FORMATION OF A SPINAL CORD DOMINANT DURING THE ACTION OF A CONSTANT CURRENT ON AN AFFERENT NERVE

F. D. Sheikhon

Electrophysiological Laboratory (Head, Dr. Biol. Sci. O. V. Verzilova), Institute of Normal and Pathological Physiology (Director, Active Member AMN SSSR, V. V. Parin) of the AMN SSSR, Moscow
(Presented by Active Member AMN SSSR, V. V. Parin)
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In our previous investigations [12, 13] we showed that the formation of a flexor spinal-cord dominant as a result of the application of subthreshold stimuli of current from an induction coil to a sensory nerve is accompanied by changes in the functional state of the peripheral neuromuscular apparatus. The changes taking place in these circumstances in the thresholds of excitability of the ipsilateral nerve and muscle and in the rate of accommodation of the motor nerve are analogous to those developing during catelectrotonus, whereas changes similar to those in anelectrotonus develop in the corresponding motor nerve and muscle of the contralateral limb.

Because of these facts and of existing ideas concerning the role of electrotonus and perielectrotonus in the mechanism of the activity of the nervous system [1-8, 10, 11], we undertook to investigate whether, in experimental electrophysiological conditions, it was possible to form a spinal cord dominant during the action of a constant current of subthreshold strength on an afferent nerve.

EXPERIMENTAL METHOD

Experiments were conducted on large specimens of the frog Rana ridibunda. The cerebral hemispheres were removed from the animals and the semitendinosus muscles, and peroneal and ulnar nerves dissected on both sides. The peripheral end of the ipsilateral peroneal nerve was divided and placed on nonpolarizing electrodes ($Zn-ZnSO_4$), for use in stimulation with a constant current (distance between electrodes 1 cm).

We used a modification of N. P. Rezvyakov's nonpolarizing electrodes [9]. A polarizing current (voltage from 0.01 to 0.4 V) was used, and its strength in the different experiments varied from 2 to 20 μA.

At a distance of 2 cm from the nonpolarizing electrodes were placed other electrodes used for stimulating the nerve with an induction current or with impulses from a thyratron stimulator, and at a further distance of 2 cm were the silver electrodes used to record the potentials of the nerve. The action potentials of the semitendinosus muscle were picked up by means of silver needle electrodes. Steps were taken to remove the loops of the stimulating current. A 4-channel alternating current amplifier (transmission band 1-1500 cps) and an 8-loop oscillograph (type MPO-2) were used in the experiments.

At the beginning of the experiment we recorded the reflex contractions and action potentials of the semitendinosus muscle in response to stimulation of the ipsilateral afferent nerve, and against this background we tested the effect of stimulating the contralateral peroneal and ulnar nerves. A constant current of subthreshold strength (50-80% of the threshold of stimulation) was then passed through the afferent nerve for 3 to 10 min. The passage of a subthreshold constant current of this strength through the nerve did not itself cause a flow of impulses in the afferent nerve. Investigations by means of the tests described above were carried out in association with the action of an ascending or descending constant current, and at various intervals of time after removal of the current. In each experiment the action of the constant current in different directions was tested repeatedly.

EXPERIMENTAL RESULTS

When a constant current of subthreshold strength was passed through the afferent nerve, changes took place in the functional state of the spinal cord centers; an ascending current (the cathode situated nearer the cord) brought about a dominant state in the corresponding flexor center, while a descending current (anode nearer the spinal cord) depressed the dominant formed earlier, and strengthened the reciprocal inhibition. Before application of the polarizing current to the nerve, stimulation of the contralateral peroneal nerve caused inhibition of the reflex contractions of the ipsilateral semitendinosus muscle (Fig. 1, 1, 2). Initially there was a sharp decrease in the frequency and amplitude of the action potentials of the muscle, and this was followed by their gradual and complete disappearance (Fig. 2, 1). Polarization of the afferent nerve with a constant current (2 μA) in an ascending direction for 10 min caused a modification of these effects, as shown by the fact that instead of reciprocal inhibition in response

