitivity of their spindles to SCh. Comparing mean  $\Delta$ DD and mean  $\Delta$ IF for  $b_1$   $b_2$  c units by Student's *t* test between masseter and temporalis showed no significant difference. In addition, analysis of variance (ANOVA) applied to  $\Delta$ DD and  $\Delta$ IF for all units in the three muscles showed no significant dependence of these measures on the muscle of origin.

*Properties of the different afferent types in the passive and activated states*

The properties of the different types as defined above are well summarized by the bar graphs for mean values in Fig. 7. The upper row shows mean values for  $\Delta IF$ ,  $\Delta DD$  and  $\Delta DI$  displaying the differences to be expected from the way the types were

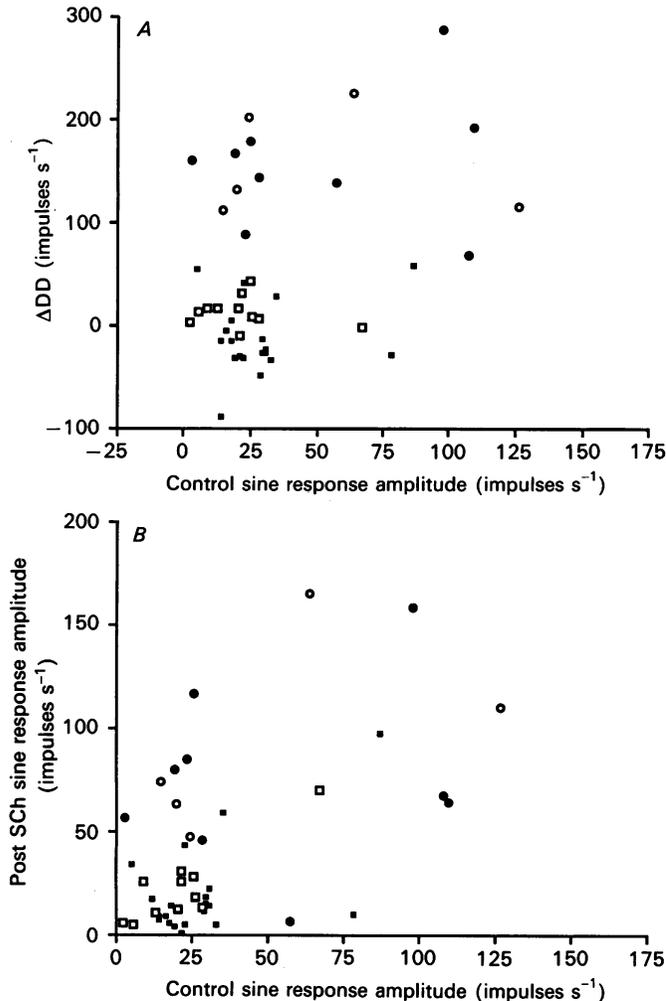


Fig. 8. Responses to sinusoidal stretching of forty-five spindle afferents related to the effect of SCh on DD (*A*) and on sine wave response amplitude (*B*). Different symbols indicate the unit types as follows:  $\circ$ , type 1;  $\bullet$ , type 2;  $\blacksquare$ , type 3; and  $\square$ , type 4.

defined. The second row shows the mean values for control SD, DD and DI. It is seen that while mean control DD does not differ significantly between the four types (*E*), mean control DI is very significantly higher for types 1 and 2 than for types 3 and 4 (*F*). Evidently, this difference depends neither on a greater dynamic stretch sensitivity (DD), nor on a higher peak firing rate (PF) for types 1 and 2, but instead

on lower values for SI and SD. Thus the high DI of type 1 and 2 units *in passive conditions* depends on marked adaptation of firing rate rather than on inherently high stretch sensitivity. Another aspect of the passive behaviour is that the static stretch sensitivity, as measured by mean control SD appears to be higher for types 3 and 4 than for types 1 and 2.

