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Ganglionic neuronal mechanisms involved in circulatory control system

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Abstract. Intracellular tonic activity and responses to orthodromic stimuli were recorded from the neurones of rabbit superior cervical ganglion and compared with those recorded from the nerves containing pre- and postganglionic nerve fibres, with the use of a coherent recording technique. It was found that: (1) firing of each ganglion neurone is triggered by two presynaptic inputs, single and multiple, formed by a single preganglionic nerve fibre whose discharges evoke the postsynaptic spikes correlated with cardiac rhythm, and by a few converging preganglionic nerve fibres which evoke the postsynaptic spikes, either correlated with cardiac rhythm or irregular, only if two or more of them discharge together, correspondingly; (2) about 240 neurones of the ganglion, on the average, fire synchronously during their tonic activity, being driven by only three preganglionic nerve fibres; (3) only about 9% of a "neural unit", the number of the ganglion neurones receiving innervation from the same preganglionic nerve fibre, are discharged during their tonic activity through a single input, while the rest of neurones are either discharged through a multiple input (17%), or generate only the excitatory postsynaptic potentials subthreshold for spike generation (73%). The results obtained suggest that the ganglionic neuronal mechanisms responsible for vasomotor control involve much more complex ganglionic integrative processes than it has been commonly thought.

Key words: ganglionic integrative mechanisms, sympathetic tonic activity, sympathetic vasomotor control

INTRODUCTION

It has been commonly accepted that the sympathetic outflow which controls the circulatory system is mainly formed in the central nervous system, while sympathetic ganglia only serve as the "relays" where the nerve impulses are multiplied (see, e.g., Skok and Ivanov 1989). This model is consistent with a relatively simple organization of singly innervated B cells of amphibian sympathetic ganglia (Nishi et al. 1975). In contrast, multiple preganglionic innervation is observed in mammalian sympathetic ganglia. For example, 12 and 8.5 preganglionic nerve fibres, on the average, converge upon the same neurone in the superior cervical ganglion of the guinea-pig (Purves and Wigston 1983) and rabbit (Tatarchenko et al. 1990), correspondingly. These observations suggest that the sympathetic ganglia in mammals may fulfil integrative functions which, however, have been scarcely studied. Their study was the aim of this work, the main part of which was made using the *in situ* preparation, with preganglionic supply of the ganglia left intact. This allowed us to study tonic activity of the ganglion neurones, rather than only their responses to artificial preganglionic stimuli, and to investigate the integrative functions of the ganglia important for their normal physiological activity.

METHODS

The experiments were performed on the superior cervical ganglion of the rabbit anaesthetized with urethan (1.0 g/kg, i.v.). In the *in vitro* experiments, the ganglion was isolated and perfused throughout the experiment by Krebs solution saturated with 95% O_2 + 5% CO_2 at 22-25°C. In the *in situ* experiments, the ganglion was kept under the level of the solution, with its blood supply and connections to the spinal cord left intact. Intracellular recording of either evoked or tonic activity from the ganglion neurones was performed with the conventional glass microelectrodes filled with 2.5 M KCl. A single ganglion neuron was directly stimulated through the recording intracellular microelectrode using a bridge circuit. The ganglion nerves were stimulated, and their electrical responses were recorded, with either wire or sucking electrodes. Large myelinated preganglionic nerve fibre was dissected, under visual control by a dissecting microscope, cut, and its end attached to the ganglion was pulled into a sucking electrode for stimulation.

For estimation of how many ganglion neurones and preganglionic nerve fibres correlate their discharges with each other during their tonic activity, the cross-correlation analysis between the intracellular spikes and the records obtained from the internal and external carotid nerves containing postganglionic nerve fibres, or the cervical sympathetic nerve containing preganglionic nerve fibres, was performed. For this purpose, the 50 to 80 ms records obtained from the nerves were digitized at the frequency of 7.8 kHz (in the *in vitro* experiments) or 3.5 kHz (in the *in situ* experiments), stored, and averaged synchronously with the tonic intracellular spikes or with the direct stimulation of single preganglionic nerve fibre or single ganglion neurone, correspondingly, to improve the signal-to-noise ratio. The signals thus obtained were compared with those recorded from the nerves in response to the direct stimulation of a single neurone or single preganglionic nerve fibre, correspondingly.

