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THE VARIABILITY OF MUSCLE NERVE SYMPATHETIC ACTIVITY IN RESTING RECUMBENT MAN

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SUMMARY

1. Pulse synchronous bursts of multi-unit sympathetic activity was recorded from median or peroneal muscle nerve fascicles in fourteen subjects resting in the recumbent position. The neural activity was quantitated in terms of burst incidence, i.e. the number of bursts in the mean voltage neurogram/100 heart beats, during successive rest periods of 2–4 min.

2. For each individual the burst incidence was fairly constant between different rest periods but the mean burst incidence varied widely between individuals, the range being from less than 10 to more than 90 bursts/100 heart beats.

3. Simultaneous double nerve recordings were made on one subject from median and peroneal nerves and on eight subjects from the two peroneal nerves. There was always close similarity between the two records in such experiments regardless of which muscles the nerve fascicles innervated. When analysed separately the difference in burst incidence between the two sides ranged from 0·7 to 5·1 bursts/100 heart beats. The findings suggest that sympathetic neurones destined to skeletal muscles are subjected to a homogenous central drive and that contributions to the activity from ganglionic or segmental sources are of lesser importance.

4. On seven subjects repeated recordings at rest were made with intervals of 3 weeks–21 months between recordings. In each subject mean burst incidences were similar in all recordings (range of differences 0·5–11·2 bursts/100 heart beats) suggesting an individually constant level of sympathetic activity in muscle nerves.

5. For each individual the variability of burst amplitudes in the mean voltage neurogram was described by burst amplitude spectra. Most subjects had a relatively larger proportion of small than high amplitude bursts, but there was a tendency for more even amplitude distributions in subjects with high burst incidence. The finding may be an indication of inter-individual differences in the average number of impulses/burst.

6. It is concluded that the multi-unit recording technique can be used for comparisons of the level of muscle nerve 'sympathetic tone' between different subjects.

INTRODUCTION

Previous micro-electrode recordings of multi-unit sympathetic activity in resting man showed that spontaneously occurring sympathetic impulses destined for skeletal muscles are discharged in a characteristic temporal pattern of short sequences of pulse-synchronous bursts with interposed periods of more or less total neural silence (Hagbarth & Vallbo, 1968). Simultaneous blood pressure recordings revealed that the waxing and waning of the neural activity are inversely correlated to spontaneous blood pressure fluctuations in a way indicative of baroreflex modulation of the sympathetic outflow (Delius, Hagbarth, Hongell & Wallin, 1972*a* and *b*; Wallin, Delius & Hagbarth, 1973; Wallin, Delius & Sundlöf, 1974; Wallin, Sundlöf & Delius, 1975). It still remains uncertain, however, whether the patterning and strength of the muscle nerve sympathetic activity (MSA), as recorded from a given site in a limb muscle nerve and visualized in a 'mean voltage' display, is representative of sympathetic outflow to extremity muscles in general and can provide a quantitative measure of muscle nerve 'sympathetic tone' in a given subject. These questions are dealt with in the present study. Attempts are made to estimate whether under resting conditions the patterning and strength of the MSA is similar in different muscle nerves of a given subject, whether there are significant variations in this activity from day to day and whether there are reproducible differences between individuals. Instead of measuring the absolute amplitude of sympathetic bursts in the 'mean voltage' neurograms, a variable critically dependent upon electrode positioning within the nerve fascicle, the *number* of such bursts in relationship to the number of heart beats was used as a quantitative measure of the strength of the sympathetic outflow.

METHODS

Material. Recordings of MSA were made on fourteen volunteers, 21–54 years of age, twelve of whom were healthy and two of whom had untreated essential hypertension with blood pressures of 170/100 and 170/105 mm Hg, respectively. All gave their informed consent to the investigation. In nine of the subjects (eight healthy and one hypertensive) *simultaneous recordings* were made from two nerves. In eight subjects the recordings were made from the left and right peroneal nerves and in one subject from the left median and the right peroneal nerves. In seven subjects (six healthy and one hypertensive) *repeated* recordings of MSA were made either in the peroneal or the median nerve. The recordings were made in four subjects on two occasions and in three healthy subjects on three occasions. In those three cases in which three recordings were made, one was a simultaneous double nerve recording.

In each subject the interval between recordings varied between 3 weeks and 21 months.