TABLE 1. Effect of SCh on the sine wave response of the different afferent types

<i>n</i>	Afferent type			
	$b_1 c$ 5	$b_1 b_2 c$ 9	$b_2 c$ 20	<i>c</i> 11
Control sine response amplitude	49.9	52.4	28.3	21.8
SD	47.1	42.0	20.2	17.3
$\Delta$ sine response amplitude	42.0	23.2	-8.0	0.6
SD	43.6	54.9	20.9	8.7
Control sine response mean	-11.0	-8.1	20.3	19.7
SD	35.2	28.5	22.6	17.2
$\Delta$ sine response mean	34.8	84.2	37.6	11.5
SD	45.9	37.1	37.1	14.6

All values of frequency and SD in impulses  $s^{-1}$ .

### *Sine wave responses*

For forty-seven units responses to 1 Hz sine waves of 0.85 deg amplitude were recorded after ramp stretch responses. From previous reports (Price & Dutia, 1987) the most obvious use of this test is to derive a figure for sensitivity to stretch, which is expected to be higher for primary endings than for secondaries (Matthews & Stein, 1969). Figure 8A shows the control response amplitude compared with  $\Delta DD$  taken as an index of  $b_1$  influence. The correlation is weak ( $r = 0.38$ ), but significant at the 1% level. Of the nine units with sine response amplitude  $> 50$  impulses  $s^{-1}$ , six would be classified as having significant  $b_1$  influence by virtue of having  $\Delta DD > 60$  impulses  $s^{-1}$ . The less sensitive units have  $\Delta DD$  values scattered over the whole observed range.

Figure 8B shows that the units with low control sine wave sensitivity, but with  $\Delta DD > 60$  impulses  $s^{-1}$ , are shifted up by SCh to make a very clear and significant correlation. The existence of this correlation with the bimodally distributed  $\Delta DD$  implies that sine wave sensitivity in the presence of SCh should also be bimodally distributed. However, the separation of the units into two subpopulations on the basis of SCh enhanced sine wave sensitivity or by the increment in sensitivity is not as clear as with  $\Delta DD$ . The statistics of the sine wave responses are summarized in Table 1.

Change in mean firing rate during sine wave stretches in the presence of SCh reflect the  $\Delta IF$  seen with trapezoids ( $r = 0.53$ ,  $P = 0.001$ ), though there is much residual variation. The mean control phase advance of the sine wave responses was 60 deg, with no difference between unit types. There was no significant correlation of the  $\Delta$  phase with any other measure. Thus the ramp stretch testing seems to be superior to sine wave testing for estimating both  $b_1$  and  $b_2$  influences. The phase measurements appear to be of little value for purposes of classification.

*Other unit properties*

Conduction velocity was measured for fifty-four units capable of being excited by stimulation of the masseter nerve or the combined masseter and temporalis nerve. The histogram of values seen in Fig. 9*A* is not distinguishable from a single normal