To differentiate between the ganglion neurones projecting to the skeletal muscles and to the cutaneous vasoconstrictors, the systemic chemoreceptors were stimulated by inhalated CO_2-enriched air for 15-20 s through the intubating cannula in the *in situ* experiments (Gregor and Jänig 1977). For more detailed description of the methods used see Skok and Ivanov 1983, Ivanov 1987, Tatarchenko et al. 1990, Ivanov and Skok 1992).

RESULTS

How are the sympathetic ganglion neurones activated during their normal tonic activity?

Two types of intracellular spikes appear in the ganglion neurones during their tonic activity (Skok

and Ivanov 1983, 1989), as shown in Fig. 1A. The spikes of the first type (marked by dots in Fig. 1A) are characterized by a steep rising phase and, being evoked by a single preganglionic stimulus of the gradually increasing intensity, appear in an all-or-none fashion, together with the excitatory postsynaptic potential (e.p.s.p.) which triggers the spike (Fig. 1B, left record). Strong hyperpolarization of the neuronal membrane is needed to block the spike initiation. These features indicate that the spike of the first type is evoked by a discharge of a single preganglionic nerve fibre. In contrast, the spikes of the second type possess a smooth rising phase and appear only when two or more preganglionic nerve fibres converging on the same neurone discharge synchronously with each other, while a discharge of a single fibre evokes only an e.p.s.p. subthreshold for the spike initiation (Fig. 1B, left and right records). Therefore, each ganglion neurone is activated during its normal tonic activity *via* the two presynaptic inputs, single and multiple, formed by a single preganglionic nerve fibre and a few converging preganglionic nerve fibres, correspondingly. The former input, if activated, always triggers a

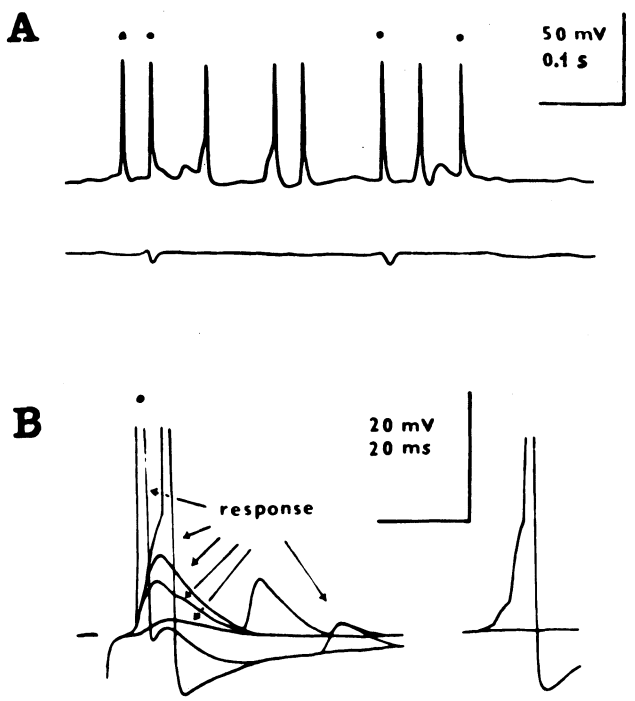

Fig. 1. Two types of intracellular spikes in the neurones of rabbit superior cervical ganglion. A, tonic activity (upper trace) and ECG (lower trace). The spikes marked by dots are evoked through a single presynaptic input, while the rest spikes and excitatory postsynaptic potentials (e.p.s.p.s) are evoked through a multiple presynaptic input. B, the superimposed responses (marked by arrows) of another neurone to single preganglionic stimuli of different intensities. The spike evoked through a single presynaptic input is marked by dot. Note that one e.p.s.p. appeared spontaneously (the preganglionic nerve fibres in A and B were left intact). Right panel shows the spike evoked by single preganglionic stimulus in the absence of tonic activity (modified from Skok and Ivanov 1983).