Nerve electrodes, recording and display systems. The nerve recordings were made with insulated tungsten micro-electrodes, the uninsulated tip of which had a diameter of 1–5 μm. The reference electrodes were similar but with a larger part of the tip uninsulated and they were inserted subcutaneously 1–2 cm from the recording electrodes. The electrodes were connected to a differential preamplifier with a FET input stage with a fixed gain of 1000 and the nerve signal was then further amplified with an additional gain of 20. During the experiments the neural activity was monitored continuously on a storage oscilloscope (Tektronix 549) and a loudspeaker. To improve the signal-to-noise ratio the nerve signal was fed through a bandpass filter with a band width of 700–2000 Hz and then through an amplitude discriminator to reduce remaining noise. A RC integrating network with a time constant of 0·1 sec was used to obtain a mean voltage display of the nerve signal. Both the unfiltered nerve records and the mean voltage neurograms were stored together with the e.c.g. on an 8 channel FM tape recorder (PI 6200, Precision Instruments). In the simultaneous double nerve recordings two identical recording systems were used and careful controls were made to exclude electronic overhearing between the two systems.

For analysis the mean voltage nerve records were displayed together with the e.c.g. on an inkjet recorder (Mingograph 800, Siemens-Elema Ltd) with a paper speed of 3–5 mm/sec. The amount of neural activity was then determined from the chart by counting the number of pulse synchronous sympathetic bursts in the mean voltage record in relation to the number of heart beats. Measurements of burst amplitudes were also made from the chart. In the simultaneous double nerve recordings each nerve record was analysed independently of the other. To determine the difference in latency between corresponding bursts in the two nerves the filtered neurograms were displayed on a fibre optic ultra-violet recorder (Medelec MS6) with a paper speed of 50 mm/sec. In the figures to be presented amplitude calibrations of the nerve signals are omitted because of the amplitude distortion inherent in the filtering process.

E.c.g. was recorded by surface electrodes on the chest.

Experimental procedure. Subjects were in a comfortable recumbent position. The nerve recording electrode was inserted manually through the intact skin into the median nerve at the elbow or the peroneal nerve at the fibular head. Muscle nerve fascicles were identified by the following criteria: (a) weak electrical stimuli delivered through the recording electrode gave rise to muscle twitches without concomitant skin paraesthesiae, (b) taps on the muscle belly and passive muscle stretch evoked afferent mechanoreceptive impulses, and (c) no afferent neural response was induced by skin stimuli. On penetration of a muscle nerve fascicle small electrode adjustments were made until a recording position was found in which spontaneously occurring bursts of sympathetic impulses could be recorded. Evidence that the impulses derive from sympathetic vasoconstrictor fibres has been discussed in detail previously and only the most important points will be summarized here: (1) by injections of local anaesthetics around the nerve proximal and distal to the recording point the impulses were found to be efferent (Hagbarth & Vallbo, 1968; Delius *et al.* 1972*a*), (2) the conduction velocity of the impulses was found to be approximately 1 m/sec (Hagbarth & Vallbo, 1968; Delius *et al.* 1972*a*), (3) I.V. infusion of a sympathetic ganglion blocking drug (Trimetaphan) reversibly blocked the impulses (Delius *et al.* 1972*a;* Wallin *et al.* 1973), (4) an increase in the number of pulse synchronous bursts was regularly followed by blood pressure elevation or muscle vasoconstriction both at rest and in response to tests such as the Valsalva manoeuvre

(Delius *et al.* 1972*a*, *b*), (5) electrical stimulation of the carotid sinus nerves caused a reduction of the number of bursts and at the same time a decrease in calf vascular resistance (Wallin *et al.* 1975), (6) sympathetic vasodilator fibres are probably not present in man (Bolme & Fuxe, 1969). Even if they exist one would not expect them to be active at rest and since they are not supposed to be under baroreflex control (Uvnäs, 1960), they can hardly be the generators of the pulse synchronous bursts studied here.

Although equivalent recording sites could not be obtained in different experiments, attempts were always made to obtain recordings of similar quality and only such sites were accepted in which some of the sympathetic bursts had an amplitude of at least 3–4 times that of the noise in the mean voltage neurogram. When an acceptable recording position was found the subject had usually been in the recumbent posture for 30–90 min and the activity at rest was then recorded for varying periods of time. In some experiments the rest was interrupted by manoeuvres such as deep breathing, fist clenchings, mental stress. The effects of these manoeuvres will be reported separately. The first 20 sec after each manoeuvre was not included in the quantitative determinations of the number of sympathetic bursts at rest.

During the rest periods the subjects were repeatedly instructed to remain relaxed and if unintentional muscle contractions occurred in the extremity recorded from, the resulting electrical activity was recognized both because such signals occurred continuously without being grouped in pulse synchronous bursts and because they had different frequency content than the sympathetic impulses when the nerve activity was monitored on a loudspeaker.

