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PROJECTION OF CAT JAW MUSCLE SPINDLE AFFERENTS RELATED TO INTRAFUSAL FIBRE INFLUENCE

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SUMMARY

1. A method of classification of muscle spindle afferents using succinylcholine (SCh) and ramp stretches has recently been described, which appears to estimate separately the strength of influence of bag_1 (b_1) and of bag_2 (b_2) intrafusal fibres. Increase in dynamic difference (ΔDD) indicates b_1 influence whilst increase in initial frequency (ΔIF) indicates b_2 influence. The significance of this classification has now been examined by correlation with the strength of synaptic projection of jaw muscle spindle afferents to the fifth motor nucleus (MotV) and the supratrigeminal region (STR) in anaesthetized cats.

2. Projection strength was estimated by computing the extracellular focal synaptic potential (FSP) from spike-triggered averages of 1024 sweeps at 100 μm intervals along tracks through STR and MotV. Trigger pulses were derived from spindle afferent cell bodies of the jaw-closer muscles recorded in the mesencephalic trigeminal nucleus, and characterized by the effect of SCh on their responses to ramp-and-hold stretches.

3. The maximum size of FSPs in tracks traversing STR and MotV ranged from 2·08 to 36·99 μV with a mean of 7·55 μV. The amplitudes were bimodally distributed into roughly equal-sized groups with high and low amplitude FSPs.

4. Mean values of ΔIF were significantly greater for the group with large FSPs than for those with small FSPs. There were no significant differences in ΔDD. FSP amplitude was significantly positively correlated with ΔIF, but not with ΔDD.

5. Spindle afferents with high values of FSP amplitude in MotV had a wide range of values of ΔDD (b_1b_2c and b_2c groups), while units with large FSPs in STR were all in the b_2c category. Some evidence is presented to indicate that this reflects a preferential projection of secondary afferents to the STR.

6. For those units with projection to both STR and to MotV, there was a significant positive correlation between FSP amplitude in the two nuclei.

7. These results indicate that the extent of the b_2 influence on spindle afferents predicts the central projection strength better than does the b_1 influence. This finding is discussed from the viewpoint of possible developmental and functional issues.

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INTRODUCTION

The classification of muscle spindle afferents into primary and secondary types has a strong historical basis (Ruffini, 1898; Matthews, 1972) and, considering the simple morphological observation upon which it was originally founded, has served remarkably well in the design of physiological studies. However, recent years have yielded many reports of spindle structure and behaviour which are difficult to classify confidently into this binary system. On the other hand, with the growth of knowledge of the intrafusal muscle fibre types and the recognition that afferents may have a variety of combinations of termination upon them it becomes worthwhile considering whether a more functionally useful classification might be based on the relative influence which each afferent receives from the bag_1 (b_1), bag_2 (b_2) and chain (c) fibres. The feasibility of this approach was examined in two recent papers (Taylor, Durbaba & Rodgers, 1992*a*; Taylor, Rodgers, Fowle & Durbaba, 1992*b*) by the use of the drug succinylcholine (SCh) which strongly activates b_1 and b_2, but paralyses c fibres. It was proposed that the b_1 influence was best indicated by increases in dynamic responsiveness as indicated by the increment in dynamic difference (ΔDD) in cyclically repeating ramp-and-hold stretches. The b_2 influence was thought to be indicated by the increment in initial frequency (ΔIF). The distributions of these measurements in both jaw and hindlimb muscle spindles were demonstrably bimodal but uncorrelated, which was taken to indicate four groupings. These were thought to correspond to b_1c, b_1b_2c, b_2c and c fibre influences.

The validity of this approach could be tested in two different ways. Most obviously, attempts should be made to relate the morphology of individual endings with their classification by SCh. This is likely to be extremely difficult in the case of the cat jaw muscles, because of their bulk and complexity, but might be tried on a very small muscle in a way similar to that used for tenuissimus by Price & Dutia (1989). The other possible way is to examine the central projection patterns for each afferent. For any classification to have real functional validity it may be argued that information from the different groups should be processed differently. Specifically we have examined in the present study the monosynaptic excitatory termination of individual afferents within and adjacent to the fifth nerve motor nucleus (MotV) using spike-triggered averaging of extracellular focal synaptic potentials (Appenteng, O'Donovan, Somjen, Stephens & Taylor, 1978). A brief presentation has recently been made of some of the resulting data (Taylor, Durbaba & Rodgers, 1990).

METHODS

The experimental arrangements for these observations have mostly been reported in the paper on the jaw spindle afferent classification (Taylor *et al.* 1992*a*) for which the same animals were used. Briefly, cats were anaesthetized with sodium pentobarbitone (40 mg kg^{-1} I.P. with I.V. supplements of 6–12 mg). Anaesthesia was kept deep enough to effectively suppress fusimotor activity and this together with monitoring of blood pressure ensured the effectiveness of anaesthesia during the administration of the muscle relaxant SCh. Animals were prepared for stereotaxic extracellular recording from muscle spindle first-order afferent cell bodies in the mesencephalic trigeminal nucleus (MeV) and from the MotV. The latter recording was via a glass-coated or varnished stainless-steel electrode with a relatively large tip exposed (20–40 μm) in order to average field potentials over such a distance rather than to be unduly affected by unitary spikes (Taylor, Stephens, Somjen, Appenteng & O'Donovan, 1978). This electrode was advanced with a