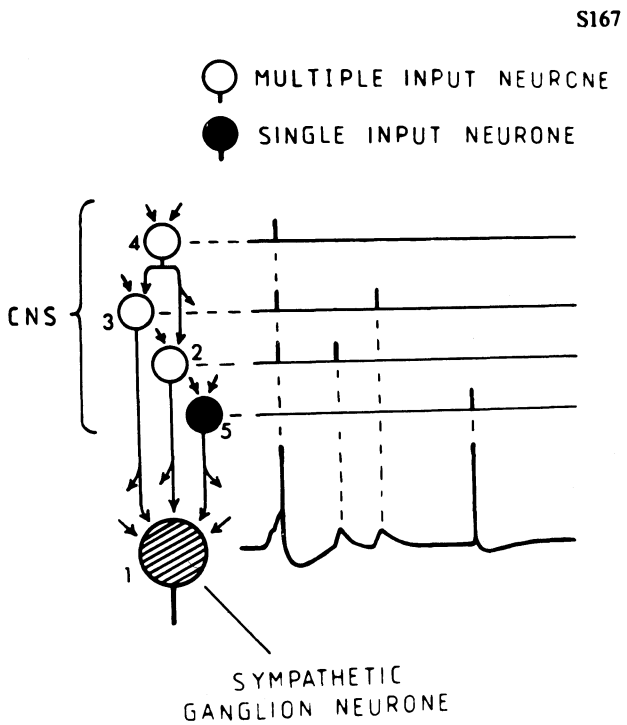

Fig. 2. A hypothetical scheme of neuronal organization responsible for tonic activity of the sympathetic ganglion neurone (1) which receives a multiple presynaptic input from preganglionic neurones 2 and 3 (whose activity is synchronized by a neurone 4) and a single presynaptic input from a preganglionic neurone 5. Arrows indicate additional presynaptic inputs or axon collaterals. The discharge of each CNS neurone is indicated by vertical bar at the right part of the scheme; the resulting tonic activity of the ganglion neurone is drawn arbitrary below, comprising the step-preceded spike, the sharp-rising spike and two e.p.s.p.s. According to the scheme, a postsynaptic spike appears if either the neurone 5 fires, or the neurones 2 and 3 fire synchronously, while their non-synchronous firing yields only e.p.s.p.s. For further details see text (Tatarchenko et al. 1990).

postsynaptic spike, while the latter one can trigger it only through the cooperative firing of two or more preganglionic nerve fibres.

It is essential that the synchronization itself of the firing of preganglionic nerve fibres is not an occasional process, as it occurs much more frequently than one should expect supposing its occasional occurence (Skok and Ivanov 1989). This means that firing in the two or more converging preganglionic nerve fibres can be driven by one more neurone located central to them. A hypothetical scheme of the neuronal organization responsible for the features of tonic activity described above is shown in Fig. 2.

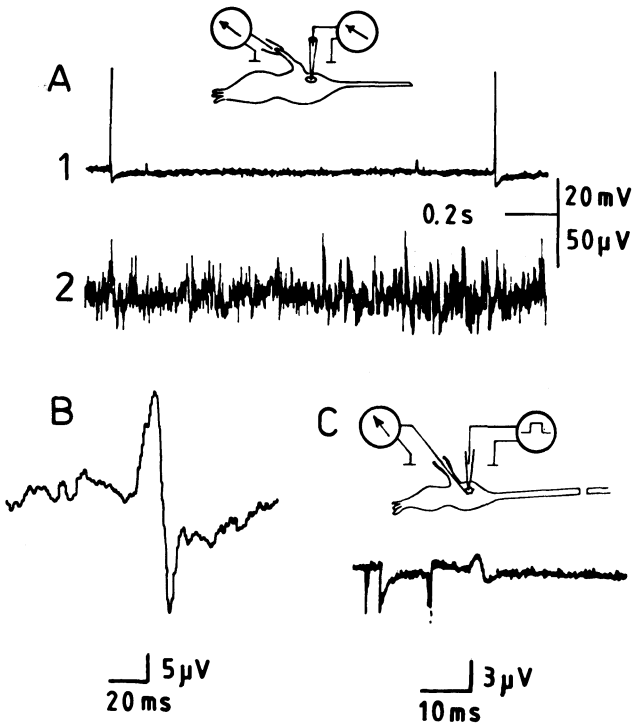

Fig. 3. Estimation of the number of the ganglion neurones firing synchronously with each other during their tonic activity. A, tonic activity recorded simultaneously with an intracellular microelectrode from the ganglion neurone (1) and with a sucking electrode from the external carotid nerve containing postganglionic nerve fibres (2). The inset shows the experimental arrangement. B, a signal obtained by the averaging of 100 nerve records synchronized with the intracellular spikes. C, a signal obtained by averaging of 200 nerve records synchronized with the direct suprathreshold stimuli applied to a single ganglion neurone through an intracellular electrode. The inset shows the experimental arrangement. The number of the synchronously firing neurones during their tonic activity was estimated by dividing the area of a signal in B by the area of a signal in C (modified from Skok and Ivanov 1987).