RESULTS

In all recordings the sympathetic impulses were grouped in pulse-synchronous bursts separated by variable periods of apparent neural silence. The strength of individual bursts varied widely in each recording; some were weak and difficult to distinguish from the background noise but the majority were distinct and easy to identify in the mean voltage neurogram. The sequential pattern of discharges also varied; sometimes bursts occurred fairly regularly in periodically repeated sequences (e.g. Fig. 1), sometimes sequences were more irregular or single bursts occurred in a staccato fashion (as in Fig. 6*B*). The average incidence of sympathetic bursts relative to the number of heart beats varied markedly between different subjects, the range for the whole material being from less than 10 to more than 90 bursts per 100 heart beats. In contrast, for a given subject the average burst incidence was quite stable, not only when comparing consecutive rest periods during continuous recording from a given intraneural site but also when comparing simultaneous recordings from two nerves or recordings obtained on different occasions.

Continuous recording from a given intraneural site. If during a continuous recording the number of bursts were determined for consecutive rest periods of approximately 3 min duration (range 2–4 min) there were fairly small differences between different periods and values that deviated from the mean by more than 10 bursts/100 heart beats were rare. This is illu-

strated in Figs. 3 and 7 which show examples of the burst variability at rest in many different recording sites. In general, the largest variations occurred in those experiments in which the rest was interrupted by different manoeuvres and in such cases there was often a high value during the first rest period after a manoeuvre (e.g. subject H.J. in Figs. 3 and 7). For those recording sites in which 4 or more rest periods were analysed the variability between rest periods was expressed as the standard deviation of the burst incidence. The range of variability for all such sites (twenty-five neurograms in eleven subjects) was then 1·6–9·2 (mean 5·0) bursts/100 heart beats.

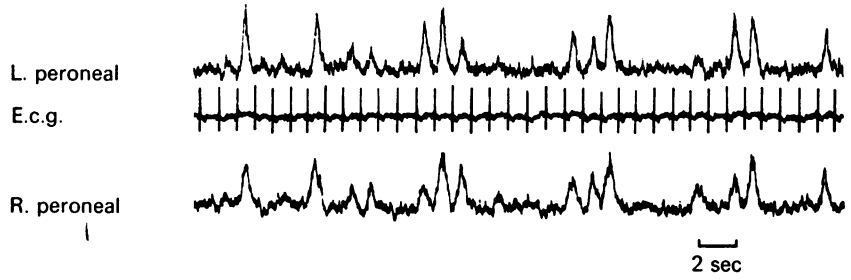

Fig. 1. Relationship between mean voltage records of MSA in simultaneous recordings from both peroneal nerves in the same subject.

Simultaneous recordings from two muscle nerve fascicles. The major finding in the simultaneous recordings of MSA from two nerves was the pronounced synchrony of the neural activity, regardless of which muscles the two fascicles innervated. As illustrated in Fig. 1, when the mean voltage nerve records were compared, almost every sympathetic burst could be identified in each, and the variations in amplitude between successive bursts often occurred in parallel. The only deviations from the bilaterally synchronous pattern were seen with weak bursts which could, at times, be distinguished only in one nerve. This type of 'drop-out' of bursts shifted back and forth from one nerve to the other and as a rule occurred with about the same incidence on both sides. When signal-to-noise ratios were not optimal, random variations in noise on either side could obscure small burst deflections in the mean voltage neurogram, and so contribute to such 'drop-outs'. However, recordings of the quality illustrated in Fig. 2, demonstrated that this was not the only reason, but that in addition true shifts in sympathetic outflow did occur. In Fig. 2 the recording from the right leg was a typical multi-unit recording displayed as a mean voltage neurogram. The recording from the left leg was dominated by impulses from a fairly small number of fibres which stood out clearly from the background. As usual most bursts can be identified in both records but on

two occasions (marked by asterisks) a single impulse was recorded from the left leg in the appropriate phase of the heart cycle without a counterpart in the mean voltage neurogram of the right side. On the other hand there is also a small multi-unit burst in the right nerve record (indicated by an arrow) without a corresponding unitary discharge on the left side.