stepping motor drive at an angle of 25 deg to the vertical with its tip directed rostroventrally. Tracks were aimed at MotV initially 4 mm lateral and 2·5 mm caudal to the ear bar zero (Berman, 1968). The recording amplifier was a JFET operational amplifier (type 071, Texas Instruments) connected as a voltage follower and then to a recording system (Medelec MS6, Medelec Ltd, Woking, Surrey) to give sensitivity of 50 μV cm^{-1} and bandwidth of 1·6 or 8 Hz to 3·2 kHz. Field potentials resulting from stimulation of the ipsilateral inferior alveolar nerve (IAN) or masseter nerve or from minute transient muscle stretches ('quick stretch') were used to help to locate the MotV. Spindle afferent cells were characterized by standardized ramp-and-hold stretches in control conditions and 1 min after an I.V. dose of 200 μg kg^{-1} of SCh as previously described (Taylor *et al.* 1992*a*). The tonic firing of each unit was then used to trigger a signal averager, the input of which was derived from the MotV electrode, after passing through a 2 ms analog delay circuit. Usually 1024 sweeps were summated and displayed at a final gain of 16 or 32 times that of the original recording and on a time scale of 1 ms cm^{-1}. The averager used sampled 1024 ordinates in 10 ms. The averaged signal was transferred to disk files via a CED 502 computer system for subsequent scaling and plotting. Spike-triggered averaged unitary field potentials were recorded in this way at 100 μm intervals along tracks spaced on a 0·5 mm grid. The usual protocol was to track in this way with one spindle unit and while recording compound synaptic field potentials caused by stimulating IAN or masseter nerve or by quick stretch, until it appeared that the centre of the MotV was being traversed. Unitary field potentials were then recorded at fifteen to twenty successive points at 100 μm intervals along this track centred on the MotV for a number of subsequently isolated spindle afferents.

At the end of the experiment two iron marks were made spaced by a known distance on one track by passing current (10 μA, electrode positive) for 30 s. The animal was killed by anaesthetic overdose then perfused via the thoracic aorta with 1 l of saline containing heparin followed by 1 l of 10% formal saline with 1% potassium ferrocyanide, to form Prussian Blue marks with the deposited iron. Serial paraffin sections were prepared at 10 μm intervals and stained with Cresyl Fast Violet and Solochrome Blue. The relationship of the electrode tracks to the MotV, the supratrigeminal region (STR) and other structures was determined from study of the series.

RESULTS

Localization of motor nucleus

Because the MotV is only about 1 mm in diameter and at a depth of 16 mm below the surface of the cerebellum, it is sometimes not easy to locate stereotaxically. It is therefore very helpful to have functional tests to apply while making tracks with the microelectrode. The most useful were the responses to IAN stimulation, minute quick stretch of the jaw muscles and antidromic stimulation (AD) of the masseter nerve. These are shown recorded at depths increasing in increments of 200 μm along a track traversing the MotV in Fig. 1. Note that with IAN stimulation at depth 4 there is a train of spikes at high frequency (maximum 1120 impulses s^{-1}) which are so repeatable as to be clearly preserved in the average of sixteen sweeps. This is characteristic of interneurones in the STR (Kidokoro, Kubota, Shuto & Sumino, 1968). At this depth quick stretch produced a small negative field potential which is consistent with excitation from jaw elevator spindle afferents known from morphological studies to project into this region (Dessem & Taylor, 1989). Masseter nerve stimulation also produced a negative focal synaptic potential (FSP) at this depth, presumably for the same reason. At subsequent depths in this track (traces 5–9) with IAN stimulation, interneurone spikes are not seen, but a positive field potential appears with a latency of 1·4 ms lasting for a maximum of 9 ms. Its first part shows a pattern of ripples consistent with its being generated by repetitive firing of interneurones such as that indicated in trace 4, and it therefore seems likely to be due to the inhibitory action of STR neurones on MotV cells as proposed by Kidokoro *et al.* (1968). In line with this we see that quick stretch produces an excitatory FSP

reaching a maximum in traces 7 and 8. Masseter nerve stimulation yields a negative field potential growing in size from traces 5–8 with a latency of 1·03 ms and this is thought to be due to monosynaptic excitation of MotV by spindle afferents. A larger and sharper negative potential with a preceding positive deflection is seen growing

