J. Physiol. (1987), **382**, 313–329
With 13 text-figures
Printed in Great Britain

ACTIONS OF TRAINS AND PAIRS OF IMPULSES FROM SINGLE PRIMARY AFFERENT FIBRES ON SINGLE SPINOCERVICAL TRACT CELLS IN CAT

BY A. G. BROWN, H. R. KOERBER* AND R. NOBLE
From the Department of Veterinary Physiology, University of Edinburgh, Summerhall, Edinburgh EH9 1QH

(*Received 26 February 1986*)

SUMMARY

1. In cats under chloralose anaesthesia single lumbosacral dorsal root ganglion cells of hair follicle afferent fibres were stimulated intracellularly to produce trains or pairs of impulses. At the same time, single spinocervical tract (s.c.t.) neurones were recorded extracellularly, from their axons in the upper lumbar spinal cord. Afferent fibre–neurone pairs were chosen in which the receptive field of the fibre was contained within the excitatory receptive field (firing zone) of the neurone.

2. Trains of impulses of 2·0 Hz were less effective in increasing the probability of s.c.t. cell firing than trains at 0·67 Hz, and this latter rate was usually less effective than trains at 0·33 Hz.

3. Successive responses to individual members of a train of hair follicle afferent impulses were variable. In some pairs of units succeeding responses declined until a fairly consistent plateau was reached. In others there was no decline and the responses remained irregular.

4. Pairs or short trains of impulses revealed two phenomena: over the first 5 ms or so following an impulse in a group II hair follicle afferent fibre, a second or small group of impulses produced a greater response from the s.c.t. neurone but at intervals of 25–200 ms there was a profound depression of the responses evoked by the second member of a pair of impulses. For Aδ afferent fibres the early facilitation lasted for at least 25 ms.

5. It is concluded that a single impulse in a single hair follicle afferent fibre from within the excitatory receptive field of a s.c.t. neurone has complex actions on transmission through that neurone. An initial excitatory influence is followed by a long-lasting depression that influences transmission through the system for at least 1500 ms. Possible mechanisms underlying this depression are discussed.

INTRODUCTION

Neurones of the spinocervical tract (s.c.t.) in the cat receive a major excitatory input from afferent fibres innervating hair follicle receptors (see Brown, 1981*a*, *b*). A single impulse in a single hair follicle afferent fibre leads to an increase in the

* Supported by an N.I.H. National Research Service Award. Present address: Department of Neurobiology and Behavior, State University of New York at Stony Brook, Stony Brook, NY 11794, U.S.A.

probability of discharge of the s.c.t. cells whose cutaneous receptive fields (firing zones) contain the receptive field of the afferent fibre. Indeed, for group II afferent fibres, one or more impulses are evoked in about 50 % of afferent fibre–s.c.t. neurone pairs in 50 % of trials (Brown, Koerber & Noble, 1987*a*). It was noted, however, (Brown *et al.* 1987*a*) that trains of single hair follicle afferent impulses at rates greater than about once every 1500 ms produced less of an effect than slower rates, suggesting some sort of depression of responses. Inhibitory post-synaptic potentials are known to be evoked in s.c.t. cells from cutaneous nerves (Hongo, Jankowska & Lundberg, 1968) and transmission through the s.c.t. is also probably affected by presynaptic inhibitory mechanisms (see Brown, 1981*b*).

When small groups of hairs within the excitatory receptive field of a s.c.t. neurone are moved, by means of an air jet, the response of s.c.t. neurones to a second air jet is greatly reduced for at least several hundred milliseconds (A. G. Brown, R. Noble & M. J. Rowe, unpublished observations). More importantly, when hairs are moved, simultaneously, at two sites within the excitatory receptive field of a s.c.t. neurone, the response to the combined stimuli is often no greater than the response to one stimulus alone or is less than the sum of the responses to each stimulus alone (Brown, Noble & Rowe, 1986). These results suggested that such attenuation of responses might be due to overlapping of excitatory and inhibitory receptive fields. Indeed, since the same type of natural stimulation that produced excitation also produced inhibition or depression of responses, it seemed possible that the same individual afferent fibre might have dual action on s.c.t. neurones, both excitatory and inhibitory.

In order to answer the question of whether a single hair follicle afferent impulse, arriving over a single afferent fibre, leads to both excitatory action on the target s.c.t. neurones and depression of transmission in the s.c.t. system, we have examined the actions of trains of single impulses in single afferent fibres on the responses of s.c.t. neurones and also the effects of pairs of impulses at different intervals. A preliminary account of some of the results has been published (Brown, Koerber & Noble, 1984).

METHODS

The results were obtained from the series of experiments described in the previous paper (Brown *et al.* 1987*a*). Briefly, in cats, anaesthetized with α-chloralose and paralysed with gallamine triethiodide, one micro-electrode was placed inside a lumbosacral dorsal root ganglion cell (hair follicle afferent neurone) and another micro-electrode used to record the responses of a spinocervical tract neurone, extracellularly, when the dorsal root ganglion cell was caused to fire single impulses by passing current through the intracellular electrode.

RESULTS

The present studies were obtained from the series of experiments described in the previous paper (Brown *et al.* 1987*a*) but the sample of neurones was limited to some of the hair follicle afferent fibre–s.c.t. neurone pairs in which the afferent fibre's receptive field was contained within the excitatory field (firing zone) of the s.c.t. neurone. As mentioned in the Introduction, we had noted that single impulses in the hair follicle afferent fibre at rates faster than once every 1500 ms produced smaller

responses in the s.c.t. neurone than slower rates. In order to examine this response depression in more detail we investigated the effects of different stimulation rates and also the effects of pairs of hair follicle afferent fibre impulses at different intervals on the responses of s.c.t. neurones.

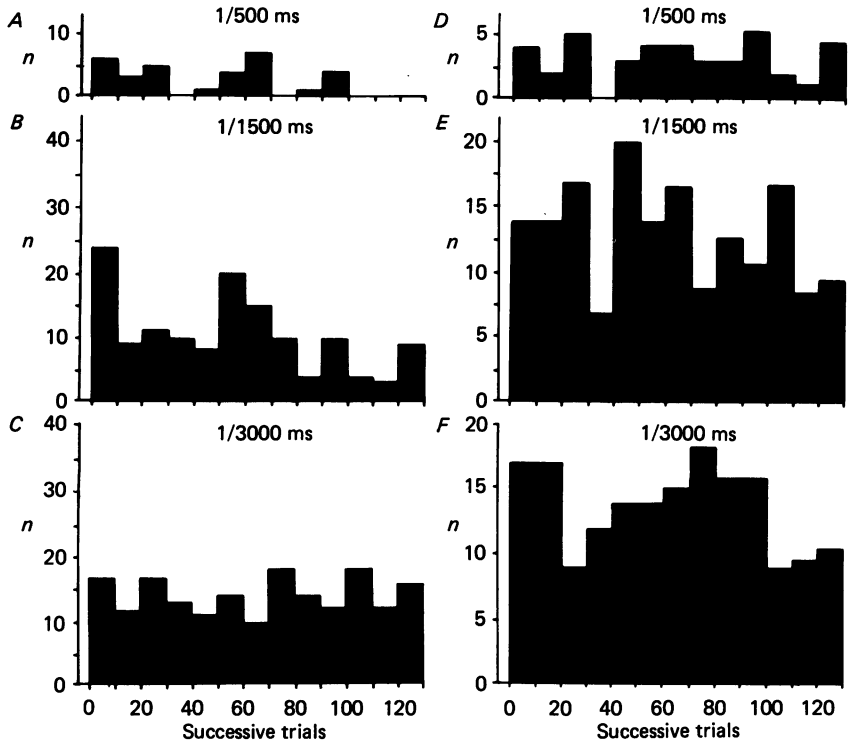

Fig. 1. Variation in the responses of s.c.t. cells to single hair follicle afferent impulses at different rates. *A–C* and *D–F* show the responses of two neurones to stimulation at 500, 1500 and 3000 ms intervals. The responses to ten successive stimuli have been summed for each bar of the histograms. The responses to stimulation at 500 ms intervals are small and very variable, failing completely for the unit shown in *A*. Responses to stimulation at 1500 and 3000 ms intervals are greater.