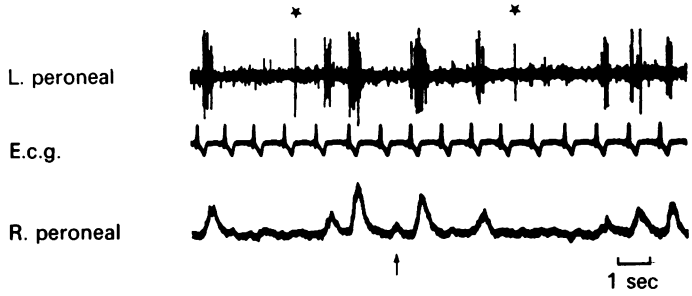

Fig. 2. Double nerve recording showing occasional discrepancies between the two neurograms. Upper record: filtered neurogram, dominated by activity in limited number of axons; lower record: mean voltage neurogram. The asterisks indicate single impulses in the upper record and the arrow indicates a small burst in lower record without a corresponding contralateral discharge.

For a quantitative comparison of the sympathetic outflow in the two nerves the recordings were divided into 3 min rest periods and the number of bursts were determined in each record separately. As illustrated in Fig. 3 there were as a rule only small differences between the two nerves and apart from some random variation, there was a clear tendency for activity changes to occur in parallel in both. Table 1 summarizes the differences between the total number of bursts in both records for all experiments in which integrated neurograms with acceptable signal-to-noise ratios were obtained. In only two subjects did the difference exceed 10 % of the total number of bursts counted. Expressed in terms of number of bursts/100 heart beats the differences between the sides ranged from 0·7 to 5·1. After separate analysis, comparison of the two neurograms from each recording revealed that on the average close to 80 % of all bursts had been identified in both neurograms. The remaining 20 % were either 'drop-outs' or weak bursts, the amplitudes of which were too low to be identified in one of the integrated neurograms when these were analysed separately.

In five double nerve recordings with good signal-to-noise ratios some corresponding bursts were distinct enough in the filtered neurograms to allow a determination of the starts and/or ends of the bursts. From such measurements latency differences and burst durations were calculated. The histograms in the left part of Fig. 4 show the variability in latency

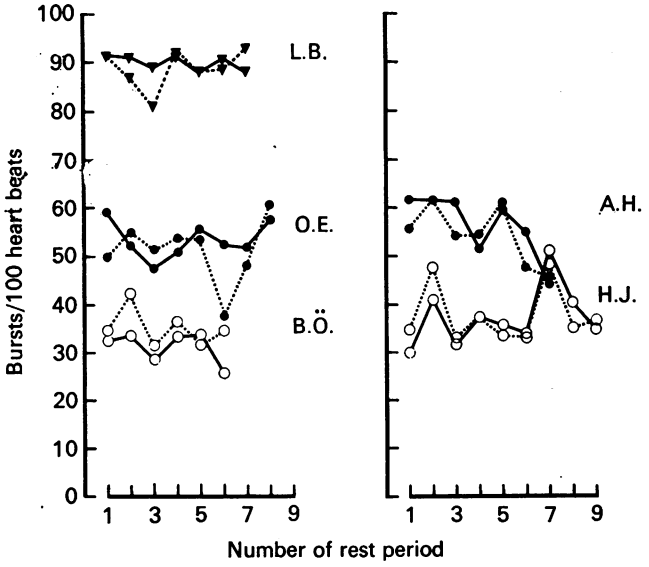

Fig. 3. Quantitative analyses of mean voltage records from simultaneous double nerve recordings in five different subjects at rest. Each point represents the number of sympathetic bursts/100 heart beats determined from a rest period of approximately 3 min. For each subject, the recordings from the left side (hatched lines) and right side (solid lines) were analysed independently. Left recording in subject LB made from the median nerve, all others from the peroneal nerves.

TABLE 1. Differences in total number of sympathetic bursts in simultaneous recordings from two nerves. Subjects at rest

Subject	Duration of recording (sec)	No. of bursts			Difference (no.)	Difference in % (of total in nerve with least bursts)
		n. med. sin.	n. per. sin.	n. per. dx.		
S.P.*	293	—	242	261	19	7·9
O.R.	352	—	197	191	6	3·1
B.B.†	725	—	70	79	9	12·9
B.Ö.	986	—	412	366	46	12·6
A.H.	1207	—	722	799	27	3·5
L.B.	1260	1185	—	1200	15	1·3
O.E.	1332	—	716	752	36	5·0
H.J.	1655	—	700	690	10	1·4

* Subject with essential hypertension.

† Due to extreme scarcity of bursts at rest, several manoeuvres were included in analysis.

differences in one subject for the start and end of corresponding bursts in the two nerves. For the same subject the variability of the duration of the bursts are shown in the right part of the figure. Similar histograms were obtained in all five subjects and in Fig. 5 the results are summarized by schematic representations of the time relationships between average corresponding bursts in both nerves for each individual. As shown in Fig. 4 the variability in latency and duration could be fairly large for individual bursts in a pair but in the recordings from the two peroneal nerves the mean values showed only small differences.