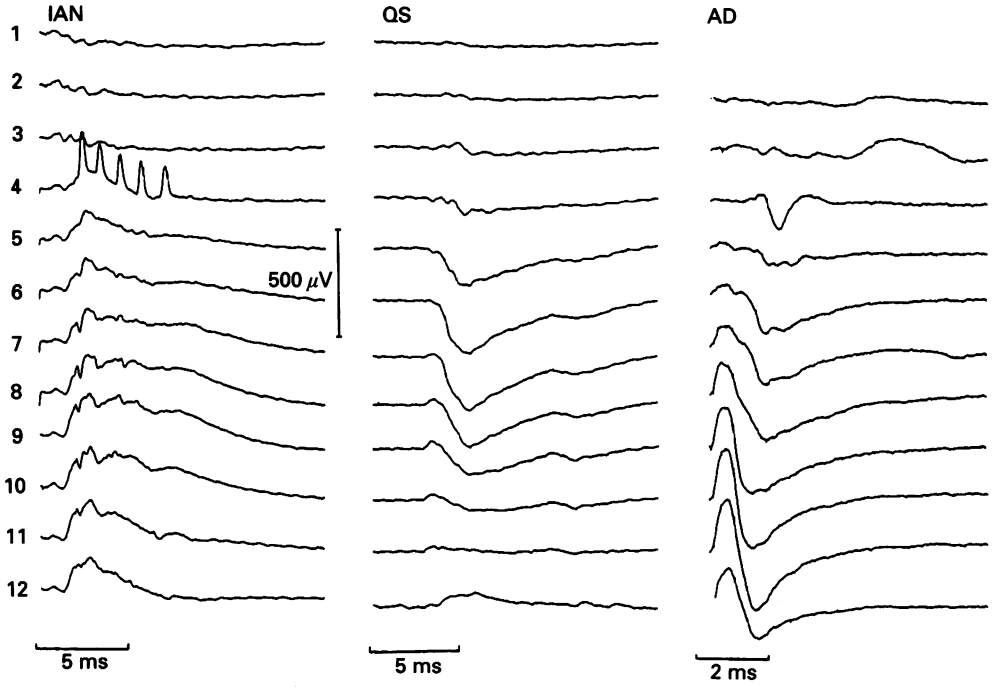

Fig. 1. Field potentials recorded at intervals of 200 μm along an electrode track passing through the STR and the MotV. Responses are shown to stimulation of IAN (left column), masseter nerve (AD, right column) and to quick stretch of the jaw elevator muscles (QS, middle column). The electrode tip was dorsal to the STR in trace 1 and ventral to MotV in trace 12. Each trace is an average of sixteen sweeps, with positive shown upward. Stimulus strength: IAN, 1·2 × threshold; AD, 2 × threshold; QS, 100 μm stretch.

from traces 8–11. The negative phase has a latency of 0·91 ms and is believed to be due to antidromic invasion of MotV cell bodies. The proposed interpretation of Fig. 1 therefore is that the microelectrode tracked successively through the STR and MotV and this was borne out by the subsequent histological analysis.

Focal synaptic potentials due to single afferents

As an example of the FSPs obtained by STA from single afferents Fig. 2 shows records obtained in the same experiment as in Fig. 1. Though averaged FSPs were recorded at 100 μm intervals they are shown here at 200 μm intervals to correspond with the traces in Fig. 1. The uppermost trace shows the triggering spike recorded in the MeV through the same delay as used for the field potentials. A negative FSP is seen very clearly at depth 4, starting 0·22 ms after the positive peak of the trigger spike and increasing to a maximum in trace 6. This corresponds well with the depth

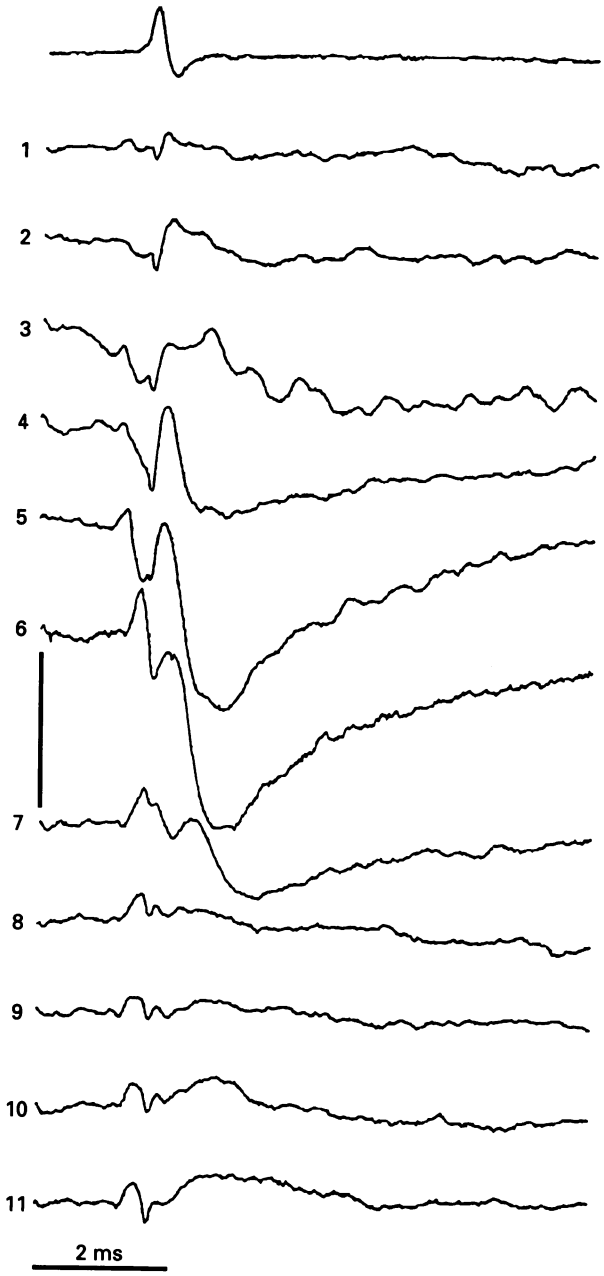

Fig. 2. Extracellular focal synaptic potentials recorded by averaging 1024 sweeps each with the trigger pulse derived from a spindle afferent cell in MeV. The uppermost trace is the averaged version of the trigger spike recorded with the same delay (2 ms) as used for the rest of the traces. The other traces are numbered to correspond with the recording depths in Fig. 1. Voltage calibration, 160 μV for afferent spike and 10 μV for FSPs.