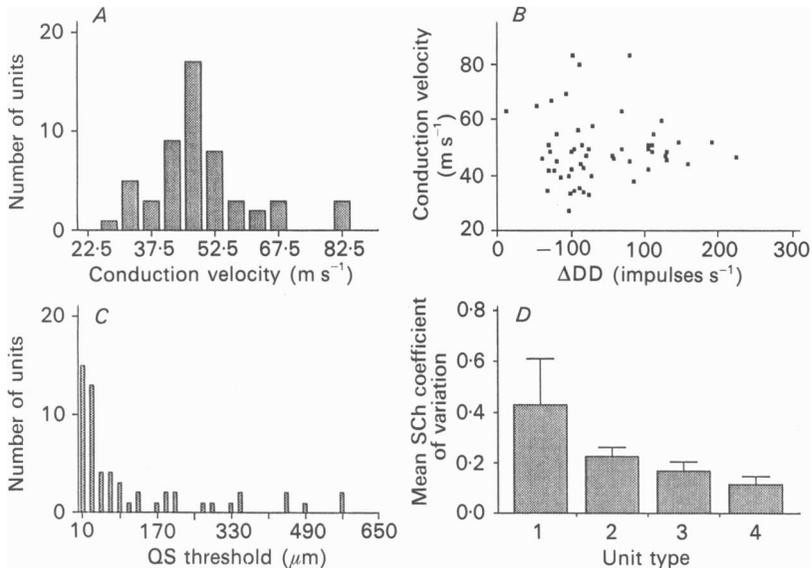


Fig. 9. Various properties of spindle afferent units. *A*, distribution of conduction velocities of masseter units. *B*, scatter plot of conduction velocity against  $\Delta DD$ . *C*, distribution of threshold amplitude of units to transient stretch ('quick stretch', QS). *D*, mean coefficient of variation for the four unit types. Bars represent s.e.m.

distribution and is therefore unlikely to be helpful in separating subtypes. Indeed, the scatter plot of  $\Delta DD$  and conduction velocity in Fig. 9*B* reveals no correlation and no sign that the different groups defined by  $\Delta DD$  or  $\Delta IF$  might differ in conduction velocity. This conclusion was confirmed by ANOVA.

The threshold amplitude for brief transient stretches was recorded for fifty-eight units as a possible alternative to studying high frequency vibration following. However, as seen in Fig. 9*C* thresholds fell into a single highly skewed population with 50% below 50  $\mu\text{m}$ . Testing by two-way ANOVA showed no relation to the groupings defined above.

Coefficient of variation of interspike intervals is another possible discriminating factor, being generally higher in primary endings than in secondaries (Stein & Matthews, 1965). Some units would not fire continuously at constant muscle length, but only during activation by Sch. Activation by Sch did not significantly alter the coefficient of variation of units with control discharge, therefore this condition was used for all units. Figure 9*D* indicates a tendency for variability to be greater for unit types 1 and 2 than for the others and lowest for type 4. Two-way ANOVA showed the apparent difference between groups separated on the basis of  $\Delta DD$  not to quite reach the 5% level of significance ( $P = 0.085$ ) and that between high and low  $\Delta IF$  to have no significance ( $P = 0.86$ ).

*Time course of SCh effects in the different unit groups*

In view of the description by Dutia (1980) of three phases in the onset of effects of infusions of SCh on hindlimb spindle afferents, recordings have been made of changes in trapezoidal stretch responses for 90 s following single i.v. injections of  $200 \mu\text{g kg}^{-1}$ . Examples of the behaviour of one unit of each type are shown in Fig. 1. Of sixty-two units so tested, fourteen had very little response to SCh and so were classed as type 4. Only two were classed as type 1 and are not considered further here. The mean changes for twelve type 2 units and for thirty-three type 3 units showed no evidence of the responses being divisible into three distinct phases, as reported to be the case for primary endings in hindlimb muscles (Dutia, 1980). However, in view of the fact that the latter work generally involved i.a. infusions of the drug, it was thought important to try that route also in the present series. SCh was therefore infused into the carotid artery via its lingual branch at doses of  $100 \mu\text{g kg}^{-1} \text{min}^{-1}$  or  $1 \text{mg kg}^{-1} \text{min}^{-1}$  in a volume of saline of  $0.5 \text{ml min}^{-1}$ . In some cases the effect on ramp stretch responses was much slower in onset with i.a. infusions than with a single i.v. dose, though the final sizes of the effects were the same. It seems likely that in these cases the i.a. infusion was not being carried as expected directly to the muscle, but only reached it indirectly after passing into the general circulation. This would happen if there should occur immediately after the tip of the cannula a branch of the artery passing to tissues other than the muscle in question. In other cases there was little difference in the time course of the effects according to which route was used, though with a very large i.a. dose of  $1 \text{mg kg}^{-1} \text{min}^{-1}$  the maximum size of the effects was larger than for the i.v. dose of  $200 \mu\text{g kg}^{-1}$ . However, taking all the data into consideration, whether the effects of SCh were prompt or delayed, there was no sign of distinct phases in the responses. In particular, we did not see a late enhancement of static index (cf. position response in Dutia, 1980). Thus the use of i.a. infusions had the disadvantage of uncertainty as to the time course of delivery of SCh to the muscle. Moreover, it did not appear to offer any additional help in the classification of responses at least in the case of the jaw muscle spindles (Durbaba, Rodgers & Taylor, 1991).

