THE PHYSIOLOGICAL PROPERTIES OF THE SENSORY FIBERS OF THE PHRENIC AND INTERCOSTAL NERVES

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The presence of sensory fibers in the phrenic nerve has been known from the work of N. O. Kovalevskii and E. Adamyuk [2]. Reflex changes of respiration and blood pressure following stimulation of this nerve were described much later [3, 6, 16 and others]. These reflexes are regarded as components of a pain reaction occurring in response to strong stimulation [13, 9], when the fine afferent pain fibers of the phrenic nerve, which have a low excitability, are stimulated [10].

It remains to find whether there are present in the phrenic nerve sensory fibers of a high excitability and conduction rate originating in stretch receptor fibers of the limb muscles. An answer to this question is essential for a correct evaluation of the significance of proprioceptors of the diaphragm in regulating respiration. Muscle spindles are present in the diaphragm [1, 7, 17]. A small number of sensory fibers, which from their diameter are classified as α-fibers have been found by histological methods in the phrenic nerve [12]. However, the physiological properties of thick sensory nerve fibers in the phrenic nerve have not been sufficiently studied.

Still less is known of the sensory nerve fibers which supply the intercostal muscles.

We here report results bearing on the excitability and rate of conduction of the sensory nerve fibers of the respiratory muscles.

METHOD

We carried out 14 experiments on cats. The spinal cord we divided at C_1, and artificial respiration was then maintained by a pressure pump, without anesthesia. Action potentials from sensory nerves of the diaphragm were led off from the peripheral ends of the dorsal roots of the 5th and 6th cervical segments of the left side. Laminectomy of the cervical vertebrae was complicated by hemorrhage from the venous sinuses. In this region, the dorsal roots are short, and they extend subdurally into fine bundles which proceed fanwise to their point of entry into the cord. Sometimes we extirpated the 5th and 6th spinal segments, which made it possible to place the whole of the subdural portion of the roots on the electrode. To reduce the inflow of "stray" afferent impulses from parts other than the diaphram, in some of the experiments we divided the cervical and brachial plexuses distal to the origin of the trunks of the phrenic nerve. We usually ligatured this nerve immediately above the diaphram, and above the ligature we placed the implanted Ag – AgCl stimulating electrode. As stimuli we used square pulses of 0.2 mseconds at a frequency of 100 per second. To record the responses we synchronized the sweep of the cathode ray oscillograph to the frequency of stimulation, and used an exposure of 20-40 sweeps. The temperature of the preparation was maintained between 36 and 37°. After the experiment the nerves were isolated along the whole of their length. The distance between the stimulating and the pickup electrodes was measured while the nerve was stretched with a load of 20 g.

RESULTS

Sensory fibers of the phrenic nerve enter the spinal cord together with a large number of afferent fibers of the cervical and brachial plexuses. Therefore from the dorsal roots records are always obtained also of numerous asynchronous action potentials due to stimulation of fibers other than those in the phrenic nerve. When we placed on the electrodes the whole of roots V and VI, or a considerable proportion of them, usually potentials due to stimulation of the phrenic nerve could not be distinguished from the other spontaneous potentials. It was only when the scan was synchronized to the stimulus that one or more action potentials from the sensory fibers of the phrenic nerve could be made out (Fig. 1a).

In order to improve the lead-off conditions, we used the peripheral ends of fine bundles of fibers of the posterior roots. From the fibers composing the V and VI roots, we were able to separate 6-12 such bundles. In most of them, only the unsynchronized electrical activity could be observed. But from certain bundles, which usually made up 1/3-1/4 of their total number, action currents synchronous with the stimulus to the phrenic nerve were obtained (Fig. 1b, c, d, e). They were of low amplitude, of the same order as that of the spontaneous waves. They could therefore be recorded only from repeated sweeps of the beam synchronized to the stimulus. On three exceptional occasions, waves from the sensory fibers were recorded from a single sweep, when the fiber was in a very fine bundle from the dorsal root (see Fig. 1b).

Fig. 1. Action potentials of the posterior roots induced by stimulation of the phrenic (a – e) and intercostal (f) nerves. a) Lead taken from the whole of the dorsal root C_5; action potential due to stimulation of the phrenic nerve, as indicated by the dots; b-e) lead-off from bundles of fibers from the dorsal roots C_5 and C_6. Action potentials of fibers having conduction velocities of 118 m/second (b), 91 m/second (c), 70 m/second (d), 43 m/second (e); f) combined action potential from the dorsal root of C_8 due to stimulation of the 6th intercostal nerve. Calibration: a-e) 10μv, f) 100 μv. Time marker (1 msecond).

Usually, when the stimulus reached threshold value, the action potentials were of maximal amplitude, and therefore evidently indicated excitation of a single fiber. Sometimes, when the stimulus amplitude was increased, the received potential was doubled in amplitude, indicating the excitation of two fibers of closely similar conduction velocity. In one bundle, 2-3 fibers might be found having different excitabilities and different conduction rates. The distribution of the sensitive fibers in the roots of the phrenic nerve was not constant; the majority of them were found in some preparations in the root of C_6, and in others in root C_5, but never in root C_4 or C_7.