in Fig. 1 at which the quick stretch field potential reached a maximum, though it is a little above the depth for maximum positive field for IAN stimulation and 800–1000 μm above the point of maximum AD field potential following masseter nerve stimulation. Preceding the FSP recorded by STA there is in all cases a biphasic

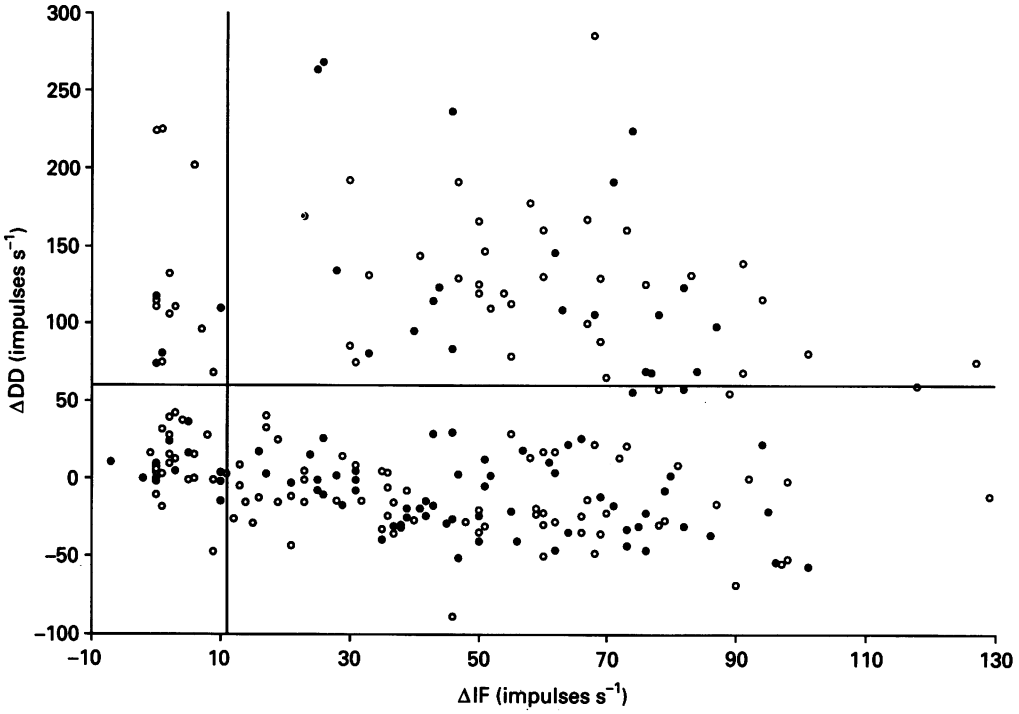

Fig. 3. Scatter plot of the increments in dynamic difference (ΔDD) against the increment in initial frequency (ΔIF) caused by a single I.V. injection of 200 μg kg^{-1} of succinylcholine for 234 jaw elevator muscle spindle afferents. The units used for the present field potential study are shown by filled symbols. The horizontal line indicates the best division into two subpopulations with low and high values of ΔDD, the vertical line similarly for ΔIF.

or multiphasic wave which may be interpreted as due to the invasion of the presynaptic axon terminal or of an adjacent presynaptic afferent branch (see Watt, Stauffer, Taylor, Reinking & Stuart, 1976; Munson & Sypert, 1979). The predominantly negative form and small size of the wave in traces 1–4 is consistent with recordings from axonal branches, while the larger size and positive–negative sequence in trace 6 is typical of invasion of presynaptic terminals. The interval between the positive peak of the presynaptic spike and the onset of the negative FSP is 0·58 ms. The FSP rise time from 10 to 90% is 0·43 ms (trace 6) and the duration at 50% of maximum is 1·87 ms. The peak amplitude in this case (between traces 5 and 6) is 15·2 μV. It is interesting to note that in traces 10 and 11 the field potentials have become positive as the electrode has passed through the motoneurone pool. It is presumably detecting the source of current from the region ventrolateral to MotV where the motor axons are concentrated as they leave the nucleus.