Effects of trains of afferent impulses on s.c.t. neurone responses

Change of response with time. When a single dorsal root ganglion cell (innervating hair follicle receptors) was caused to fire impulses repetitively at rates of 0·33–2·0 Hz the responses of the s.c.t. neurone to which the afferent fibre was coupled varied with time. Response variation was usually greatest at 2·0 Hz, when some units quickly failed to respond at all, or only rarely, after twenty to fifty trials (Fig. 1), but even at 0·67 and 0·33 Hz the responses varied sufficiently for differences to be revealed even when sets of ten successive responses were pooled (Fig. 1). Altogether twelve pairs of units, with group II afferent fibres, were examined at 0·33–2·0 Hz and in all of them the responses were greater at 0·33 Hz (more impulses per ten trials) and usually the response variation was the least at this rate. For two pairs of units there was a steady response decrement to a plateau level at impulse intervals of 1500 ms

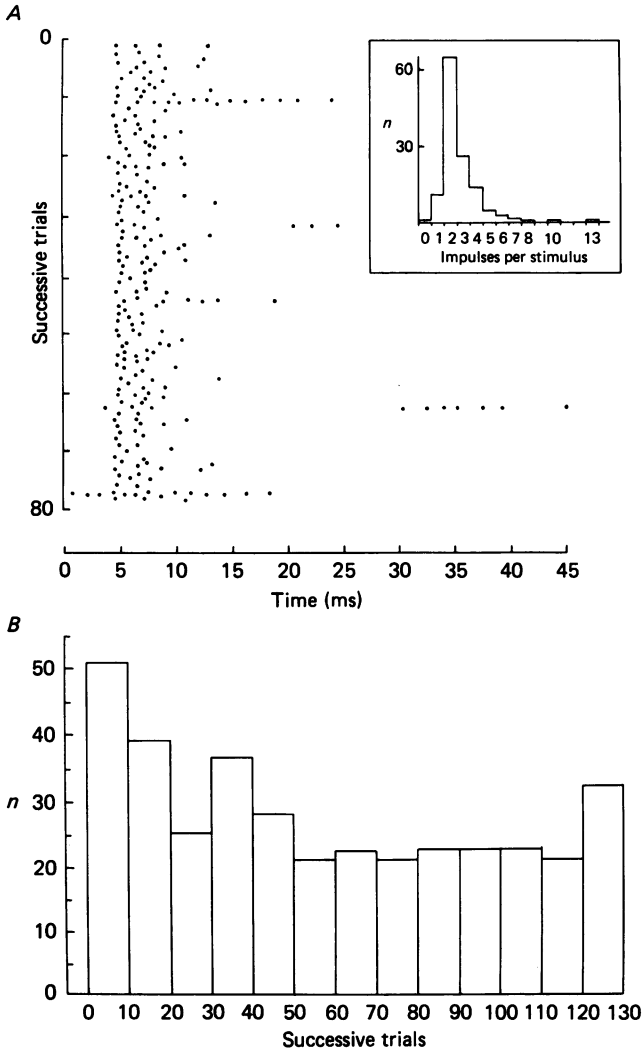

Fig. 2. Responses of a s.c.t. neurone to repetitive hair follicle afferent impulses at 1500 ms intervals. *A* shows a raster display of the raw data for the first eighty trials, with the inset showing the distribution of responses. *B* shows the numbers of impulses evoked in the neurone in succeeding trials with responses collected in groups of ten. This afferent fibre–neurone pair was strongly linked (at least one impulse was evoked in 99% of trials) and there was a decline in responsiveness during the first thirty to forty trials.

(0·67 Hz), such that the responses to the first ten or twenty trials were much greater than succeeding ones (Figs. 2 and 3). In one of these pairs where no impulses were evoked in the majority of trials the initial ten responses were still greater than succeeding ones (Fig. 3). Figs. 2*A* and 3*A* show part of a raster display of the raw data, with the early responses at the top, and the inset in Figs. 2*A* and 3*A* show the distribution of responses, the large number of 'failures' for the pair shown in Fig. 3 being apparent.

Effects of different rates of stimulation. For twelve hair follicle afferent fibre–s.c.t. neurone pairs the effects of altering the rate of afferent input was examined.

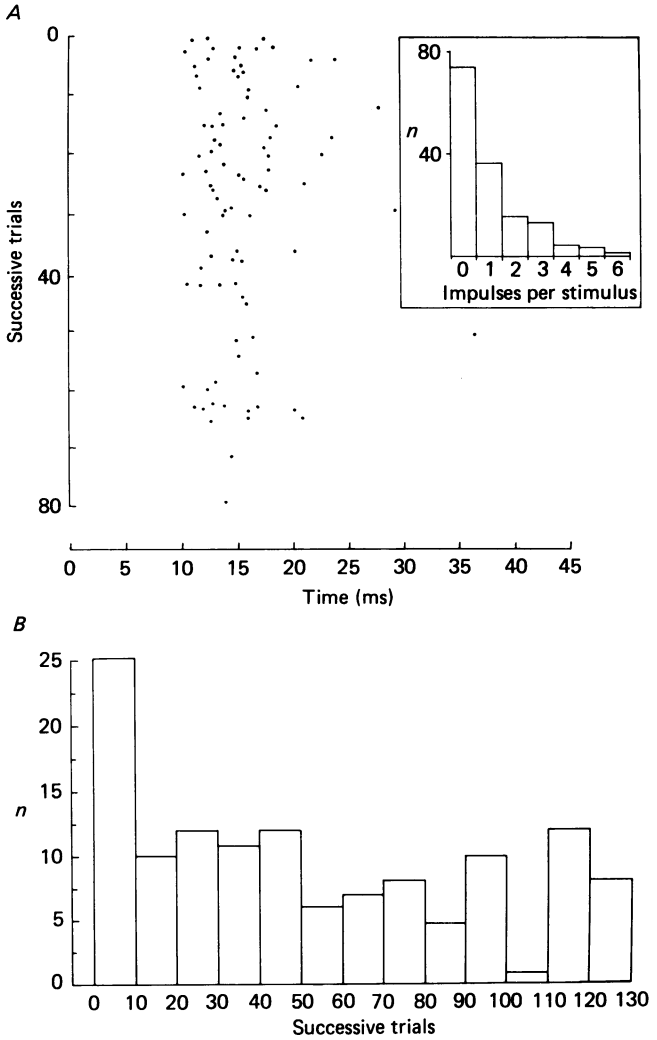

Fig. 3. Responses of a s.c.t. neurone to repetitive hair follicle afferent impulses at once every 1500 ms (0·67 Hz). This Figure is similar to Fig. 2 except the afferent fibre–neurone pair was much less strongly coupled (at least one impulse was evoked in 51 % of trials). There was a steep reduction in responsiveness of the s.c.t. neurone during the first ten trials.

