EFFECT OF CARBON DIOXIDE ON THE EXCITABLE MEMBRANE OF THE SINGLE RANVIER NODE

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Addition of 5% CO_2 to the atmosphere in the chamber with the specimen caused no significant change in the recorded parameters of the Ranvier node membrane. Increasing the CO_2 concentration to 50% (50% CO_2 + 50% O_2) caused a significant increase in the resistance and critical depolarization level of the membrane, a decrease in amplitude of the spike and maximal steepness of its rise. Spike generation ceased 2 min after the beginning of exposure to the gas mixture. The action of CO_2 was completely reversible. After-potentials of the node were virtually unchanged by the action of CO_2 in these concentrations.

KEY WORDS: single Ranvier node; isolated nerve fiber; membrane resistance.

Experiments on whole frog nerve [2-4] have shown that an increase in the CO_2 concentration in the surrounding atmosphere or solution leads to a marked increase [4] of after-depolarization (AD) and abolition [2] of posttetanic hyperpolarization (PTH) of the membrane. It is difficult to interpret the results of experiments on a whole nerve, and for that reason the mechanism of the effects of CO_2 as described above remains unexplained.

In the investigation described below it was accordingly decided to study the action of CO_2 on the excitable membrane of single Ranvier nodes of isolated nerve fibers.

The classical method of isolation, stimulation, and derivation of action potentials (AP) of single Ranvier nodes of myelinated nerve fibers of *Rana ridibunda* as described previously [1, 3] was used. Carbon dioxide was introduced into the chamber containing the specimen as a mixture with O_2 (5% CO_2 + 95% O_2 or 50% CO_2 + 50% O_2).

EXPERIMENTAL RESULTS

During exposure of the specimen to an atmosphere of 5% CO_2 + 95% O_2 (the pH fell to 7.1) only a small increase took place in the critical level of membrane depolarization. The after-potentials remained unchanged. Exposure to this gas mixture combined with a shift of pH of the solution toward the alkaline side had a similar action. In this case modified Ringer's solution containing 20 mM $NaHCO_3$ (pH 8.2) was used. The $NaHCO_3$ concentration in the solution was increased at the expense of a corresponding decrease in the NaCl concentration. The pH of the solution on saturation with a gas mixture containing 5% CO_2 fell from 8.2 to 7.8.

Since the expected change in after-potentials of the single Ranvier node was not obtained in an atmosphere of the above composition, the CO_2 concentration in it was increased to 50% (50% CO_2 + 50% O_2). When modified Ringer's solution was saturated with this gas mixture and the same gas mixture was introduced into the chamber containing the specimen (pH of the solution 7.1), within 1 min a significant change was observed in the properties of the excitable membrane of the nerve fiber: the resistance (R_m) measured relative to the amplitude of the anodal pulses increased, the critical level of membrane depolarization (ΔV) increased sharply, but the spike amplitude V_s and the maximal steepness of its rise ($\dot{V}_{max}$) were reduced (Fig. 1). In the experiment illustrated in Fig. 1 a small decrease in the resting potential of the fiber also took place. In the other experiments the changes in the resting potential were extremely small, and sometimes there was actually slight and transient hyperpolarization of the membrane.

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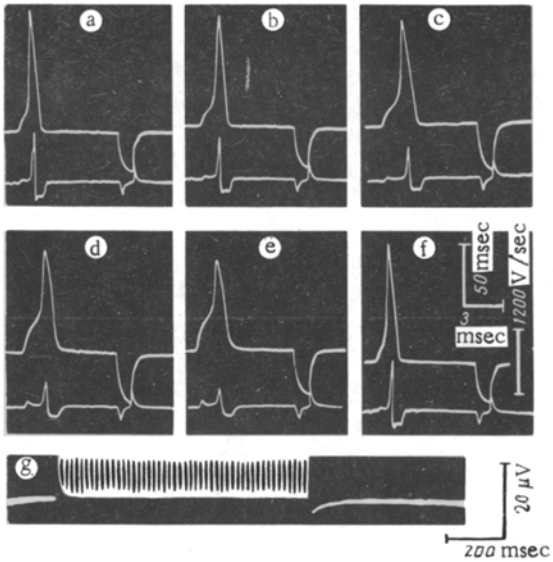

Fig. 1. Changes in properties of excitable membrane of single Ranvier node following introduction of gas mixture of 50% CO_2 + 50% O_2 into chamber containing specimen. a) Initial action potential and resistance (R_m) measured relative to amplitude of nodal pulses of constant strength applied 5 msec after spike (top beam) and differentiation with respect to time (bottom beam); b-e) the same during exposure for 1.5 min to gas mixture; f) 3 min after change of gas mixture and external solution for ordinary air and Ringer's solution; g) response of nerve fiber kept for 1 min in atmosphere with increased CO_2 concentration to repetitive stimulation at 300 Hz.