Properties of the spindle afferents

A total of ninety-five spindle afferents were used derived from eleven animals. They constituted a subset of the 234 units for which the classification by SCh effects has been described previously (Taylor *et al.* 1992*a*). That classification was based on

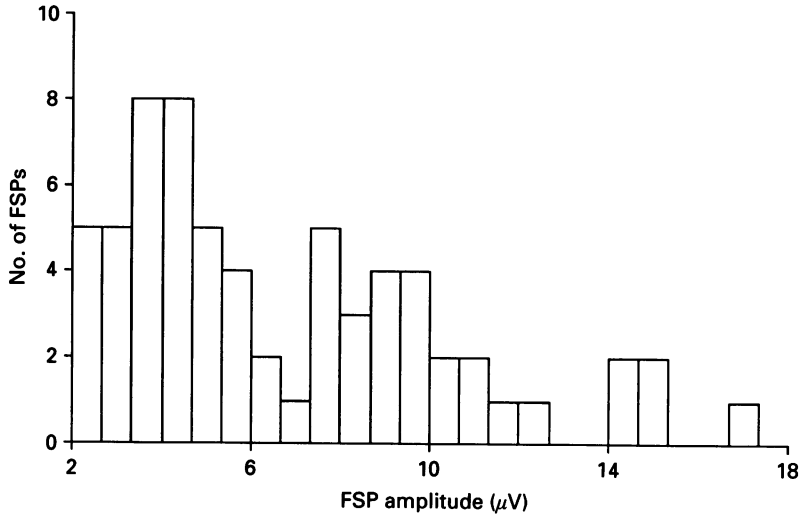

Fig. 4. Histogram to show the distribution of the maximum amplitudes of sixty-five unitary FSPs recorded along electrode tracks passing through the STR and MotV. Each FSP was derived by triggering from a different spindle afferent characterized by testing with SCh. Two other very large FSPs have not been shown; their amplitudes were 31·37 and 36·99 μV.

the increase in dynamic difference (ΔDD) and the increase in initial frequency (ΔIF) caused by a standard I.V. dose of 200 μg kg^{-1} of SCh during cyclically repeated ramp-and-hold stretches. The strength of the influence of b_1 fibres was taken to be indicated by ΔDD and of b_2 fibres by ΔIF. As these measures were both bimodally distributed and were uncorrelated they were taken to define four groups as shown by the scatter plot in Fig. 3. The whole population of units is shown, with those used in this field potential study indicated by filled symbols. For the analysis which follows attention was restricted to data from the sixty-seven afferents recorded in nine animals for which STA was carried out at 100 μm intervals along a complete track traversing the MotV region. For the fifty-eight units for which the muscle of origin could be clearly identified, 65% were in temporalis, 14% in pterygoid and 21% in masseter.

Amplitude of FSPs

The amplitudes of the mean unitary FSPs were measured simply as the maximum negative values found along the track. Values ranged from 2·08 to 36·99 μV with a mean of 7·55 μV (S.E.M. = 0·73 μV). The distribution of these values is shown in Fig. 4 which gives a strong impression of the existence of two subpopulations. The best dividing point may be taken as 6·7 μV dividing afferents into those with high values of FSP amplitude and those with low values. The question arises as to whether

attribution to these two classes relates to the response of units to SCh as estimated by ΔDI, ΔDD and ΔIF. Figure 5 presents the data relevant to this question. There is no significant difference, using the t test, between the two classes for ΔDI (P = 0·89) or for ΔDD (P = 0·139). However, mean ΔIF is very significantly higher for the

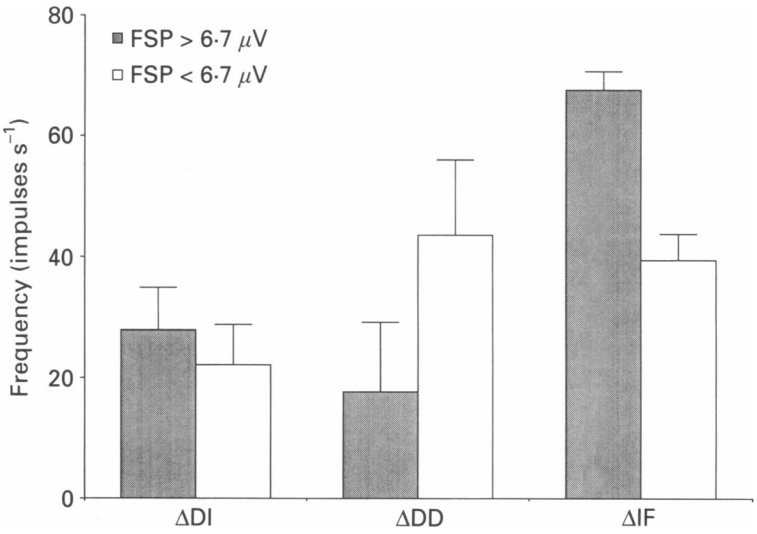

Fig. 5. Comparison of the mean values of ΔDI, ΔDD and ΔIF for spindle afferents giving high (filled columns) or low (open columns) values of FSP amplitude. Bars indicate standard errors of mean. Unpaired t tests showed the probabilities of observing the differences by chance to be 0·89 for ΔDI, 0·14 for ΔDD and < 0·001 for ΔIF.

units with high FSP values than for those with low values (P < 0·001). Thus it appears that it is the strength of the influence upon the afferent of the b_2 fibre (as estimated by ΔIF) rather than that of the b_1 fibre (as estimated by ΔDI or ΔDD) which best predicts the strength of the synaptic projection. This conclusion is reinforced by examination of the correlations between FSP amplitude and ΔDI, ΔDD and ΔIF (Fig. 6*A–C*). Only in the case of the third of these variables is there a significant positive linear correlation (P < 0·001). Two of the units were seen to have had usually large values of FSP amplitude. Why they should have been so far outside the main body of the data is not clear but their removal from Fig. 6*C* still left a significant correlation. Included within Fig. 6*D* is a plot of FSP amplitude against conduction velocity for the nineteen masseter units, in which this was measured. No significant correlation is seen. Two other measures of projection strength were also tried. First, the mean areas under the FSP curves were computed for all the points along a track. Second, in order to reduce the effects due to differences between animals and to differences in recording conditions, the maximum FSP amplitude in each track was normalized by division by the maximum amplitude of the compound field potential evoked by the standardized quick stretch. Though in all cases the data processed in these ways led to the same conclusions, there seemed to be no useful reduction in random variation. These methods were therefore not used in any further analysis.