Stimulation rates at intervals of 500, 1500 and 3000 ms were used, six pairs being examined at 500, 1500 and 3000 ms inter-impulse times and six pairs at two of these values. Figs. 4 and 5 show typical examples of the effects observed. In each pair 130 trials were collected at inter-stimulus intervals of 500, 1500 and 3000 ms and the responses of the s.c.t. neurones displayed as post-stimulus time histograms. Stimulation at 500 ms intervals produced far smaller responses (fewer s.c.t. neuronal discharges) than stimulation at the longer intervals. The differences between responses at 1500 and 3000 ms intervals were small (Figs. 4 and 5) but at 3000 ms stimulus intervals there were usually more impulses evoked than at 1500 ms.

Effects of pairs or short trains of impulses in single hair follicle afferent fibres on the discharges of s.c.t. neurones

Effects of pairs and trains of impulses at short intervals. Twenty-five hair follicle afferent fibre–s.c.t. neurone pairs (twenty-two with group II afferent fibres and three with group III fibres) were examined with pairs or short trains of three to four stimuli at short intervals, i.e. total time between the first and last impulse of 2·5–10 ms.

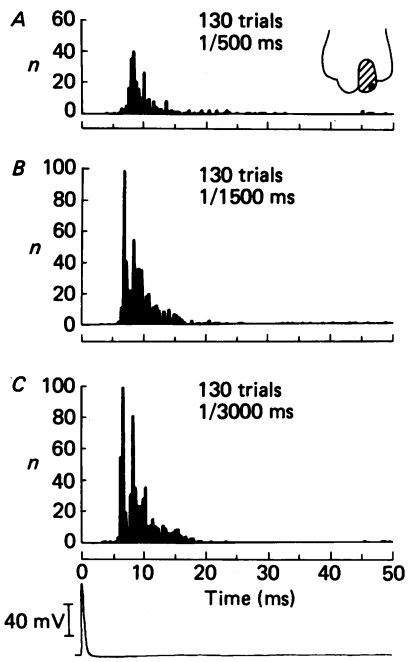

Fig. 4. Responses of a s.c.t. neurone to single hair follicle afferent impulses at different rates. *A*, *B* and *C* show responses, post-stimulus time histograms (bin width: 0·4 ms), of a s.c.t. cell to single hair afferent input at 2 Hz (*A*), 0·67 Hz (*B*) and 0·33 Hz (*C*). Note the depressed response in *A*. The inset in *A* shows the receptive fields of the hair follicle afferent fibre (filled area) and the s.c.t. neurone (hatched area).

Within 5 ms of the first, conditioning, impulse a succeeding, testing, impulse or impulses produced greater responses than the first impulse alone in twenty of twenty-one pairs tested at these intervals. This is shown in Fig. 6 for pairs of impulses in larger (group II) hair follicle afferent fibres. A similar result was shown in the previous paper (Brown *et al.* 1987*a*, Fig. 6) for Aδ hair follicle afferent fibre–s.c.t. neurone pairs with inter-impulse intervals of 5 ms. For pairs with Aδ hair follicle afferent fibres the early facilitatory period lasted at least as long as 25 ms (Fig. 7).

The responses of s.c.t. neurones during this early facilitatory period added to each other so that it was not easy to separate the responses to individual afferent impulses (see Fig. 6). In addition to the marked facilitatory effect of impulses at short intervals Fig. 6 also shows the other striking observation: although the responses to two impulses at short intervals were greatly facilitated they were, in general, no longer

in duration than the response to a single impulse. Of the twenty-one afferent fibre–neurone pairs examined in this way sixteen had post-stimulus time histograms with total durations within 5 ms of each other whether they were in response to single impulses or pairs of impulses at up to 5 ms intervals, one pair had a shorter response

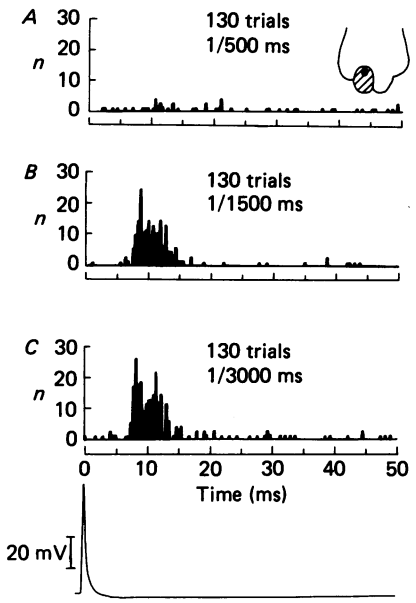

Fig. 5. Responses of a s.c.t. neurone to single hair follicle afferent impulses at different rates. This Figure is similar to Fig. 4, but responses at 2 Hz (*A*) are severely depressed and even at 0·67 Hz (*B*) there is obvious depression in comparison with responses at 0·33 Hz (*C*).

to a pair of afferent impulses and four had longer responses, although in the latter case two were responses to four stimuli (in 5 ms) and one was a response to a pair of stimuli at an interval of 2·5 ms. None of the afferent fibre–s.c.t. neurone pairs tested at intervals of up to 5 ms showed a reduced response to the second impulse of the pair even though that response was often riding on the first.

In contrast to the relatively straightforward results observed with pairs and trains of afferent impulses within a 5 ms period, when the interval was 10 ms the effects were more complex. Six afferent fibre–s.c.t. neurone pairs with group II afferent fibres were tested with a pair of stimuli 10 ms apart. Three of the pairs showed a facilitated response to the second (test) impulse in contrast to the response to the first (conditioning) impulse alone (Fig. 8*A*); whereas three other pairs showed a reduced response (Fig. 8*B* and *C*). For five of the pairs the total duration of the post-stimulus time histograms produced by two impulses 10 ms apart was similar to that of the histogram produced by a single impulse (Fig. 8): for the other pair the duration was longer by 7 ms. As mentioned above, at intervals of up to 25 ms the pairs with Aδ afferent fibres showed facilitation.

Effects of pairs of impulses at 20–200 ms. Ten hair follicle afferent fibre–s.c.t.