The number of rapidly conducting sensory fibers in the phrenic nerve is shown in Fig. 2b, representing the results of three experiments. The greatest conduction rate corresponded to a maximum velocity in the muscle nerves of the limbs of 120 m/seconds. These fibers were solitary, and were not found in all preparations. More frequently, fibers having velocities of about 90, 70, or 60-36 m/second were encountered. However, the total number of fibers with these impulse velocities was very small. In most successful experiments the activity of no more than 8-9 such fibers could be detected. From a histological study of the phrenic nerve, the number of thick sensory fibers which would be expected to correspond to such conduction rates was rather greater [12]. These results are shown in Fig. 2a (the abscissa scale of Fig. 2a and b is chosen so that the velocity in meters per second is equal to the diameter of the fiber in $\mu \times 6$ [14]).

The excitability of the sensory fibers of the phrenic nerve was high, and greater than that of the motor fibers having the same conduction velocity. For example, the threshold for the motor fibers was 180 μa, the maximum conduction rate was 103 m/second (potentials led off from the peripheral end of the anterior root of C_6, phrenic nerve stimulated by implanted electrodes in the diaphragm equivalent resistance between them 2.3 kohm). The thresholds for the sensory fibers having conduction velocities of 95 and 75 m/second was 2.3 times less (82 μa) and 1.2 times less respectively than that of the motor fiber. The threshold for the slower sensory fibers was above that of the motor nerves.

The high excitability of the sensory fibers made it possible to observe their action potentials when leading off from the peripheral ends of the cut mixed trunks of the phrenic nerve in the region of the neck. To do so, we compared the thresholds for the appearance of electrical responses in the nerve fibers and in the muscles of the diaphram with unipolar stimulation of the nerve (which in these experiments was not ligatured at the diaphragm). Response of the muscle evidently corresponded to the threshold of excitability of the motor fibers. It was found that the action currents of the nerve could be observed at stimulations which were much weaker than those evoking contraction of the muscle (Fig. 3 lead from trunk of phrenic nerve branching from 5th cervical nerve). The threshold of excitation of the muscle of the diaphragm was 29 μa (equivalent resistance between electrodes 4.4 kohm). The action currents of the nerve fibers appeared at a threshold 2.6 times lower (11 μa). With increased amplification, there was no change in the amplitude of the action potential, indicating probably that a single fiber was excited. At a stimulus strength of 27 μa, a second wave appeared. Further increase of excitation led to a very rapid increase in the size of the second wave representing excitation of motor fibers. At the onset of the high-voltage wave of the combined action potentials, the first wave could be distinguished as a scarcely perceptible hump. Evidently this first wave was due to the activity of a sensory fiber having a lower threshold and higher conduction velocity than the most sensitive motor fiber. Observations of this kind were made on three preparations. When action potentials were led off from

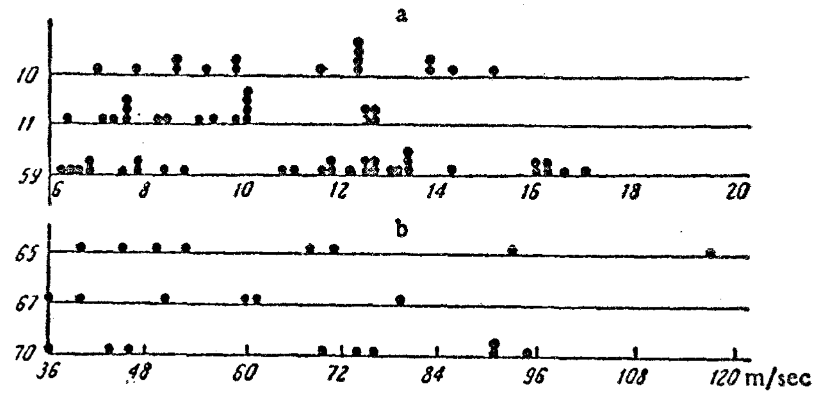

Fig. 2. Diameter (a) and conduction velocity (b) in sensory fibers of the phrenic nerve of the cat. Abscissa: a) diameter of fibers (in μ); b) rate of conduction (in meters per second). Each point corresponds to an identified fiber; a) results of Hinsey, Hare and Phillips [12]; b) our own data.

the trunk of the phrenic nerve, in all cases several fibers were found in the 6th cervical nerve whose excitability was 1.75-2.9 times greater than that of the motor fibers, as shown by the fact that the first wave increased with increase of the stimulus. A rapid increase in the amplitude of the action potential of the nerve began at stimulus strengths which were threshold for the excitation of muscle, and were therefore associated with the excitation of motor fibers. In one experiment, the thresholds for action potentials picked up in the 5th cervical nerve and derived from the muscle and the trunk of the phrenic nerve were identical, which showed that here there were no highly excitable sensory fibers.