## DISCUSSION

Systematic use of SCh for classification of muscle spindle afferents was introduced by Rack & Westbury (1966). The principal effect noticed was a marked rise in dynamic sensitivity of primaries similar to the effect of dynamic fusimotor stimulation, but at this stage the two distinct bag fibres had not been recognized. The study of soleus spindle afferents by Dutia (1980) was the first to be able to draw on the results from Gladden (1976) indicating that the effects of acetylcholine were due to contraction of  $b_1$  and  $b_2$  intrafusal fibres and that  $b_1$  fibres were more sensitive than  $b_2$  (see also Boyd, 1985*b*). Considering particularly the afferents with conduction velocities intermediate between those thought to be clearly primary ( $> 80 \text{m s}^{-1}$ ) or secondary ( $< 60 \text{m s}^{-1}$ ), it was possible to attribute most of these to one or other type, leaving only a small proportion with intermediate properties. Later, Price & Dutia (1987) sought to use a similar approach to classify afferents from the spindles of the dorsal neck muscles of the cat, in which conduction velocity measurements

were not available. They found one group to be little affected, like the hindlimb secondaries and another to have marked increases in their dynamic responses and in their static discharge rate, like typical primaries. A third group showed only enhancement of static firing, which suggested an origin in  $b_2c$  type capsules of tandem spindles, known to be common in neck muscles (Richmond & Abrahams, 1975). While these conclusions appear to be very plausible on the basis of the examples of responses used as illustrations, the data were not available in a form which permitted the objective statistical definition of boundaries between the various unit types. In the present observations on jaw muscles conduction velocity measurements were made where possible, but were found to be of no help in classification. It was therefore considered best in the first place, and in the absence of morphological checks, not to seek to separate units into supposed primary or secondary groups. Rather it was attempted to use the SCh effects to give quantitative estimates of the strength of the influence of  $b_1$  and  $b_2$  fibre contraction on each afferent.

The central finding of the present study is that the muscle spindle afferents from the jaw-closer muscles of the cat can be divided into four types on the basis of their response to SCh. This was established by using a standardized testing procedure on a relatively large population of units, so permitting statistical definition of subpopulations. It is important before proceeding further to consider which effects best indicate respectively  $b_1$  and  $b_2$  contractions and whether they act independently on the sensory endings. Gladden (1976) observed that acetylcholine applied to isolated tenuissimus spindles caused both types of nuclear bag fibres to contract, but not nuclear chain fibres, and SCh is believed to have the same action, as discussed in detail by Boyd (1985*a, b*). The best information regarding the effects of contraction of  $b_1$  and  $b_2$  fibres on afferent discharge is summarized by Boyd, Murphy & Moss (1985) and by Boyd, Sutherland & Ward (1985). Contraction of  $b_1$  fibres by dynamic fusimotor action or by SCh generally causes only a small increase in bias (equivalent to our  $\Delta IF$ ) in primaries and rarely any increase in secondaries. Its essential effect is to enhance sensitivity to dynamic length change regularly in primaries and in any occasional secondary which has a termination on a  $b_1$  fibre. This effect would show up in the present data as an increase in DD and probably in DI. There is a problem however with using DI to indicate  $b_1$  effects in isolation which can be expressed as follows. DI is given by  $PF - SI$ , but both the latter include IF, so that  $DI = DD - SD$ . Direct observation has shown that  $b_1$  activation increases static sensitivity or SD (Boyd, 1981, 1985*a*), so making the increase in DI less than that in DD. Also  $b_2$  activation actually decreases static sensitivity or SD (Boyd, 1981), so causing DI to be contaminated by  $b_2$  effects. Attention has also been drawn previously to the different time course after SCh of changes of IF on the one hand and of DD and SD on the other (Durbaba *et al.* 1991). The fact that for  $b_1 b_2c$  units DD and SD are maintained for 1.5 min while IF falls markedly, underlines the conclusion that SD like DD is largely determined by  $b_1$  fibre contraction, unlike IF, which is largely  $b_2$  dependent. The use of  $\Delta DD$  is further justified operationally by the clearer separation of two distinct subpopulations of units using  $\Delta DD$  rather than  $\Delta DI$ . This is the reason for the change to the use of  $\Delta DD$  in the present study from the previous use of  $\Delta DI$  (Taylor & Durbaba, 1990).