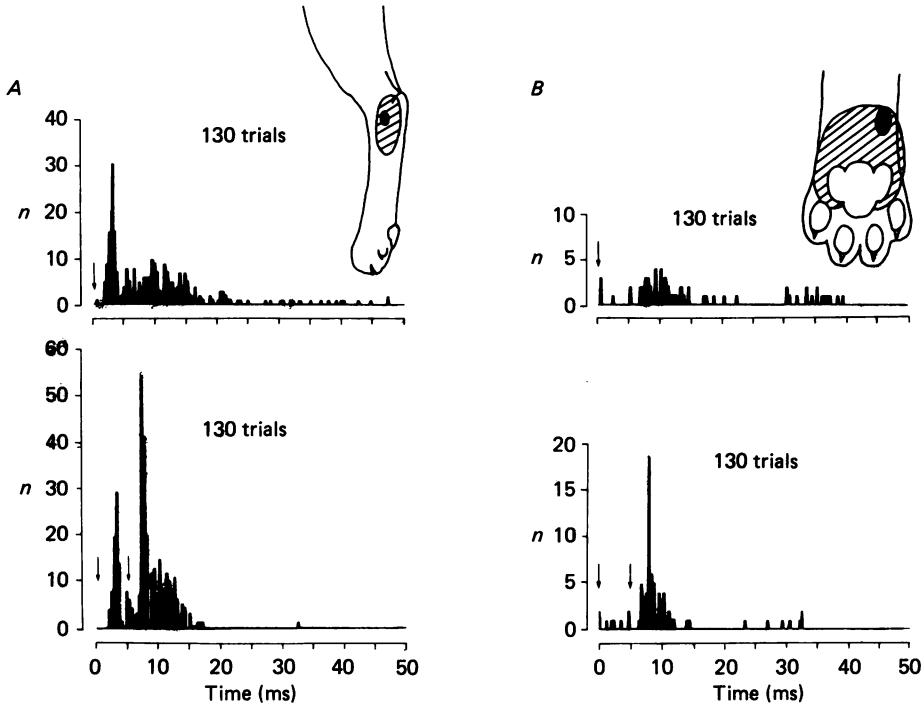

Fig. 6. Early facilitatory actions of a single hair follicle afferent fibre impulse on s.c.t. neurones. *A* and *B* show responses of two afferent fibre–s.c.t. cell pairs. The upper histogram in each pair shows the response to a single hair afferent impulse (at 0·67 Hz) and the lower histogram the actions of a pair of impulses 5 ms apart (again at 0·67 Hz). The pair of impulses produces a greater response than the single impulse alone, the response to the second member of the pair adding to that of the first. Note that the total duration of the response to a pair of stimuli 5 ms apart is similar to that to a single impulse. The receptive fields of each pair of units are shown, the hair follicle afferent fibre's field as a filled area and the s.c.t. cell's field as a hatched area. Bin width in each histogram is 0·4 ms.

neurone pairs were tested with pairs of impulses at intervals from 20–200 ms. Five of the pairs were studied at intervals of 20 (or 25), 50, 100 and 200 ms, and the remaining six pairs at one to three of these intervals. Figs. 9–11 show the post-stimulus time histograms generated by three of the pairs over the range up to 200 ms and Fig. 12 shows a summary of the results for all the intervals tested in all the pairs. From 20 ms out to 200 ms a single, conditioning, hair follicle afferent fibre impulse produced, in addition to its excitatory action, a profound depression of the responses of the s.c.t. neurone to a second (testing) afferent impulse. The responses averaged 13·6 % of the control value at 20–25 ms, 15·7 % at 50 ms, 20·1 % at 100 ms and still only 32·5 % at 200 ms. When these results are considered together with those described above for trains of impulses at different rates, it seems reasonable to conclude that this depression lasts for at least 1500 ms.

For most of the afferent fibre–s.c.t. neurone pairs tested with two impulses, the s.c.t. cell's response had a latency too long to be considered due to monosynaptic excitation. Two pairs, however, had latencies to a single hair follicle afferent impulse of 1·5 and 1·75 ms, short enough to suggest a monosynaptic initial response (see

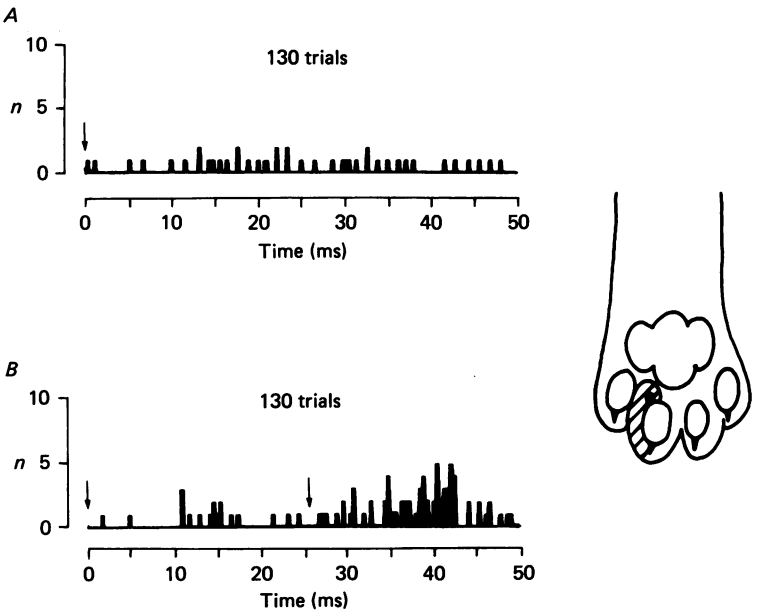

Fig. 7. Responses of a s.c.t. neurone to hair follicle afferent impulses from a group III (Aδ) hair follicle afferent fibre. *A* shows the response to a single afferent impulse and *B* the response to a pair of impulses 25 ms apart (bin width: 0·4 ms). The early facilitatory period for this pair lasts at least as long as 25 ms. The receptive fields are shown on the right of the Figure.

Brown *et al.* 1987*a*). These pairs allowed an assessment of whether the monosynaptic component was as affected by the depressed transmission as were the later components. Fig. 13 shows results for these two pairs and it can be seen that at 25 ms impulse separation there was a clear depression of the earliest components of the post-stimulus time histograms.

DISCUSSION

In the previous paper it was shown that a single impulse in a single hair follicle afferent fibre usually has a marked excitatory action on a s.c.t. neurone if that neurone's excitatory cutaneous receptive field (firing zone) contains the receptive field of the afferent fibre (Brown *et al.* 1987*a*). Indeed, about one-half of the group II hair follicle afferent fibres have a sufficiently strong excitatory action on s.c.t. neurones that a single impulse in the afferent fibre will cause the neurone to fire at least one impulse in about 50 % of trials in about 50 % of pairs (when the trials are conducted at rates of once every 1500 ms). The present paper has shown that this excitatory action lasts for a relatively short time. Although an additional impulse within 5 ms or so will produce a facilitated response in the s.c.t. neurone such facilitation does not lead to a response of longer duration. From about 10 ms following the arrival of the first impulse (after 25 ms at least for Aδ afferent fibres), the response to a second impulse is much reduced and this depression is very profound by 20–25 ms and lasts for a period on the order of 1500 ms.