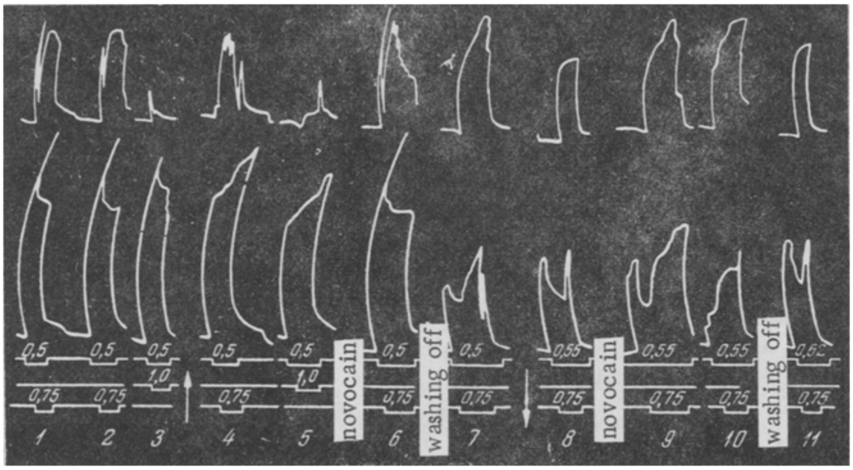

Fig. 1. Formation of a spinal cord dominant during the action of a subthreshold constant current in an ascending direction (↑) on an afferent nerve, and inhibition of the dominant during the action of a descending constant current (↓) on the same nerve. Significance of the curves (from above down): reflex contraction of the contralateral semitendinosus muscle; the same of the ipsilateral semitendinosus muscle; marker of stimulation of the ipsilateral peroneal nerve; the same of the ulnar nerve; the same of the contralateral peroneal nerve. The numbers above the stimulus marker denote the intensity of stimulation in volts. 1-11) Serial numbers of sections of the tracing.

to stimulation of the contralateral nerve, the amplitude of the reflex contractions of the ipsilateral semitendinosus muscle was increased (Fig. 1, 4) and the frequency of its action potentials rose (Fig. 2, 4). Meanwhile there was no change in the action potentials of the afferent nerve as a result of polarization.

After the passage of a constant current in an ascending direction, stimulation of the ulnar nerve, hitherto having no effect (Fig. 1, 3), also began to cause an increase in the amplitude of the reflex contractions (Fig. 1, 5) and a marked rise in the frequency and amplitude of the action potentials of the semitendinosus muscle (Fig. 2, 5). Similar results were obtained in the other experiments. Consequently, the passage of a constant current in an ascending direction greatly increased the powers of summation of the flexor center. In many cases this was also expressed by the fact that isolated stimulation of the ulnar or the contralateral peroneal nerve began to cause contraction of the ipsilateral semitendinosus muscle.

The formation of a dominant in one of the flexor centers of the hind-limbs was usually accompanied by the development of reciprocal inhibition in the antagonistic center.

Important factors in the formation of the dominant were the strength of the constant current and the duration of its passage. The optimal value of the strength of the constant current in an ascending direction for formation of a dominant was between 2 and 10 μA, with a voltage of 0.05-0.2 V. When the action of the polarizing current was prolonged (over 30 min), the dominant was usually weakened and replaced by inhibition. In this case, after the constant current was switched off, the dominant reappeared and could be reinforced by the passage of a constant current in an ascending direction for a short time.

The dominant caused by a constant current possessed considerable inertia: it persisted for a long time (1-2 h) after discontinuation of the constant current. During the action of a constant current in an ascending direction the formation of the flexor dominant took place much more quickly and in a higher proportion of cases than when produced in the usual manner—by stimulation of the afferent nerve with a threshold and subthreshold induction current. A well marked dominant was obtained in 110 of the 130 cases (85%) in which a constant current was applied in an ascending direction. Hence, the passage of a subthreshold constant current in an ascending direction through an afferent nerve can be used experimentally to form a spinal cord dominant.