How many ganglion neurones discharge synchronously with each other during their normal tonic activity?

To answer this question, the cross-correlation analysis between the intracellular tonic activity (Fig. 3A: 1) and the activity recorded from the whole nerve containing postganglionic nerve fibres (Fig. 3A: 2) was performed within the 40 ms periods before and after each intracellular spike. The averaged signals thus obtained (Fig. 3B) had the amplitudes of 33.0 ± 9.5 μV in the internal carotid nerve and 48.0 ± 2.4 μV in the external carotid nerve (mean ± SE, $n = 22$), correspondingly. If correlated with the intracellular spike evoked by a direct stimulation of the neurone, instead of the spikes in its tonic activity, the signals of 1.1 ± 0.1 μV ($n = 5$) and 1.6 ± 0.1 μV ($n = 6$) amplitudes, correspondingly, were obtained (Fig. 3C). The number of the neurones discharging synchronously with each other during their tonic activity was estimated simply by dividing the signal area by area, and appeared equal, on the average, to 113 and 124 neurones projecting into the internal and external carotid nerves, correspondingly. It thus can be concluded that a total of about 240 ganglion neurones fire synchronously with each other within a 80 ms time interval during their tonic activity (Tatarchenko et al. 1990).

How many preganglionic nerve fibres evoke the correlated firing of the ganglion neurones during their tonic activity?

A response to this question was obtained using a cross-correlation analysis between the intracellular tonic spikes (Fig. 4A: 1) and the activity recorded from the intact cervical sympathetic nerve which contains the preganglionic nerve fibres (Fig. 4A: 2). The averaged signal (Fig. 4A: 3) of a 1.8 ± *0.2* μV amplitude ($n = 11$) was obtained and compared with that of 1.3 ± *0.1* μV ($n = 5$), obtained with the same method, but using for the cross-correlation

the stimuli applied to a single preganglionic nerve fibre, instead of the intracellular spikes (Fig. 4B). It was found with an area by area dividing that, on the average, only three preganglionic nerve fibres (the number ranging from one to six in different experiments) fire synchronously within the 80 ms time interval. This surprising result means that synchronous firing of only three preganglionic nerve fibres is enough to evoke discharges in about 240 neurones of the ganglion during their tonic activity (Ivanov and Skok 1992).