At the beginning of the second minute of action of CO_2 the amplitude of V_s was reduced almost by half, and $\dot{V}_{max}$ by 60%. The R_m which was considerably increased during the first minute of action of CO_2 fell somewhat but still remained higher than initially. By about the end of the second minute of action of the mixture of CO_2 and O_2, AP generation ceased completely. Anodal hyperpolarization of the fiber did not restore AP. In all probability CO_2, like tetrodotoxin, depresses the maximum of sodium permeability ($\overline{P}_{Na}$).

As Fig. 1d and e show, AD increased a little as a result of the action of CO_2 on the node. However, the duration still remained not more than a few milliseconds. The small increase in AD which occurred in these experiments was probably the result of weakening of the outward I_K as a result of a decrease in membrane depolarization during the spike (its amplitude was reduced). The potassium permeability was evidently unchanged in the presence of high CO_2 concentrations. This was shown by preservation of PTH (Fig. 1g). The writers showed previously [3] that the onset of PTH of an isolated nerve fiber is connected with summation of the increased P_K of the membrane.

The data described above thus show that CO_2, in high concentrations, has a marked effect on R_m, $\overline{P}_{Na}$, ΔV, and $\dot{V}_{max}$ for the membrane of the single Ranvier node. The observed effects of CO_2 are completely reversible. Replacement of the atmosphere with CO_2 and O_2 in the chamber with the specimen by ordinary air and replacement of the external fluid by Ringer's solution led to the virtually complete recovery of the above parameters of the node membrane within 1-3 min.

The data on the effect of CO_2 on after-potentials of the single Ranvier node described above do not agree with previous observations [2, 4] made in experiments on the whole nerve. These disagreements between the results can be attributed to the fact that CO_2 has a specific effect only on the long phases of AD [2, 4] and PTH [2] of the whole nerve which, for as yet insufficiently clear reasons, are not present in single Ranvier nodes of isolated nerve fibers [1, 3].

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ELECTROPHYSIOLOGICAL, MORPHOMETRIC, AND HISTOCHEMICAL CHARACTERISTICS OF MUSCLE FIBERS OF THE FROG SARTORIUS MUSCLE

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Investigation of succinate dehydrogenase (SD) activity in the fibers of the frog sartorius muscle revealed three groups of muscle fibers (dark, pale, and intermediate). The SD activity in the muscle fibers was inversely proportional to their diameter. The outer surface of the sartorius muscle consists mainly of dark muscle fibers, the inner surface mainly of pale fibers. A microelectrode study showed that fibers of the outer surface have lower values of action potentials, a longer negative afterpotential, a lower quantum composition of the end-plate potentials, and higher amplitude and lower frequency of miniature end-plate potentials than fibers of the inner surface. Analysis of the results reveals definite relations between the histochemical profile of frog sartorius muscle fibers and their electrophysiological characteristics.

KEY WORDS: frog sartorius muscle; types of muscle fibers; succinate dehydrogenase; electrophysiological differences.

Three types of muscle fibers are distinguished in the amphibian motor system: phasic, tonic, and intermediate. Phasic fibers are characterized by a high transmembrane potential (TMP), by generation of an action potential (AP) in response to single stimulation of the motor nerve, by a short latent period and high quantum composition of synaptic potentials [4, 5], by weak summation of synaptic potentials in response to repetitive stimulation [4-6], and by other electrophysiological features. Phasic muscle fibers also differ from tonic and intermediate by their greater diameter [7, 9], the morphology of the motor nerve endings (endings of the "end brush" type), low activity of oxidative enzymes [9, 11], and various other structural and histochemical features.

The frog sartorius muscle is a typical phasic muscle, all fibers of which are regarded as functionally homogeneous. However, recent observations indicate that the fibers of the sartorius muscle vary in amplitude and quantum composition of their end-plate potentials (EPP), the dynamics of amplitude of EPP during repetitive stimulation [1], the frequency of their miniature end-plate potentials (MEPP), the duration of their AP [3], the area of synaptic contact [10], and activity of their oxidative and glycolytic enzymes [9].

The question naturally arises whether electrophysiological differences between muscle fibers of the sartorius muscle are connected with morphological and histochemical heterogeneity. The following investigation was carried out to study this problem.

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