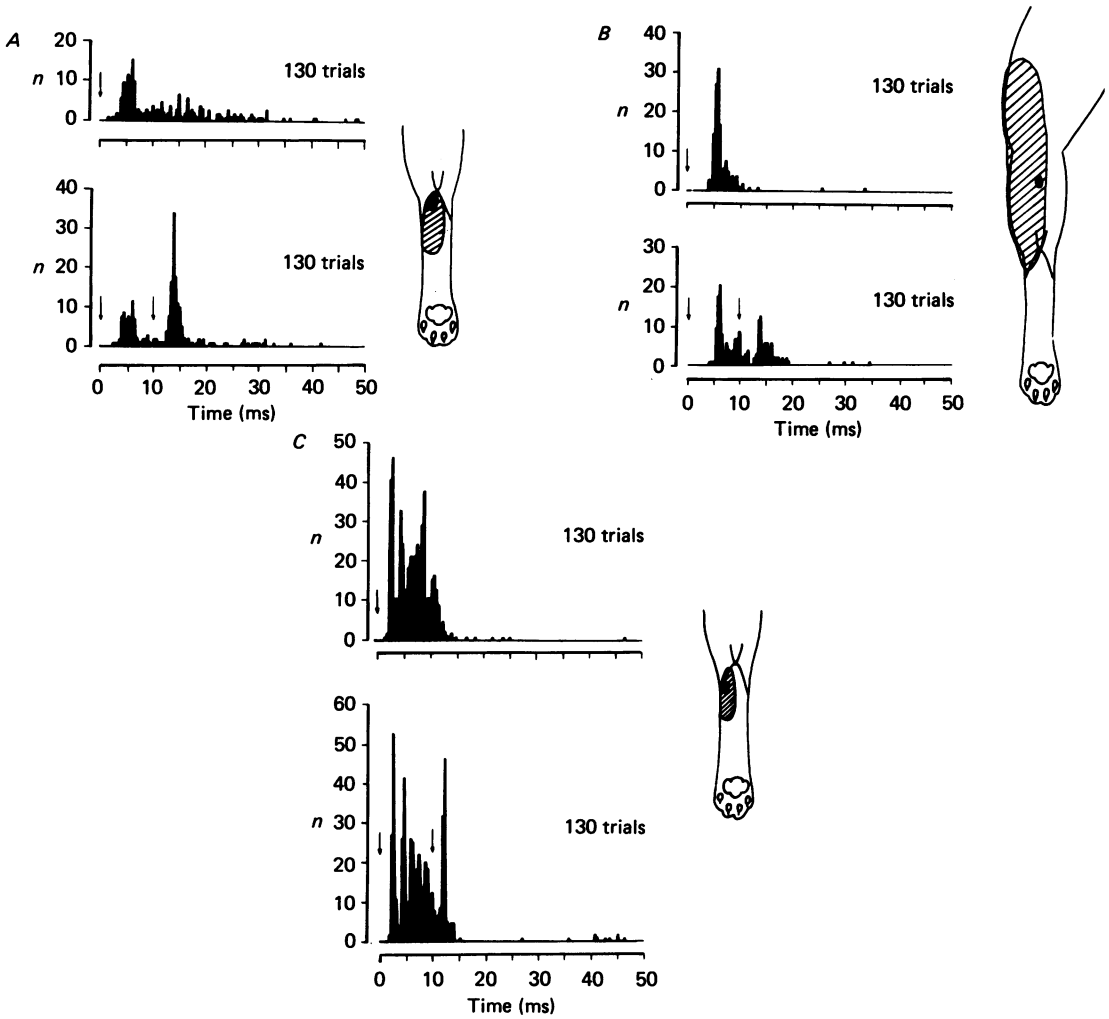

Fig. 8. Responses of s.c.t. neurones to pairs of hair follicle afferent impulses 10 ms apart. *A* and *C* show responses in three afferent fibre–s.c.t. cell pairs. The upper histogram showing the response to a single impulse at 0·67 Hz and the lower histogram showing the response to two impulses 10 ms apart (also at 0·67 Hz). In *A* the second impulse produces a facilitated response; in *B* and *C* the second impulse is much less effective than the first. Note that in *A* and *C* the total duration of the response to two impulses is similar to that to one alone, whereas in *B* the response is about 7 ms longer. Bin widths in each histogram are 0·4 ms. Receptive fields for the pairs of units are shown on the right of the histograms.

The mechanisms underlying this depression are presumably complex. Some component may to be due to the initial part of a long-lasting decay in responsiveness of the system, since for some pairs long trains of impulses produce decreasing responses, especially during the first ten or so trials, until a plateau phase is reached. Most pairs of units, however, did not show much evidence of this decrementing type of response and much of the depression in response that peaks at about 20–25 ms and lasts for 1500 ms is presumably due to other causes. The present experiments, in which the

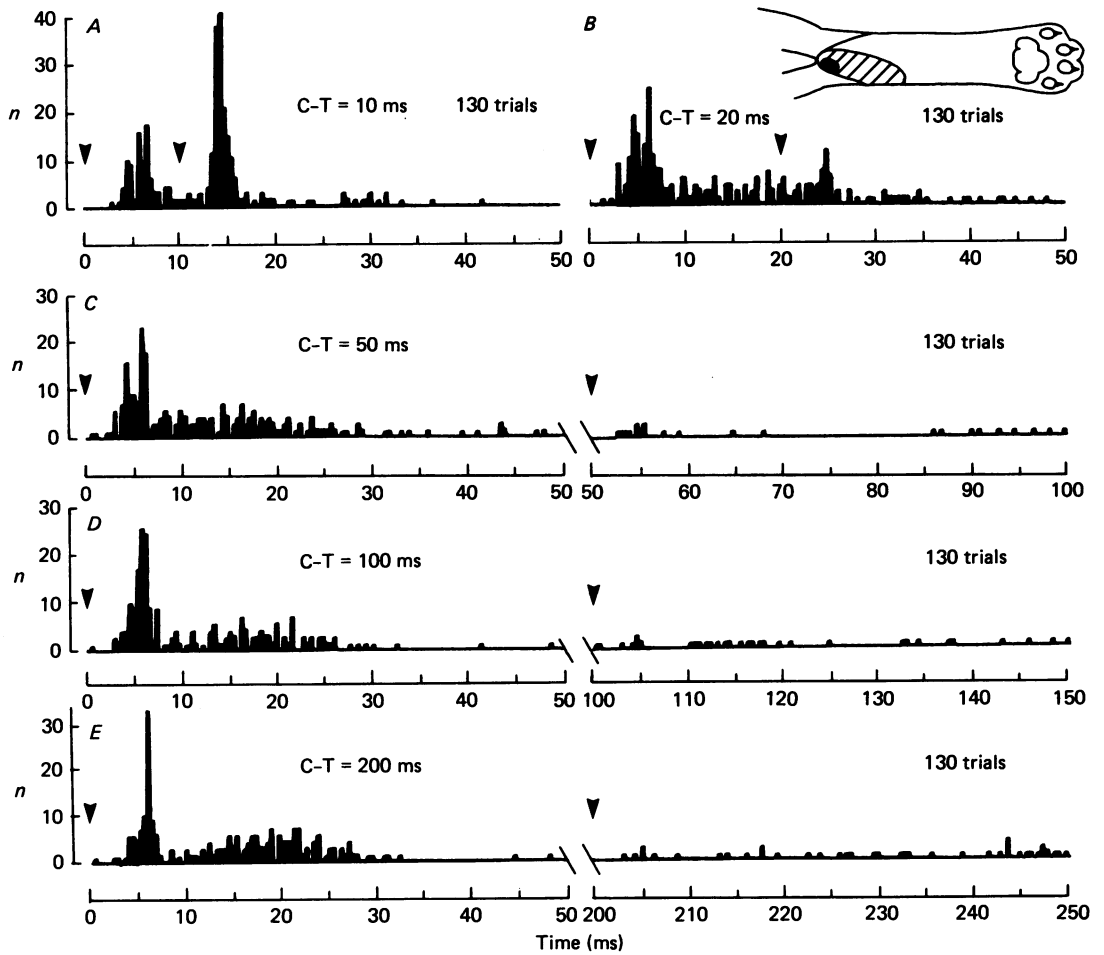

Fig. 9. Responses of a s.c.t. neurone to pairs of hair follicle afferent impulses at different conditioning–testing (C–T) intervals. Each histogram (*A–E*) is the sum of 130 individual trials at a repetition rate of 0·67 Hz. Note the early facilitation at 5 ms and 10 ms, and the marked depression of responses to the second (test) impulse starting at 20 ms and lasting for at least 200 ms. Responses of two other s.c.t. cells are shown in Fig. 10 and 11. The response of the s.c.t. cell in Fig. 11 recovers earlier than those in Figs. 9 and 10. Bin width: 0·4 ms. The receptive fields of the hair follicle afferent fibre (filled area) and the s.c.t. neurone (hatched area) are shown.