Contraction of  $b_2$  fibres strongly biases primary afferents and has a similar but smaller effect on secondaries having endings on  $b_2$  as well as on  $c$  fibres. Thus SCh should cause a significant rise in IF in any afferent terminating on a  $b_2$  fibre.

It could be suggested that the observation of a large number of units with little or no  $b_1$  effect ( $b_2c$  type) might result from inadequate delivery of SCh to some spindles to activate the  $b_1$  fibres. This can be discounted however because the  $b_2$  fibres are well known to be less sensitive than the  $b_1$  fibres to SCh and units showing no significant increase in DD nevertheless usually showed increases in IF. It is also worth noting from Fig. 8F that for the populations designated as having  $b_1$  influence (types 1 and 2), the mean control value of DI is much higher than that of the non- $b_1$  afferents (types 3 and 4).

It is clearly important to relate this classification to the conventional primary/secondary distinction originally established for hindlimb spindles. There is no problem in assigning our first and second groups (designated as  $b_1c$  and  $b_1b_2c$ ) as primary afferents as it is generally accepted that primary endings are the main sensory terminals on  $b_1$  fibres. Any secondary ending making contact with a  $b_1$  fibre seems to be little affected by it (Boyd, 1985a). It is equally clear that the fourth group must represent units with predominantly  $c$  fibre endings, i.e. secondary afferents. The third group, which is designated  $b_2c$ , however, needs special consideration as it may include not only primary afferents from  $b_2c$  capsules of tandem spindles, but also secondary afferents with endings on  $b_2$  as well as on  $c$  fibres. As described in the Results section, attempts to subdivide this group into primaries or secondaries on the basis of conduction velocity, coefficient of variation, transient stretch threshold or various measures of adaptation have not been successful. If the  $b_2c$  units are actually capable of subdivision, it must presumably be on the basis of the biophysical properties of primary and secondary nerve endings or on their central connections. The observations by Scott (1990) in which spindles were conditioned by five stimuli in the shortened state, followed by slow lengthening to a firing frequency of 20 impulses  $s^{-1}$  before the test stretch, might be helpful in this regard. In primary afferents this procedure seems to enhance the rapid adaptation phase, which is thought to be due to a property of the ending rather than of the intrafusal muscle fibres. This matter is considered further in the following paper (Taylor, Rodgers, Fowle & Durbaba, 1992).