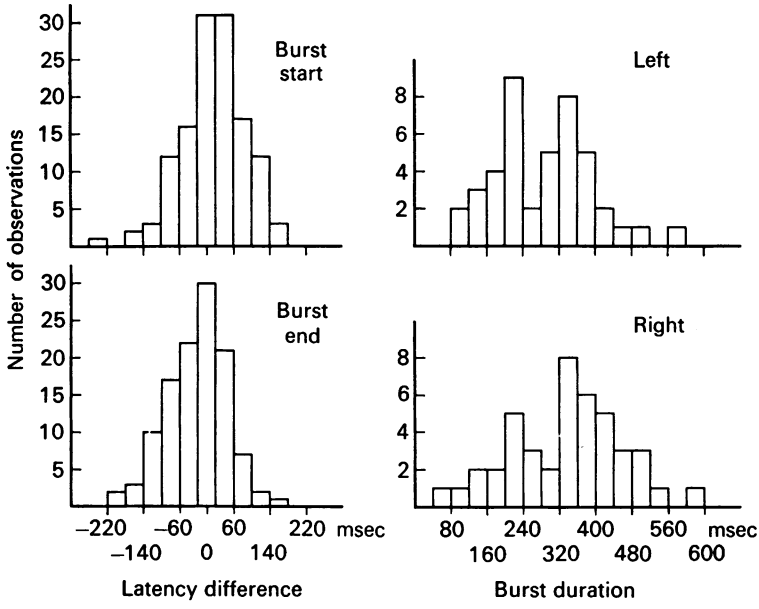

Fig. 4. Latency differences (left) and durations (right) for corresponding bursts recorded simultaneously in both peroneal nerves in subject A.H. Analysis based on bursts with good signal-to-noise ratio in filtered neurograms. In the latency difference histograms positive values indicate that bursts in right leg begin (upper) and end (lower) before bursts in left leg.

The shorter durations of the bursts in the left leg can probably be explained by the fact that in all four experiments the left recording happened to be the more selective with fewer units within the recording range of the electrode. In the simultaneous recordings from the median and peroneal nerves in subject LB there was a clear latency difference between corresponding bursts in a pair with the activity from the median nerve leading by on the average 350 msec. The difference can be explained simply as a consequence of the difference in conduction distance. Disregarding intraspinal conduction, the peripheral conduction distance from the

vertebral column (Th1 and L4 respectively) to the recording site was approximately 35 cm longer in the leg than in the arm. With a latency difference of 350 msec this corresponds to a conduction velocity of 1·0 m/sec which is well within the conduction velocity range of post-ganglionic sympathetic axons.

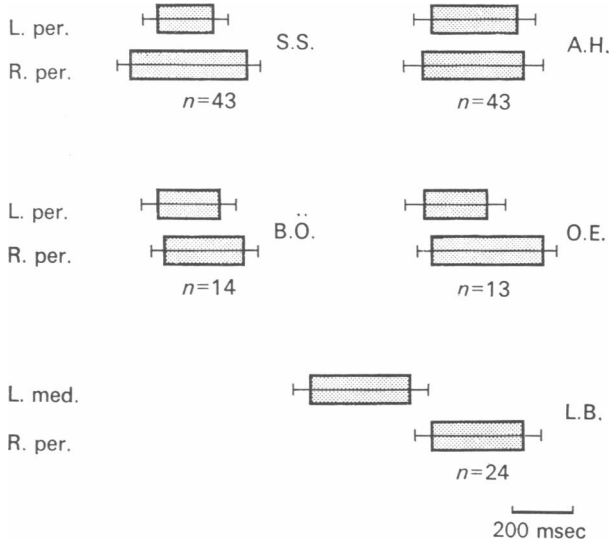

Fig. 5. Collected data from latency difference and burst duration histograms obtained from simultaneous recordings of MSA in two nerves in five subjects. For each subject the pair of rectangles illustrate the mean time relationship between corresponding bursts in the two nerve records. Horizontal lines indicate burst duration at plus 1 S.D. In subject L.B. recordings made from left median and right peroneal nerves, in all other subjects from both peroneal nerves.

If, during a double nerve recording, one electrode position was altered it was found that minor changes in signal-to-noise ratio or in the number of active sympathetic fibres recorded from could occur without seriously affecting the correspondence between the two recordings. In highly selective recordings with only a few active fibres within the pick up range of the electrode, the bursts sometimes became more difficult to identify in the mean voltage neurogram, but in such cases a close relationship could still be demonstrated if the original neurogram was used for the comparison instead of the mean voltage neurogram (cf. Fig. 2).