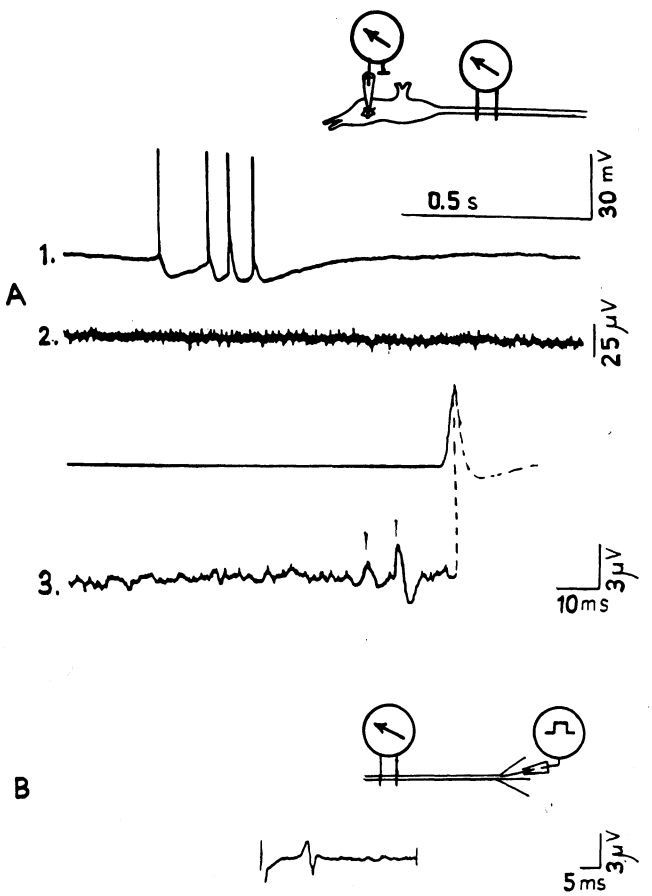

Fig. 4. Estimation of the number of the preganglionic nerve fibres correlating their firing with the appearance of intracellular spikes recorded from the ganglion neurones during their tonic activity. A, tonic activity simultaneously recorded from the ganglion neurone with an intracellular electrode (1), and from the intact cervical sympathetic nerve containing preganglionic nerve fibres, with wire electrodes (2), and a signal obtained by averaging of about 500 nerve records synchronized with the intracellular spikes during tonic activity (3; a top trace shows the position of the intracellular spike in relation to the nerve signal). The inset shows the experimental arrangement. B, a signal obtained by the averaging of the nerve records synchronized with the suprathreshold stimuli applied to single preganglionic nerve fibre through a sucking electrode. The inset shows the experimental arrangement (modified from Ivanov and Skok 1992).

It seemed of interest to know in what proportion of the above number of 240 neurones the spikes are evoked through a single presynaptic input, and in what proportion through the multiple one. These proportions were estimated in the following experiments.

How many ganglion neurones synchronously firing during their tonic activity are discharged through a single presynaptic input?

To answer this question, the area of the averaged signal evoked in a postganglionic nerve by the stimulus applied to a single preganglionic nerve fibre (Fig. 5A) was divided by the area of the signal evoked in the same nerve by direct stimulation of a single ganglion neurone (Fig. 5B). The single fibre stimulation resulted in the appearance of a 6.6 ± 0.6 µV ($n = 13$) signal in the internal carotid nerve, and 6.1 ± 0.6 µV ($n = 8$) signal in the external carotid nerve. Stimulation of single neurone evoked a 1.5 ± 0.2 µV ($n = 10$) signal in the internal carotid nerve, and a 1.3 ± 0.2 µV ($n = 10$) signal in the external carotid nerve. It was found with a dividing area by area that stimulation of a single preganglionic nerve fibre evokes discharges, on average, in the 15 neurones projecting into the internal carotid nerve and 13 neurones projecting into the external carotid nerve, i.e., altogether, in 28 neurones (Ivanov and Skok 1992). As far as the postsynaptic discharge generation did not need cooperation between the preganglionic nerve fibres, it was obviously triggered through a single presynaptic input.

Distribution of interspike intervals in tonic activity of the ganglion neurones

It has been found (Gregor and Jänig 1977, Blumberg et al. 1980, Jänig et al. 1983) that sympathetic vasoconstrictor neurones to the skeletal muscles in

their major part are characterized, in contrast to the vasoconstrictor neurones to the skin, by modulation of their tonic activity with cardiac and respiratory rhythms, and by an increase in their firing frequency following stimulation of the systemic chemoreceptors with CO_2. Using these criteria, two groups of 30 and 15 neurones that tentatively project to the muscle and cutaneous vasoconstrictors, correspondingly, were identified in our experiments (Fig. 6: A: 1-3 and B: 1 - 3). In the first group, only in 9% of neurones tonic activity was characterized by a noise-like distribution of interspike intervals, while in the major part of neurones the activity was modulated by cardiac (33%) or respiratory rhythms (17%), or by both rhythms (41%). In the second group, a noise-like distribution of interspike intervals was observed in most neurones (62%), while the respiratory rhythm was found only in 19%. In addition, in 19% of the neurones in this group the activity was modulated by a 1.5-2.5 Hz rhythm which was not identical either to the cardiac or to respiratory rhythm. These results confirmed the conclusion (see Jänig et al. 1983) that the strongest baroreceptor control is observed in the muscle vasoconstrictor sympathetic neurones.