The combined action potentials from the dorsal roots of the thoracic segments elicited by stimulation of the intercostal nerves were easier to observe, because they were of considerable amplitude (see Fig. 1f). Their shape was complex, and when the stimulus was increased above threshold, several waves developed having successively slower velocities. The amplitude of each wave increased gradually. The maximum velocity in the sensory fibers was again 120 m/second. However, the action potentials showed two more distinct peaks originating from impulses having a slower velocity. The first, which was of greater amplitude and shorter, was due to the excitation of fibers having the greatest conduction velocity of 70-88 m/second. Sometimes a wave could be found having a velocity of 46-63 m/second. The maximum rate of impulses giving the second peak was 40 m/second. With strong stimulation, superimposed on it there were a further 3-4 waves of successively smaller velocities.

Thus within the phrenic nerve there are contained afferent fibers having a high excitability and conduction rate. They enter the spinal cord through the dorsal roots of the 5th and 6th cervical nerves. Some of them have a lower threshold and a higher conduction velocity than do the most excitable motor fibers. In this respect they belong to the 1a group of sensory fibers [8]. Fibers were also found having a conduction velocity of about 90 m/second (group 1b), or 70 m/second or less (group II, [15]). In the muscle nerves of the limbs such fibers conduct impulses from stretch receptors in the muscle spindles and tendon endings. In our experiments we did not find more than 8 or 9 fibers having a conduction velocity greater than 36 m/second.

A few fibers may have been damaged during the dissection or in the experiment, but a large error on this score is unlikely. The number of fibers reported in [12] which did not undergo degeneration after division of the anterior roots was greater than found by us. It may be that in the experiments of [12], owing to the technically complicated method of dividing the anterior roots, a small number of motor fibers were preserved. In any case, the phrenic nerve must contain very few thick or moderate-sized afferent fibers. In the muscle nerves of the limbs there are many tens of such fibers (in the nerve supplying the tibialis anterior muscle, for example, there are about 150) [11]. The phrenic nerve contains a considerable number of fine afferent fibers [12, 15]. We did not study their properties in this investigation.

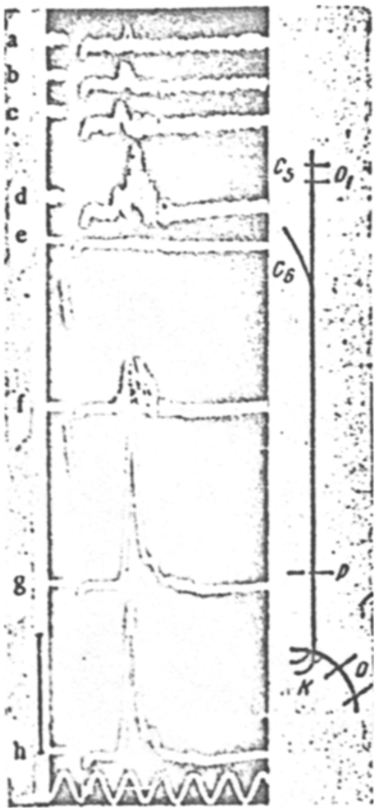

Fig. 3. Action potentials of the phrenic nerve in response to different strengths of stimulus. Leads taken from the 5th cervical nerve. Unipolar stimulation above the diaphragm. Stimulus strengths: a) 11, b) 17; c) 27; d, e) 31; f) 39; g) 51; h) 227 μa. Threshold excitation for diaphragm 29 μa. Amplification reduced ten times between d and e: calibration 100 μv for a-d, 1 μv for d-i. Time marker (1 μsec). On the right – diagram of the experiment. K) Arch of the diaphragm, L and L_1) lead-off electrodes, P) stimulating electrode (see text).

The intercostal nerves are richer in rapidly conducting sensory fibers, as was shown by the greater amplitude of their action potential. Here too fibers are found which belong to group Ia. Here we must note that in the intercostal muscles, muscle spindles are present [4]. In the combined action potentials the principal peaks are those which spread with the smaller velocity characteristic of fibers of group II. Evidently, these peaks represent excitation of fibers in the intercostal nerves conducting impulses from both muscular and cutaneous receptors.

SUMMARY

Action potentials from the 5th and 6th cervical dorsal roots induced by electrical stimulation of the phrenic nerve in the diaphragm were recorded from spinal cats. Action potentials were found corresponding to sensory fibers having conduction rates of about 120, 90, and 70 meters per second and less. The sensory fibers had a high excitability which was greater than that of motor fibers of the same conduction velocity. These sensory fibers are similar to those which conduct impulses from the stretch receptors of muscles. No more than 8 or 9 sensory fibers in the phrenic nerve were found having conduction rates of above 36 meters per second. The intercostal nerves contain more rapidly conducting sensory fibers, among which fibers of group 2 prevail.

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