Repeated recordings in the same subject. When MSA was recorded on more than one occasion in the same subject the general character of the activity was similar in each recording. This is illustrated in Fig. 6 which shows examples of the mean voltage nerve records obtained in repeated

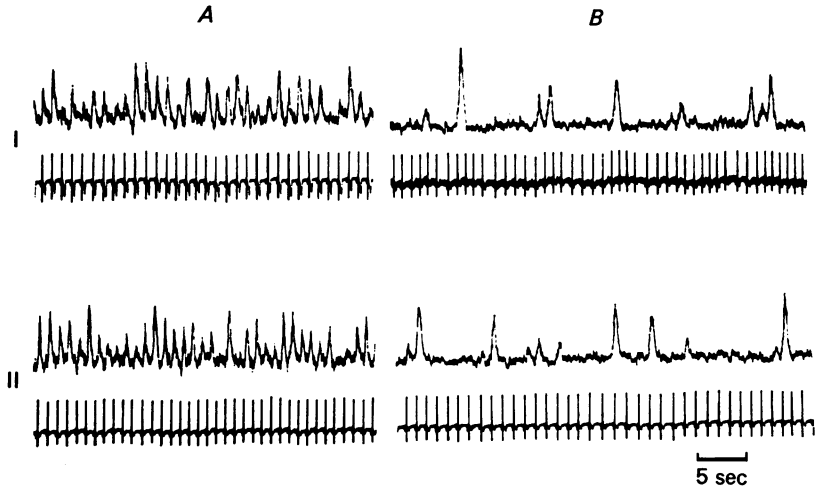

Fig. 6. Similarity of MSA in repeated recordings in the same subjects. Time interval between recordings was 2 months for subject A and 3 weeks for subject B. Upper traces: Mean voltage neurogram. Lower traces: e.c.g.

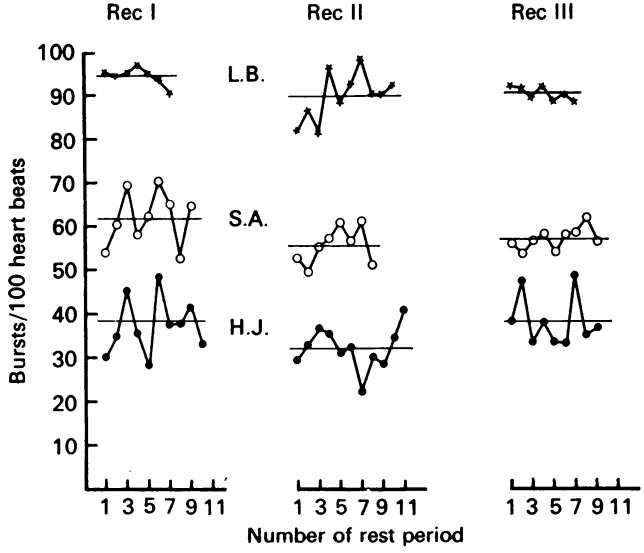

Fig. 7. Quantitative analyses of repeated recordings of MSA in three different subjects at rest (subject initials between rec. I and II). Each point represents the number of bursts/100 heart beats determined from a rest period of approximately 3 min duration. The thin horizontal lines represent the mean value for each experiment. Recording I in subject S.A. made in the right median nerve, all others in either of the peroneal nerves. Recording III in subjects H.J. and L.B. were double nerve recordings and diagram shows results from one nerve only.

recordings on two different subjects. In both recordings from subject *A* pulse-synchronous discharges occurred almost continuously with only occasional pauses, whereas in both recordings from subject *B* the bursts occurred much more sparsely, often in a staccato pattern.

After each recording the number of sympathetic bursts relative to the number of heart beats was determined for all rest periods. Fig. 7 shows examples of the results for repeated recordings in three subjects and the collected data for all subjects are summarized in Table 2. For a given subject the mean difference in burst incidence between recordings was only 4·8 bursts/100 heart beats (range 0·5–11·2), despite the fact that the interval between recordings varied from 3 weeks to 21 months, and the fact that in some subjects different manoeuvres were interposed between some rest periods.