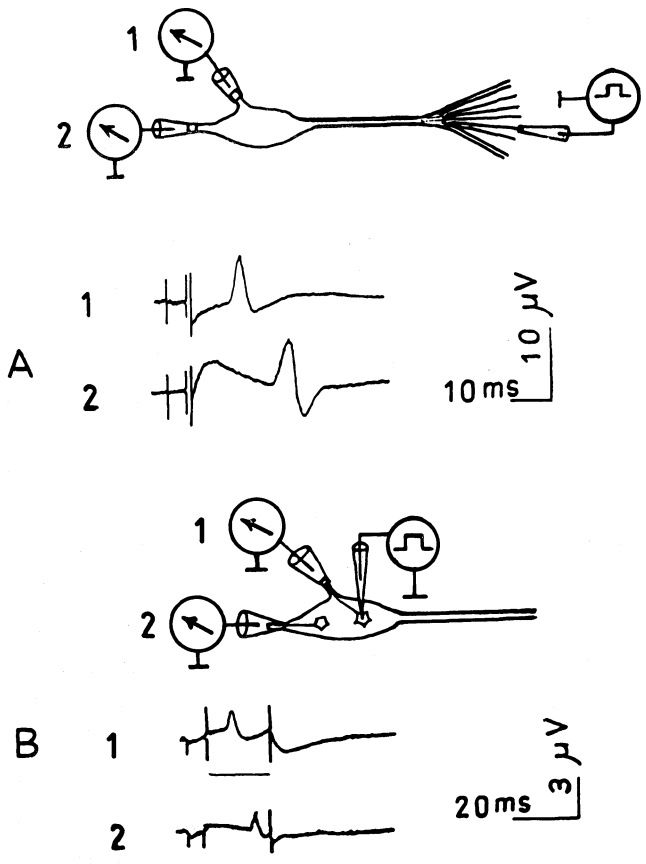

Fig. 5. Estimation of the number of the ganglion neurones discharged by single preganglionic nerve fibre. Action potentials were recorded with sucking electrodes from external (A: 1 and B: 1) and internal (A: 2 and B: 2) carotid nerves in response to stimulation of a single preganglionic nerve fibre (A) or single ganglion neurone (B). The action potentials were obtained by averaging of 50 records (A) and 100 records (B) synchronized with the corresponding stimuli. The insets show the corresponding experimental arrangements. The number of ganglion neurones discharged by a single preganglionic nerve fibre was estimated by dividing an area of the signal shown in A: 2 by an area of the signal shown in B: 2.

Modal specificity of single and multiple presynaptic inputs

The proportions of the neurones whose tonic spikes were evoked only through a single input, only through a multiple input, and through both inputs, were equal to 23%, 31%, and 46% in the muscle vasoconstrictor neurones, and 23%, 54%, and 23% in the cutaneous vasoconstrictor neurones (Fig. 6A: 4 and B: 4). Although there is a difference in the proportions of the neurones whose tonic spikes are triggered though the multiple input and through both single and multiple inputs, it is clear that both inputs are operating in each of the groups. Thus, multiple presynaptic input is typical of the mammalian vasoconstrictor neurones, supplying both the skeletal muscles and the skin, rather than of sympathetic neurones of other modalities.

The single input interspike intervals may have a bimodal normal distribution, with the two respective means corresponding to the mean interval between the R_{ECG} and between the two respiratory cycles. As regards a multiple input, the interspike interval histograms either fit a Poisson distribution or were intermediate between this type of distribution and normal distribution (Tatarchenko et al. 1990). In about 50% of the neurones whose spike in tonic activity are triggered by a multiple input the interspike intervals revealed modulation with a car-