It could be proposed that a false association of ΔIF with FSP amplitude might result if the latter depended on the muscle of origin and the proportion of afferents with strong b_2 influence varied significantly between the muscles. However, this possibility may be discounted because analysis of variance showed no significant

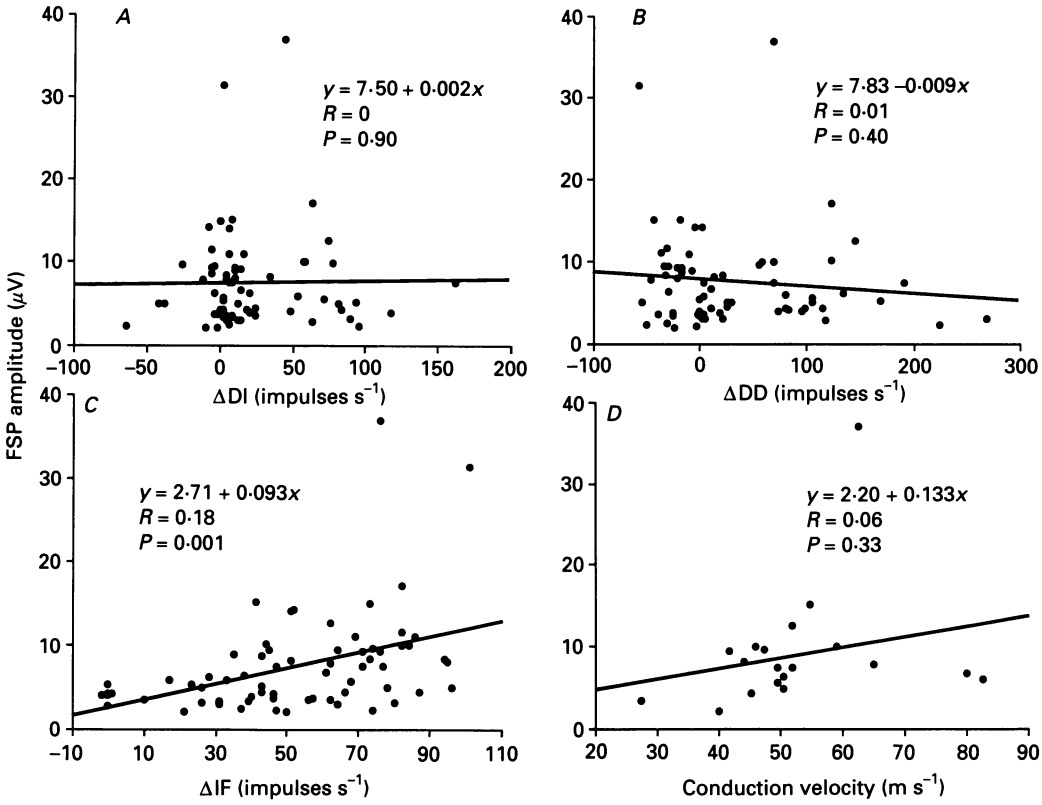

Fig. 6. Scatter plots of maximum amplitude of FSPs generated by sixty-seven spindle afferents against ΔDI (*A*), ΔDD (*B*), ΔIF (*C*) and conduction velocity (*D*). In each case the best-fit straight line is shown with its equation and the value of correlation coefficient (*R*) and the probability of this being observed by chance (*P*).

variance of ΔIF attributable to muscle of origin either in the whole population (Taylor *et al.* 1992*a*) or in the sixty-seven units considered here.

Distribution of FSPs in MotV and STR

By careful examination of the electrode tracks and iron marks in the histological sections it was possible to set boundaries on the MotV and STR as judged by the outline of the cell bodies. The term supratrigeminal *nucleus* has not been used because we were not in a position to apply the strict definition of this cell group originating with Lorente de Nó (1922). From the histology, recordings of FSPs were distinguished as having been made in one or the other of these two cell groups. It was found that thirty-four (50·7 %) of the afferents had their maximal FSP within MotV

and thirty-three (49·3%) within STR. The possible relationship of this distribution to the afferent types as determined by SCh is explored in Fig. 7. The symbols for the sixty-seven units are chosen to indicate location of the maximal FSP in MotV or STR and in each case whether the FSP amplitude fell in the high or low group as defined