TABLE 2. Comparison of the amount of MSA in repeated recordings at rest in the same subject. For each recording the sympathetic activity is expressed as the mean number of sympathetic burst/100 heart beats ± S.D. For one recording with less than four rest periods only mean value given. Recording I in subject S.A. made in the right median nerve, all others in either of the peroneal nerves

Subject	Recording I	Recording II	Recording III	Time interval between recordings
H.J.	38·5 ± 5·9	32·1 ± 4·9	37·5 ± 6·3	3 weeks 3 months
A.S.	43·4 ± 9·0	37·3 ± 6·4	—	7 months
I.K.	45·4	41·8 ± 8·0	—	13 months
I.O.*	58·9 ± 4·9	69·6 ± 2·3	—	16 months
K.J.	63·5 ± 8·4	71·0 ± 4·1	—	21 months
S.A.	61·8 ± 6·2	56·0 ± 4·2	57·0 ± 2·5	5 months 11 months
L.B.	94·3 ± 2·0	89·5 ± 5·3	90·4 ± 1·6	2 months 7 months

* Subject with essential hypertension.

Burst strength. For each subject the relative strength of the sympathetic bursts was assessed by measuring burst amplitudes in the mean voltage neurograms and displaying the results as burst amplitude spectra. Since recording sites were not reproducible in different experiments burst amplitudes were expressed in percentage of the maximal amplitude in each experiment and comparisons between spectra from different sites were restricted to their general shape. In most subjects the amplitude spectra were left skewed, i.e. the number of small amplitude bursts was greater than the number of high amplitude bursts, and in a given subject there was in general good agreement between the shapes of the spectra obtained in different nerves or in repeated recordings in the same nerve. Examples of

left skewed amplitude spectra from four different recording sites in subject H.J. are shown in the left part of Fig. 8.

Not all subjects, however, had amplitude spectra with the same degree of left skewness but the tendency was that subjects with high burst incidence had, in relative terms, more high amplitude bursts than subjects with low burst incidence. The most pronounced interindividual difference in shapes between burst amplitude spectra is shown in Fig. 8 between the spectra from subject H.J. (32–38 bursts/100 heart beats) and subject L.B. (89–94 bursts/100 heart beats).

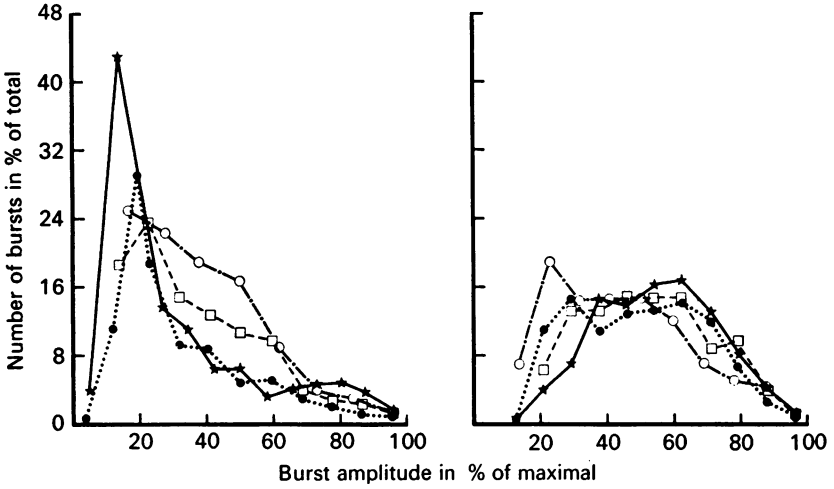

Fig. 8. Burst amplitude spectra from four different recording sites in subject H.J. with 32–38 bursts/100 heart beats (left) and subject L.B. with 89–94 bursts/100 heart beats (right). One spectrum in subject L.B. based on 200, all others on 300 burst amplitudes. For each spectrum, burst amplitudes are given in percent of the maximal amplitude in a particular recording site. For subject H.J. the spectrum indicated by □ - - □ from left and all other spectra from right peroneal nerve. For subject L.B. the spectrum indicated by ○ - · - ○ from left median, □ - - □ from left peroneal and the remaining two spectra from right peroneal nerve.

DISCUSSION

In the present investigation mean voltage records were used as an aid in quantitating the multi-unit sympathetic outflow to muscles. When recording bursts of neural activity the strength of a burst, as seen in a mean voltage record, depends both on the number of active fibres and their proximity to the recording electrode. However, in a given recording position such records do give a quantitative estimate of the fluctuations of activity. The finding of a pronounced similarity between the two mean

voltage records in all double nerve recordings, regardless of which muscles the fascicles innervated, indicates a remarkable synchrony in the sympathetic outflow to different skeletal muscles. Since in most cases even weak bursts could be identified in both neurograms when these were inspected together, it is likely that a fairly large and diffusely distributed portion of all sympathetic fibres destined to skeletal muscle discharge during most bursts detected in the integrated records. Consequently one must postulate that in intact man at rest, the central drive on post-ganglionic neurones in muscle nerves is widespread and powerful, whereas contributions to the outflow from segmental or ganglionic sources are of lesser importance.