depression is measured against the probability of impulse initiation by the s.c.t. cells (extracellular recording) can throw little light on mechanism and certainly cannot differentiate between some sort of post-activation depression and an active inhibitory process. Post-activation depression might be occurring at the s.c.t. neurone itself or within a chain of interneurones interposed between the hair follicle afferent fibre and the s.c.t. neurone. Direct activation of a s.c.t. neurone by intracellular current pulses does not lead to long-lasting post-activation depression (see Brown, Koerber & Noble, 1987*b*). If post-activation depression occurs in an interneuronal chain then any monosynaptic component of the s.c.t. neurone's response to the hair follicle

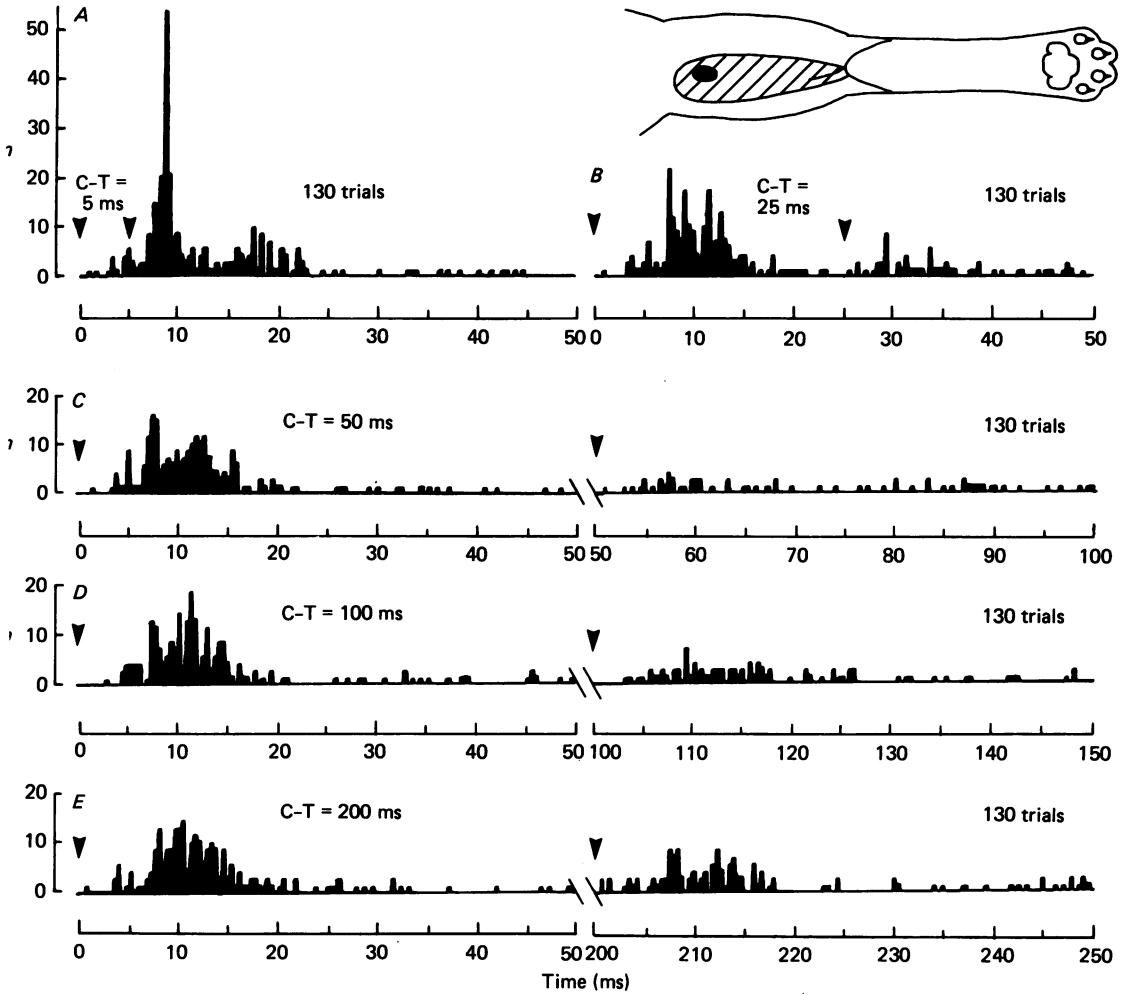

Fig. 10. Response of an s.c.t. neurone to pairs of hair follicle afferent impulses at different conditioning–test (C–T) intervals. Each histogram (*A–E*) is the sum of 130 individual trials at a repetition rate of 0·67 Hz. Bin width: 0·4 ms. The receptive fields of the hair follicle afferent fibre (filled area) and the s.c.t. neurone (hatched area) are shown.

afferent input should remain unaffected. Indeed, it has previously been suggested (Brown, Kirk & Martin, 1973) that both segmental and descending inhibitory effects act preferentially on the polysynaptic components of s.c.t. cell responses and Hongo & Koike (1975) noted that the later excitatory post-synaptic potentials were more effectively inhibited than the monosynaptic components. As discussed in the previous paper, there are difficulties in assigning a monosynaptic connexion to

Fig. 11. Responses of s.c.t. neurones to pairs of hair follicle afferent impulses at different conditioning–testing (C–T) intervals. Each histogram (*A–E*) is the sum of 130 individual trials at a repetition rate of 0·67 Hz. Bin width: 0·4 ms. The receptive fields of the hair follicle afferent fibre (filled area) and the s.c.t. neurone (hatched area) are shown.