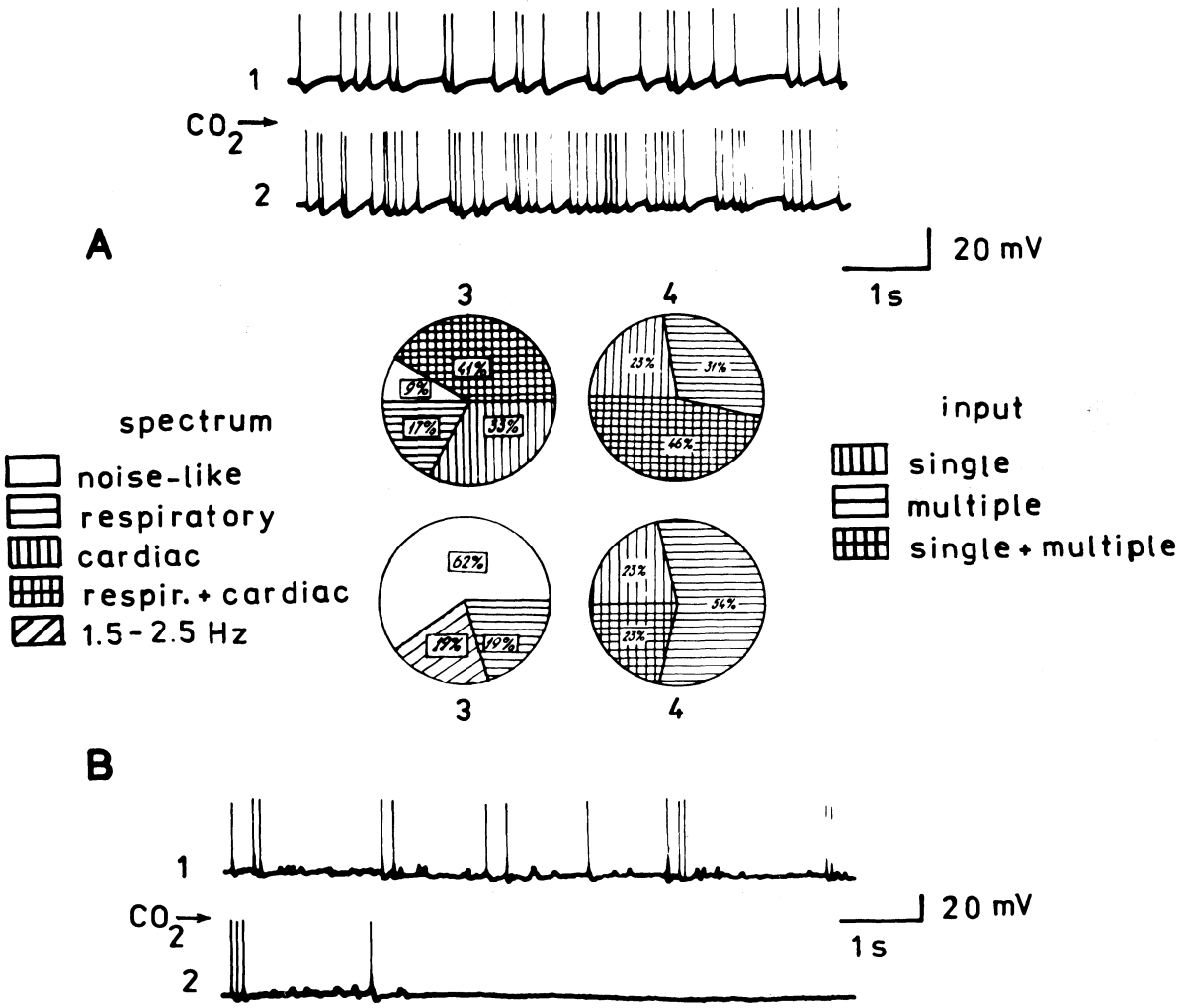

Fig. 6. Tonic activity recorded from the neurones of two groups, presumably the muscle (A) and cutaneous (B) vasoconstrictor neurones of the ganglion, before (1) and after (2) inhalation of the CO_2-enriched air. The diagrams 3 show the proportions of neurones with a noise-like distribution of interspike intervals (A: 3a and B: 3a), and with the activity modulated by a respiratory rhythm (A: 3b and B: 3b), by a cardiac rhythm (A: 3c), by the both rhythms (A: 3d), and by a 1.5 - 2.5 Hz rhythm (B: 3, c). The diagrams 4 show the proportions of neurones whose tonic activity is evoked through only a single input (A: 4a and B: 4a), only a multiple input (A: 4b and B: 4b), or the both inputs (A: 4c and B: 4c) (modified from Ivanov 1987).

diac rhythm, similar to that found in the spikes triggered by a single input (V. Maslov, unpublished observation).