Several previous studies have shown sympathetic impulses recorded in human skin nerves to be discharged in a different temporal pattern to that found in muscle nerves (Delius *et al.* 1972*a*; Hagbarth, Hallin, Hongell, Torebjörk & Wallin, 1972; Wallin *et al.* 1973, 1975; Hallin & Torebjörk, 1974). In skin fascicles sympathetic impulse bursts have variable duration, show no sign of pulse synchrony and as revealed by simultaneous double nerve recordings from one skin and one muscle nerve fascicle, occur without apparent correlation to the discharges in muscle fascicles (Wallin *et al.* 1973). On the other hand, in simultaneous recordings from two skin fascicles in different extremities (Wallin *et al.* 1973; B. G. Wallin, unpublished observations) the similarity between the mean voltage records is again quite good (although not as striking as in muscle nerve fascicles). Taken together, these observations suggest that human sympathetic ganglia contain at least two, and probably more, functionally different populations of post-ganglionic neurones, each subjected to a fairly homogeneous preganglionic influence, which differs markedly between the populations. The existence of cell populations which are distinct both anatomically and physiologically has been demonstrated by micro-electrode recordings from single cells in the avian ciliary ganglion (Marwitt, Pilar & Weakly, 1970) and toad sympathetic ganglia (Nishi, Soeda & Koketsu, 1965; Honma, 1970).

As shown by the present results the number of sympathetic impulse bursts destined for skeletal muscle differs markedly between different individuals. This cannot be explained by large fluctuations of outflow from day to day since the figures were surprisingly constant, not only during the course of a long experiment, but also when repeated recordings were made after varying time intervals. It could be argued that different degrees of emotional stress experienced during an experiment could account for the interindividual differences. Well defined periods of mental stress may alter the amount of MSA in some subjects (Delius *et al.* 1972*a*; Wallin *et al.* 1973) but usually such effects are moderate or small. Some of our subjects were more tense than others at the start of an experiment but, as a rule, when the recording was under way they relaxed without concomitant changes in

neural outflow. The similarity of the repeated recordings also speaks against acute stress as a major determinant of the amount of activity since it is unlikely that subjects would experience the same degree of stress during subsequent recordings. Therefore, on the basis of the present results it is reasonable to propose that human subjects resting in the horizontal position have a fairly constant outflow of sympathetic activity to skeletal muscles and that there are major differences in the relative number of bursts between individuals. At present little can be said about the reason for the interindividual differences but factors such as blood pressure, age, personality, physical fitness have to be considered. In this context, it should be noted that some normotensive subjects had higher burst incidence figures than the two hypertensive ones and the synchrony of the neural outflow in double nerve recordings was equally pronounced in normo- and hypertensive subjects. Consequently the results give no indication of a difference in MSA between subjects with different blood pressure.

It is likely that the pulse synchronous bursts are dominated by vasoconstrictor impulses to the vascular bed of skeletal muscles (see Methods). From this viewpoint the similarity between the double nerve recordings agrees well with common experience from haemodynamic studies that muscle blood flow variations occur in parallel in different extremities (cf. Golenhofen & Hildenbrand, 1957). The results of repeated blood flow measurements are more difficult to compare with the present results, since muscle blood flow depends not only on the neural drive but also on cardiac output, vascular basal tone, hormonal and local metabolic factors, and these influences may vary more than the sympathetic activity. However, in a carefully controlled study Browse (1962) measured calf blood flow (which is dominated by muscle flow) in the same individuals on different occasions and found no significant variations from day to day in any given subject. Between subjects however, there were clear and reproducible flow differences.

The synchrony in the simultaneous double nerve recordings and the reproducible results in repeated recordings in the same subjects indicate that the present multi-unit recording technique can be used for comparing the number of pulse synchronous sympathetic bursts between individuals. Do such figures also give estimates of true 'sympathetic tone' in muscle nerves? Since the absolute strength of the sympathetic bursts (their amplitude in the mean voltage neurogram) cannot be compared between individuals, it could be argued that interindividual differences in the average number of sympathetic impulses per burst could reduce the differences indicated by burst incidence figures. This seems unlikely. It is true that the differences in shape between burst amplitude spectra could be an indication of interindividual differences in sympathetic impulses/burst.

However, since subjects with high burst incidence tended to have relatively more high amplitude bursts than subjects with low burst incidence it is reasonable to propose that burst incidence figures do give fairly reliable measures of 'muscle nerve sympathetic tone', the maximal difference between individuals being perhaps even greater than the burst incidence figures indicate.

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