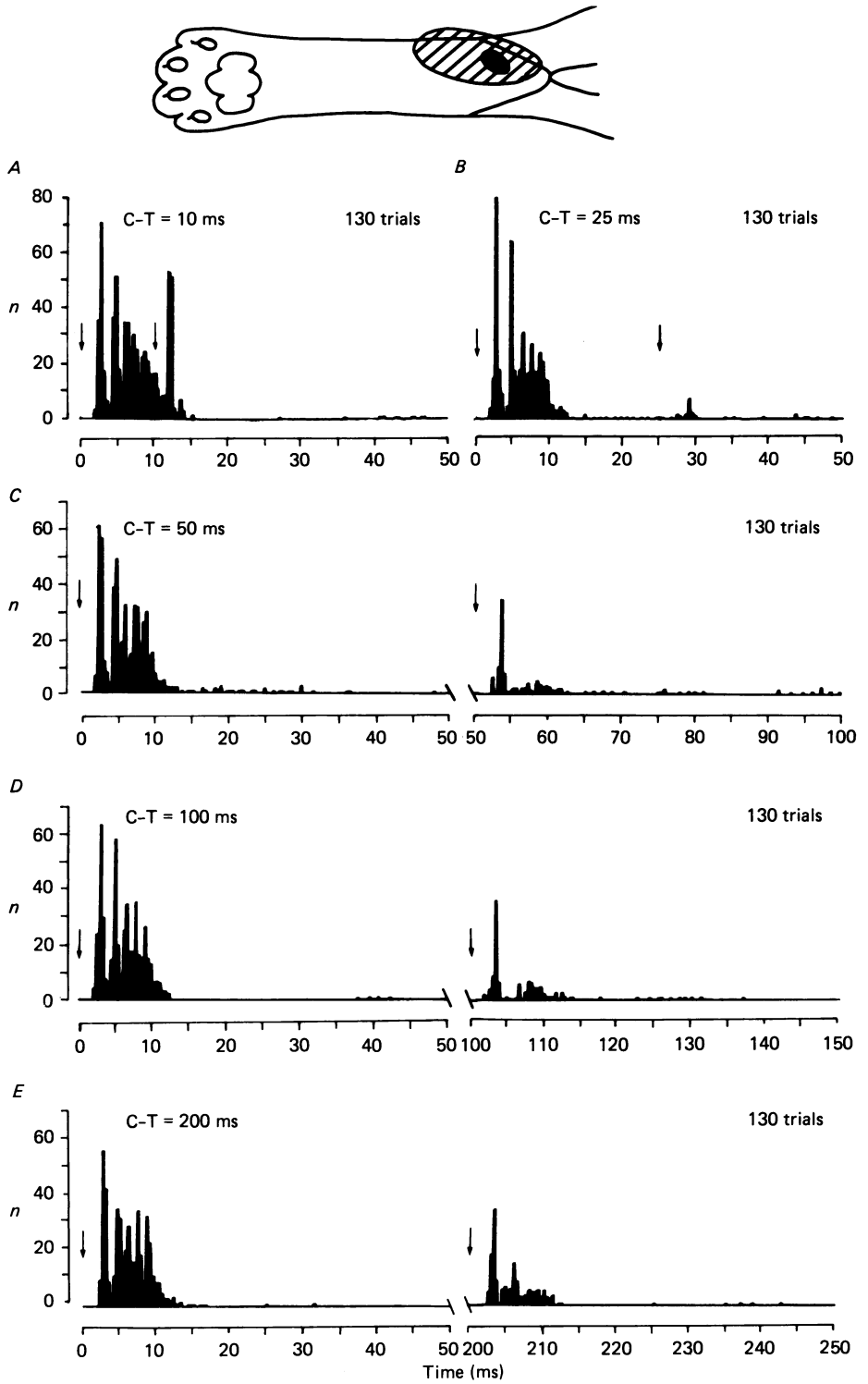

Fig. 11. For legend see opposite.

afferent fibre–s.c.t. cell pairs using the present experimental approach. However, two pairs in the present series had response latencies of 1·5 and 1·75 ms and these earliest components of the response were assumed to be monosynaptically evoked. Both of these pairs were tested with two impulses at 25 ms separation and both showed profound depression of the second response and this depression included the earliest

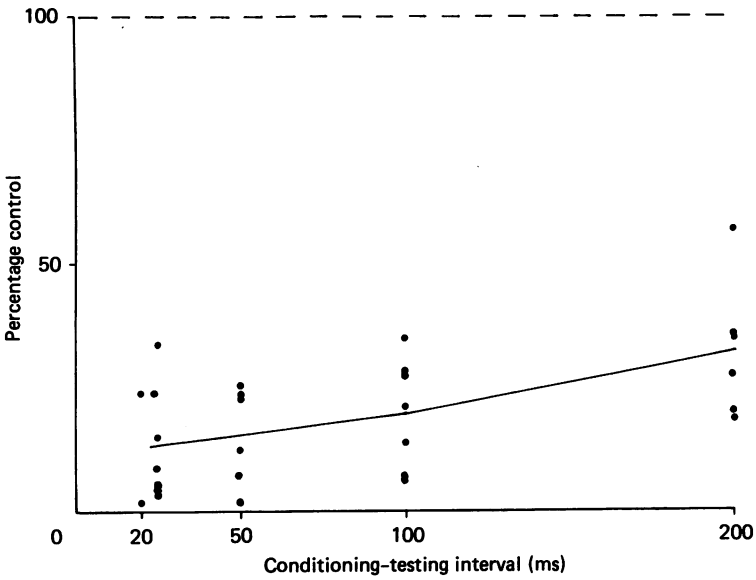

Fig. 12. Summary of the responses of s.c.t. neurones to a test impulse in a single hair follicle afferent fibre following a conditioning impulse in that fibre at the stated intervals. All points are the mean values for 130 trials except for: one at 20 ms (75 trials), one at 25 ms (100 trials) and one at 50 ms (33 trials). The line has been drawn through the average value at each conditioning–testing interval, with the responses at 20 and 24 ms pooled. Note that at 200 ms the response is still, on the average, only about 33% of control.

components. Whether such depression is really affecting a monosynaptic component is difficult to tell, but in an intracellular study (Brown *et al.* 1987*b*) we have shown, in agreement with Hongo & Koike (1975), that monosynaptically evoked excitatory post-synaptic potentials are largely unaffected by this depression whereas the polysynaptic components may be largely removed. We are left with the conclusion that a major part of the depression is due either to post-activation depression in an interneuronal chain or to an active inhibitory mechanism or mechanisms. The intracellular experiments referred to earlier in this paragraph rule out any recurrent inhibitory actions. Only detailed intracellular observations, however, will determine whether a post-synaptic inhibition is involved at the level of the s.c.t. neurone itself. Post-synaptic inhibitory potentials may certainly be recorded from s.c.t. cells in response to both electrical stimulation of cutaneous nerves and mechanical stimulation of the skin (Hongo *et al.* 1968; Hongo & Koike, 1975) but these potentials have durations in the order of 10–20 ms and are thus unlikely to be responsible for the much longer-lasting depression reported herein. In the last paper in the present series

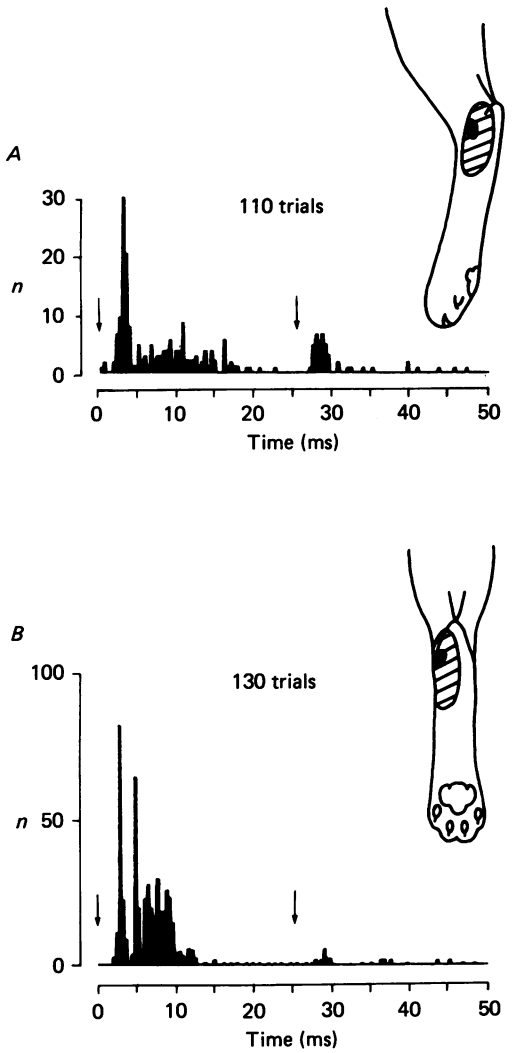

Fig. 13. Depression of the earliest components of s.c.t. cell responses to single hair follicle afferent impulses. *A* and *B* show post-stimulus time histograms (bin width: 0·4 ms), from two separate pairs of units, in which the earliest responses had latencies of less than 2 ms. In both pairs a conditioning impulse at 25 ms produced profound depression of the earliest components of the response.