The main bodies of data now available on the use of SCh to classify spindle afferents relate to triceps, tenuissimus and peroneus tertius in the hindlimb, dorsal neck muscles and jaw elevator muscles. From these some comparisons of the abundance of the various types are possible. First, it must be said that  $b_1c$  type responses have not been specifically described before, though histological studies of lumbrical muscles (Decorte *et al.* 1990) showed appreciable numbers of single bag fibre capsules which lacked the  $b_2$  fibre. In a brief report on rat jaw muscles (Banks *et al.* 1988),  $b_1$  and  $b_2$  fibres were found to be often separately innervated by primary endings, so that a marked enhancement of dynamic response with SCh without significant bias could well be interpreted in these terms. With regard to  $b_2c$  type responses, the study of soleus by Dutia (1980) may be interpreted from later reasoning to have included four of this type out of fifty-three afferents. The later study of medial gastrocnemius (Price & Dutia, 1989) indicated eight out of eighty-

two, while one  $b_2c$  unit was seen amongst eight in tenuissimus. The latter was particularly interesting as it was traced histologically to a single bag fibre capsule and so represents the only direct morphological correlation with SCh diagnosis so far. In neck muscles twenty-four out of seventy-two afferents had the properties expected of  $b_2c$  afferents (Price & Dutia, 1987), a high proportion which fits the known frequency of tandem capsules in these muscles (Richmond & Abrahams, 1975; Richmond, Bakker, Bakker & Stacey, 1986). The present data indicate 127 out of 234 units to be of this type, an unexpectedly high proportion. The most detailed of the recent morphological studies of jaw muscle spindle innervation come from the rat masseter (Banks *et al.* 1988; Rowlerson, Mascarello, Barker & Saed, 1988). Reports agree that there are many unusual spindle complexes with various innervation patterns. In particular, Banks *et al.* (1988) noted  $b_1$  and  $b_2$  fibres to be often separately innervated. This situation, if it exists also in the cat, could provide the structural basis for our observation of a high proportion of  $b_2c$  responses, irrespective of the existence of  $b_2c$  tandem spindle capsules. Various morphological studies on cat jaw muscles (Lund *et al.* 1978; Rowlerson *et al.* 1988) report the presence of conspicuous complexes of spindles, with some tandem capsules. This is suggestive of the existence of greater diversity of innervation patterns than seen in the most commonly studied hindlimb muscles. There is a clear need here for more correlative studies of structure and function.

From the experimental point of view, the jaw muscle spindles have proved to be particularly rewarding subjects for the study of afferent specialization. The absence of any useful guidance from conduction velocity forced the adoption of an unbiased statistical assessment of a wide range of properties and the effects on them of SCh. This resulted in the definition of quantitative criteria for the separation of subpopulations and these criteria can now be tried in other situations as in the following paper (Taylor *et al.* 1992). It is clear that, in the absence of intrafusal fibre activation, no reliable classification can be achieved from passive stretch responses. This conclusion has been drawn also by Banks, Ellaway & Scott (1980) in peroneus brevis and by Scott (1990) who were unable to detect subpopulations corresponding to  $b_2c$  endings. Price & Dutia (1989) found the same result in neck muscles. Even simple separation into primary and secondary types by stretch responses is difficult to justify in the absence of intrafusal activation. In the various studies in which this has been attempted (Richmond, Anstee, Sherwin & Abrahams, 1976; Wei *et al.* 1986) the separations proposed are quite reasonable, but in the absence of some morphological confirmation can hardly be accepted with complete confidence. Scott (1990) described peroneus brevis stretch testing after an arbitrary conditioning, as described above. A combination of an initial burst, a break in firing at the beginning of the hold phase (rapid adaptation) and silence during release at  $2.5 \text{ mm s}^{-1}$  was thought to identify primary afferents, but again the standard for comparison was conduction velocity and the method did not distinguish  $b_2c$  afferents. These were subsequently identified in peroneus tertius as primaries with no enhancement of dynamic response by SCh (Scott, 1991).

In conclusion, it has been demonstrated that the value of SCh for classification of muscle spindle afferents can be enhanced by a population statistical approach. It may be that by an extension of the technique to other muscle groups a case may be

made for supplementing the usual classification based on the presumed ending morphology with one based on the functional influences of the different intrafusal muscle fibre types.

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