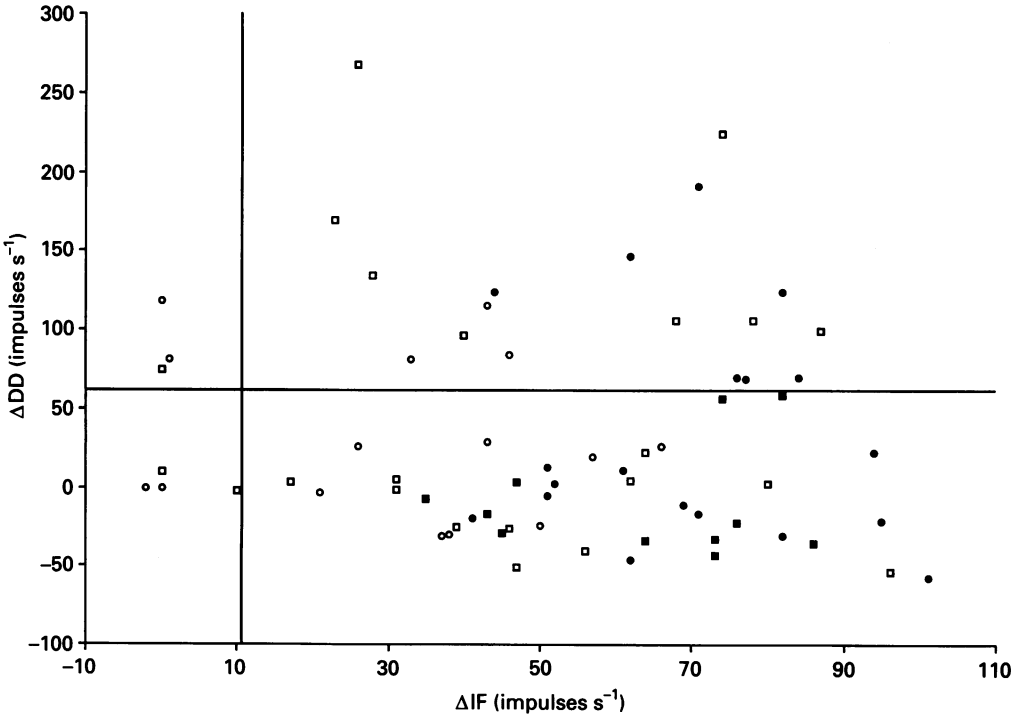

Fig. 7. Scatter plot as in Fig. 3, but showing only those sixty-seven spindle afferent units for which FSP amplitude was measured. Those units with high values of maximum FSP amplitude are shown with filled symbols and those with low values by open symbols. They are further divided according to whether their maximal FSP point was within MotV (circles) or within STR (squares).

by Fig. 3. It is evident that high values in both nuclei are associated with high values of ΔIF as expected from Figs 4 and 5 above. In addition, while units with high values of FSP in MotV have a wide range of values of ΔDD (b_1b_2c and b_2c groups), the units with large FSPs in STR are all in the b_2c category, as judged by their low values of ΔDD. The b_2c category is expected to contain those secondaries with significant endings on b_2 fibres and those primaries with no b_1 endings. For the jaw muscle spindles it is evident that these subclasses cannot be separated by afferent conduction velocity and so some other features of afferent response have to be considered. The recent study of jaw spindles with SCh (Taylor *et al.* 1992*a*) showed that mean control DI was very significantly less for the b_2c and c groups than for the b_1c and b_1b_2c groups, and therefore control DI is promising as a means of separating primaries from secondaries. However, the study of hindlimb spindles by this same method (Taylor *et al.* 1992*c*), in which this separation could be made on the basis of

conduction velocity, revealed that many primaries had low values of control DI. Thus while units with high control DI are unlikely to be secondaries, units with low control DI could be either primary or secondary. With this in mind a comparison was made between the control DI values for nineteen units with high FSP values in MotV with the nine units with high FSP values in STR. Mean control DI for the MotV group was 22·8 impulses s^{-1} while that for the STR group was 11·8 impulses s^{-1}. The difference was significant by the *t* test ($P = 0{\cdot}018$). This implies that primaries project preferentially to the MotV.

In the case of twenty-four afferents there was a clearly marked projection into both STR and MotV. Amongst these units the amplitudes of the FSPs in the two nuclei were significantly positively correlated ($P = 0{\cdot}021$). This points to the existence of a factor particular to the afferents rather than to the site of termination as influencing projection strength. From what has been said above it appears that this is the strength of the influence of the b_2 intrafusal fibre.

DISCUSSION

The usefulness of the classification by SCh appears from the present work not to rest solely on its potential for distinguishing primary from secondary afferents, because the size of FSPs produced correlates with the strength of the b_2 fibre influence as measured by ΔIF. If the primary/secondary distinction had been the more important, then b_1 fibre influence would have been expected to have been the better predictor of FSP amplitude since primary afferents on the whole are much more affected by b_1 fibre contraction than are secondaries. The correlation of FSP amplitude with ΔIF (Fig. 6*C*) suggests a graded relationship between them rather than the existence of two distinct groups. This encourages one in the idea that it is indeed the relationship with b_2 fibres which is important rather than perhaps some association of this with primary or secondary afferent type. In relation to what is known of the projection strength of primary and secondary afferents of hindlimb muscles this is a surprising result. Thus, by intracellular spike-triggered averaging secondary afferents have been found to produce individual excitatory postsynaptic potentials with mean value approximately 46% of that produced by primary afferents (Stauffer, Watt, Taylor, Reinking & Stuart, 1976). It has also been shown by spike-triggered averaging of ventral root population potentials (Lüscher, Ruenzel, Fetz & Henneman, 1979) that projection strength is highly positive correlated with afferent conduction velocity. From the present data we can see that it is not afferent conduction velocity (or afferent fibre diameter) in itself which necessarily determines central projection strength to motoneurones. As yet we do not know whether the strength of b_2 influence correlates with projection strength in the hindlimb situation as it does for the jaw muscles. However, such a result would be compatible with the established correlation with conduction velocity if primary afferents were to have on average a higher ΔIF than secondaries. The recent work on gastrocnemius spindles (Taylor *et al.* 1992*b*) shows this to be so, with mean ΔIF values of 56·1 and 22·1 impulses s^{-1} respectively ($P < 0{\cdot}001$). Further support for this conclusion can be drawn from several other lines of evidence. Morphological studies of spindle secondary endings (Banks, Barker & Stacey, 1982) have shown that those close to the