(Brown *et al.* 1987*b*) it will be shown that although moving a small group of hairs in the excitatory field of a s.c.t. neurone leads to both excitatory and inhibitory post-synaptic potentials, a single impulse in a single hair follicle afferent fibre from the s.c.t. cell's firing zone appears to evoke only excitatory post-synaptic potentials in the s.c.t. neurone. Inhibitory effects on an intercalated chain of neurones and/or presynaptic inhibitory action should therefore also be considered. The latter possibility, although attractive in view of the time course of the depression, runs into a certain amount of difficulty. Ultrastructural investigations of the synaptic boutons

terminating on s.c.t. neurones (Maxwell, Fyffe & Brown, 1982, 1984) have failed to show any axo-axonic contacts on them, even though hair follicle afferent boutons do receive such contacts (Maxwell, Bannatyne, Fyffe & Brown, 1982). Presynaptic inhibitory action would, therefore, have to be exerted on hair follicle afferent boutons that form synapses with neurones other than those of the s.c.t. A final component to the depression might be due to a spino-supraspinal–spinal loop.

Whatever the mechanisms underlying the phenomena described in this and the preceding paper, it is obvious that a single impulse in a single hair follicle afferent fibre has a series of actions that leads to excitation and then depression of transmission through an individual s.c.t. neurone, if the afferent fibre's receptive field is contained within the excitatory receptive field of the neurone. The present experiments have allowed a glimpse of the complex neuronal actions that can take place following the arrival of a single impulse into the spinal cord. Certainly, as far as the spinocervical tract is concerned, the arrival of such a single afferent impulse would appear to be a significant event. Whether such significance is a general property of afferent fibre inputs to tract neurones remains to be seen. Single impulses in single slowly adapting type I cutaneous fibres do, however, have actions on some dorsal horn neurones that are very similar to the actions described in the present series of experiments (Tapper & Wiesenfeld, 1980; Tapper, Wiesenfeld & Craig, 1983). Thus, successive reduction of responses to repeated single impulses and depression of a second response with a time course similar to that described here, following an early facilitation period, have been described. Unfortunately, the dorsal horn neurones responding to slowly adapting type I afferent inputs have not received a complete description in terms of their axonal projections. Some of them certainly project through the dorsal columns (Brown & Fyffe, 1981; Brown, Brown, Fyffe & Pubols, 1983) and are, therefore, tract cells.

We wish to thank Miss S. Brass, Mrs A. Corbett, Mr R. B. Hume, Mrs J. Wood and Mr C. M. Warwick for excellent technical assistance. The work was supported by a Programme Grant from the Medical Research Council. Animals were held in the Wellcome Animal Research Laboratory, Faculty of Veterinary Medicine, University of Edinburgh.

REFERENCES

BROWN, A. G. (1981*a*). *Organization in the Spinal Cord.* Berlin, Heidelberg, New York: Springer Verlag.

BROWN, A. G. (1981*b*). The Spinocervical Tract. *Progress in Neurobiology* **17**, 59–96.

BROWN, A. G., BROWN, P. B., FYFFE, R. E. W. & PUBOLS, L. M. (1983). Receptive field organization and response properties of spinal neurones with axons ascending the dorsal columns in the cat. *Journal of Physiology* **337**, 575–588.

BROWN, A. G. & FYFFE, R. E. W. (1981). Form and function of dorsal horn neurones with axons ascending the dorsal columns in cat. *Journal of Physiology* **321**, 31–47.

BROWN, A. G., KIRK, E. J. & MARTIN, H. F. (1973). Descending and segmental inhibition of transmission through the spinocervical tract. *Journal of Physiology* **230**, 689–705.

BROWN, A. G., KOERBER, H. R. & NOBLE, R. (1984). Single spinocervical tract cells receive both excitatory and inhibitory effects from single hair-follicle afferent fibres in the cat. *Journal of Physiology* **353**, 28*P*.

BROWN, A. G., KOERBER, H. R. & NOBLE, R. (1987*a*). Excitatory actions of single impulses in single hair follicle afferent fibres on spinocervical tract neurones in the cat. *Journal of Physiology* **382**, 291–312.

BROWN, A. G., KOERBER, H. R. & NOBLE, R. (1987*b*). An intracellular study of spinocervical tract cell responses to natural stimuli and single hair afferent fibres in the cat. *Journal of Physiology* **382**, 331–354.

BROWN, A. G., NOBLE, R. & ROWE, M. J. (1986). Receptive field profiles and integrative properties of spinocervical tract cells in the cat. *Journal of Physiology* **374**, 335–348.

HONGO, T., JANKOWSKA, E. & LUNDBERG, A. (1968). Post-synaptic excitation and inhibition from primary afferents in neurones of the spinocervical tract. *Journal of Physiology* **199**, 569–592.

HONGO, T. & KOIKE, H. (1975). Some aspects of synaptic organization in the spinocercervical tract cell in the cat. In *The Somatosensory System*, ed. KORNHUBER, H. H., pp. 218–226. Stuttgart: Georg Thieme.

MAXWELL, D. J., BANNATYNE, B. A., FYFFE, R. E . W. & BROWN, A. G. (1982). Ultrastructure of hair follicle afferent fibre terminations in the spinal cord of the cat. *Journal of Neurocytology* **11**, 571–582.

MAXWELL, D. J., FYFFE, R. E. W. & BROWN, A. G. (1982). Fine structure of spinocervical tract neurons and the synaptic boutons in contact with them. *Brain Research* **233**, 394–399.

MAXWELL, D. J., FYFFE, R. E. W. & BROWN, A. G. (1984). Fine structure of normal and degenerating primary afferent boutons associated with characterized spinocervical tract neurons in the cat. *Neuroscience* **12**, 151–163.

TAPPER, D. N. & WIESENFELD, Z. (1980). A dorsal spinal neural network in cat. I. Responses to single impulses in single type I cutaneous input fibers. *Journal of Neurophysiology* **44**, 1190–1213.

TAPPER, D. N., WIESENFELD, Z. & CRAIG, A. D. (1983). A dorsal spinal neural network in cat. II. Changes in responsiveness initiated by single conditioning impulses in single type I cutaneous input fibres. *Journal of Neurophysiology* **49**, 534–547.