DISCUSSION

The results of our work suggest that only 28 neurones of the rabbit superior cervical ganglion, on the average, are discharged by firing of a single preganglionic nerve fibre through a single presynaptic input. At the same time, 240 neurones, on the average, are discharged during their tonic activity by synchronous fiting or three preganglionic nerve fibres, which gives 80 neurones *per* fibre. In 52 neurones of this number (a difference between 80 and 28) the discharges, therefore, occur through a multiple input. Each preganglionic nerve fibre is known to innervate from 200 to 400 ganglion neurones (i.e., about 300 neurones, on the average), the number called "neural unit" (Gabella 1986, Purves et al. 1986). So, only 9% of the neurones of the neural unit are discharged through a single input, and

17% of the unit neurones are discharged through a multiple input. In the rest of the unit neurones (74%) only the e.p.s.p.s subthreshold for spike initiation should occur.

Thus, in the majority of the ganglion neurones the postsynaptic spikes occurring during their tonic activity are evoked through a multiple, rather than through a single, input. This finding rises a question about the physiological significance, in general, of multiple innervation of nerve cells. Only a single presynaptic input was found to be responsible for a very rare tonic firing in the neurones of rat superior cervical ganglion projecting to the submandibular gland, in contrast to other neurones of the ganglion, most probable, the vasoconstrictor ones, whose tonic activity, like that in the rabbit, was evoked through both single and multiple inputs (Ivanov 1989, V. Maslov, unpublished observations). Only a single innervation was found in the B neurones of amphibian sympathetic ganglia (Nishi et al. 1965) projecting to the toxic glands of the skin (Honma 1970), intracardiac nerve plexuses of the frog (Dennis et al. 1971, McMahan and Kuffler 1971) and rat (Selyanko and Skok 1992), pelvic plexus of the rabbit (A. Bobrishev, unpublished observations), and avian ciliary neurones (Marvitt et al. 1971). At the same time, other groups of neurones in the same ganglia, responsible for vasomotor effects (C neurones of amphibian sympathetic ganglia and avian choroid neurones) possess multiple innervation. Single innervation is also present in phasic skeletal muscle fibres, in contrast to the tonic ones which receive multiple innervation.

It thus seems likely that multiple innervation, in general, is related to a tonic, rather than to a phasic, functions of the target organ. One possible reason for this is that tonic activity needs persistent and relatively high-frequency impulsation which, if supplied and multiplied through a single nerve fibre, would lead to an exhaustion of its ability to synthesize and release synaptic transmitter. This may force preganglionic nerve fibres to cooperate by converging on the same ganglion neurone, triggering the postsynaptic spikes through synchronization of their firing.

One more factor that may be responsible for the development of multiple innervation of sympathetic neurones is a decrease in the number of neurones in sympathetic ganglia, if compared with the body mass (see Skok and Ivanov 1989). For example, the number of neurones in the superior cervical ganglion per a body mass unit is 6 times lower in the cat and 16 times lower in the man, than in the rat, as follows from the data presented by Gabella (1986, Tables 2.1-2.3). At the same time, it has been found that a decrease in the number of nerve cells *per* innervated target area by partial denervation of the target organ is followed by marked increases in the convergence of preganglionic nerve fibres on the ganglion cells that remain intact, and in the frequency of e.p.s.p.s and spikes in their tonic activity (Ivanov 1989, Voyvodic 1989).

An intriguing question is why a great majority of neurones (74% of the neural unit) response to tonic preganglionic volleys only by the e.p.s.p.s subtreshold for spike generation. Is this just a "side effect" of a synchronized preganglionic activity causing spikes in other ganglion neurones, or the "ineffective" e.p.s.p.s have some other functions? It was shown that preganglionic innervation, in addition to triggering spikes in the ganglion neurones, is very important for a trans-synaptic regulation of their metabolism and functions, in particular, the tyrosine hydroxilase activity (Zigmond and Chalazonitis 1979, Chalazonitis and Zigmond 1980), lipid metabolism (see Skok 1973), protein synthesis (Hall and Wilson 1979), growth and development (Black et al. 1972), and the maintenance of synaptic connections (Purves and Lichtman 1985). It is thus possible that a great number of ineffective e.p.s.p.s simply reflects this still very scarcely studied site of normal ganglionic activity.

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