equatorial (S_1) region have the largest diameter and are most likely to contact all three intrafusal fibre types. Those closer to the poles (S_{2-4}) have progressively smaller axons and have progressively less chance of contacting any other than chain fibres. It has also been found recently amongst hindlimb secondaries that ΔIF is positively correlated with conduction velocity (data of Taylor *et al.* 1992*b*). Recalling that Lüscher *et al.* (1979) showed a positive correlation between monosynaptic projection strength of secondaries to motoneurones and conduction velocity, it is evident that the presently observed correlation of projection strength with ΔIF throughout all varieties of spindle afferents should not be unexpected.

Why b_2 influence should be important in this way is not clear as yet. One possibility is that during development, since the first afferents to grow out of the CNS to innervate spindles are destined to become primaries and the first intrafusal fibres to differentiate are b_2 type, then the connection of primaries with b_2 fibres is the first to be established (see Milburn, 1984). At this stage it might be expected that these primary axons should also be growing into the CNS and establishing synaptic contacts. As the first sensory axons to arrive at the motoneurones they might therefore be expected to have the best chance of making synapses upon them. From the functional point of view it is worth noting that several lines of evidence now indicate that the b_1 fibre makes very little contribution to the sensitivity to stretch of spindle afferents in the absence of intrafusal contraction (Dutia & Price, 1990; Proske, Gregory & Morgan, 1991; Taylor *et al.* 1992*b*). In fact control DD and control SD, as measures of dynamic and static sensitivities respectively, are both strongly correlated with ΔIF in the whole population of gastrocnemius afferents recently studied (Taylor *et al.* 1992*c*). This implies that it is the b_2 fibre endings which are most important in determining passive spindle sensitivity to stretch. This could possibly contribute another influence directing the formation of central synapses and it could in addition mean that the spindle afferents most sensitive to stretch in the absence of fusimotor drive would also have most direct excitatory effect on motoneurones.

With regard to the STR this is probably best known from the work of Kidokoro *et al.* (1968) as the site of interneurones strongly excited by stimulation of alveolar nerve and intra-oral structures and probably causing inhibition of jaw elevator motoneurones. The earlier report of Jerge (1963) had, however, also indicated the presence of excitatory effects from jaw elevator muscle stretch receptors and this has been confirmed (Miyazaki & Luschei, 1987; Olsson & Landgren, 1990). A projection to this region specifically from jaw elevator muscle spindles has been confirmed morphologically by intra-axonal tracers in the rat (Appenteng, Donga & Williams, 1985; Dessem & Taylor, 1989; Luo & Li, 1991) and cat (Shigenaga, Mitsuhiro, Yoshida, Cao & Tsuru, 1988*a*; Lingenhöhl & Friauf, 1991). The present data combine single unit specificity with the ability to classify each individual afferent and to estimate the strength of its synaptic projection. It has as a result been possible to conclude that b_2 influence on spindle afferents determines the strength of projection into this region as well as to the motoneurones. In addition there is reasonably good evidence that this projection to the STR is dominated by secondary afferents, while that to the MotV is favoured by primaries. Shigenaga *et al.* (1988*a*) had suggested this to be the case, but their evidence was based only on the

presumption that one afferent with conduction velocity of 83 m s^{-1} was a primary and another of 45 m s^{-1} was a secondary. Further support comes from recent studies by intra-axonal horse radish peroxidase labelling in rats (D. Dessem & R. Donga, personal communication) in which spindle afferents with low dynamic index showed the most dense projections to the STR. In connection with the electrophysiological work it has to be recognized that some motoneurones send dendritic processes into the STR (Shigenaga, Yoshida, Tsuru, Mitsuhiro, Otani & Cao, 1988*b*; Lingenhöhl & Friauf, 1991). It is possible therefore that some contribution to the FSPs recorded in this region may be due to endings on them rather than on interneurones. This does not seem likely to have been an important disturbing factor, however, because of the evidence quoted for the differences between the two projections. From the present study we can suggest that since spindle input appears to be predominantly from secondaries, there may be some homologies to be found with the midlumbar interneurones described by Edgley & Jankowska (1987).

There are many influences which contribute to the determination of the strength of projection of individual muscle spindle afferents. The one described here for the first time, namely the strength of the influence of the b_2 intrafusal fibres, shows some promise of being of very fundamental interest. Its significance will be much more readily assessed when comparable data from hindlimb studies are available.

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