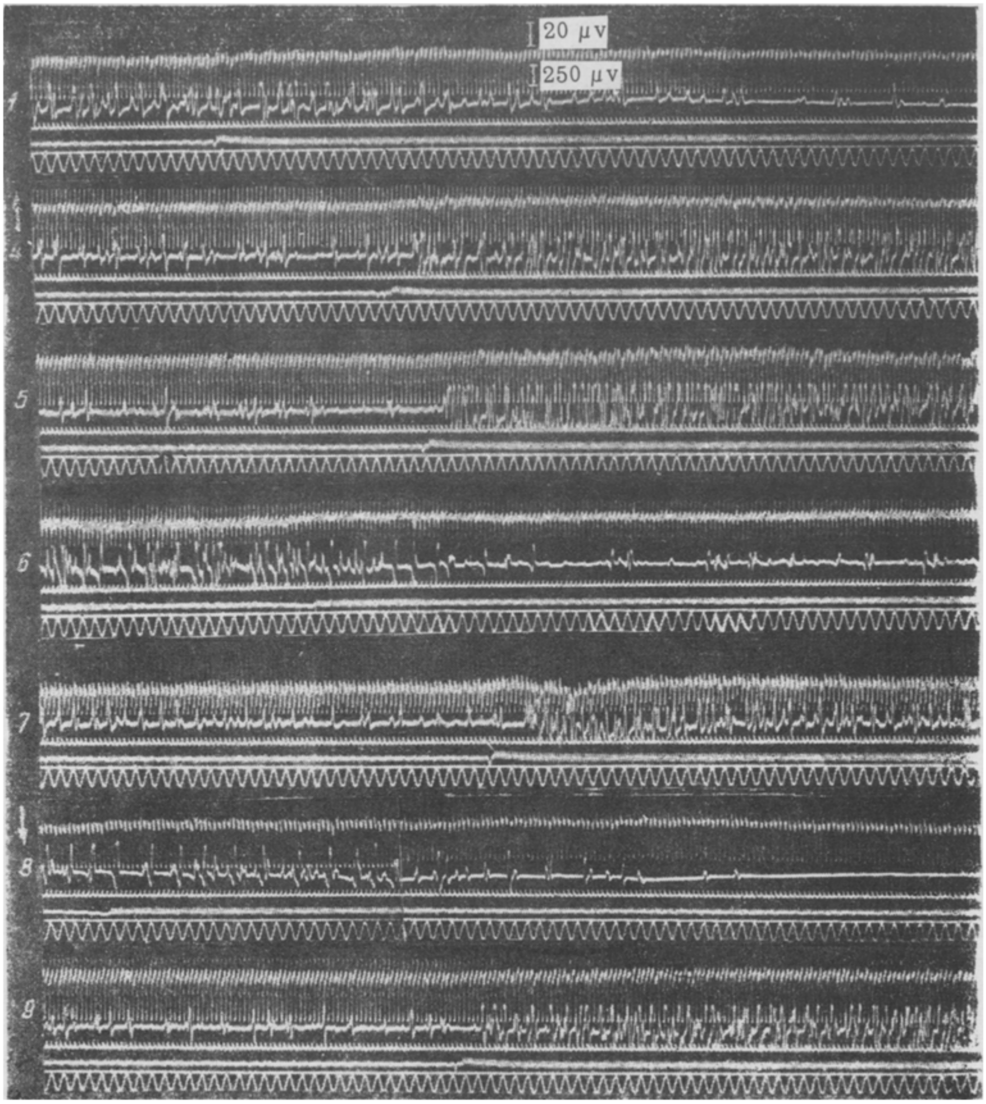

Fig. 2. Changes in the action potentials of the semitendinosus muscle and peroneal nerve during polarization of the afferent nerve with a subthreshold constant current in ascending (↑) and descending (↓) directions. Oscillogram of the same experiment as in Fig. 1. Serial numbers of the sections of the tracing the same as in Fig. 1. Sections 2 and 3, which were identical with section 1, are omitted. Significance of the curves (from above down): action potentials of the peroneal nerve; the same of the ipsilateral semitendinosus muscle; marker of stimulation of the ipsilateral peroneal nerve; the same of the contralateral peroneal and ulnar nerves; time marker (0.02 sec).

The action of a constant current of subthreshold strength in a descending direction to an afferent nerve (the anode nearer the spinal cord) depressed the dominant formed earlier. Before the action of the constant current in a descending direction, a well marked spinal cord dominant was observed, developing as a result of the passage of a current in an ascending direction through the afferent nerve (Figs. 1, 7, and 2, 7). Polarization of the afferent nerve with a constant current in a descending direction (in the time interval between 7 and 8) for a period of 10 min led to inhibition of the dominant. Under these circumstances, stimulation of the contralateral peroneal nerve again began to cause reciprocal inhibition, accompanied by a decrease in the amplitude and frequency of the action potentials of the semitendinosus muscle, followed by their gradual disappearance (Figs. 1, 8 and 2, 8). After stimulation of the contralateral nerve ceased, the amplitude of the action potentials of the muscle returned to its initial level.

In 68 (85%) of the 80 cases in which we investigated the action of a constant current in a descending direction on the afferent nerve we observed total inhibition of the dominant. In those experiments in which inhibition of the dominant was incomplete, it could be intensified by increasing the strength and duration of the constant current passed in a descending direction.

The functional state of the spinal centers could be changed repeatedly in the course of the same experiment by alternating the position of the poles of the constant current passed through the afferent nerve.

In order to discover whether the effects caused by the action of the constant current on the sensory nerve were not the result of a purely physical branching of the polarizing current along the nerve trunk towards the spinal cord, a special series of 35 experiments was carried out to study the action of novocain on the nerve during polarization by means of a constant current.

It will be clear from Fig. 1 that the application of a 2% novocain solution to a segment of the afferent nerve (5-7 mm) between the polarizing and stimulating electrodes during the passage of a constant current in an ascending direction led to disappearance of the dominant and to the appearance of inhibition of the reflex contradiction of the muscle in response to stimulation of the contralateral peroneal nerve (Figs. 1, 6 and 2, 6). Subsequent washing away of the novocain restored the previous dominant (see Figs. 1, 7 and 2, 7). For control purposes, at the beginning of the experiment the corresponding segment of the nerve was treated in the same way with Ringer's solution.

The action of novocain on the nerve polarized by a constant current in a descending direction is illustrated in Figs. 1 and 2. Before application of novocain reciprocal inhibition took place (8), and the dominant was inhibited at this time by the action of a constant current in a descending direction. Under these circumstances, the application of 2% novocain solution to the afferent nerve caused reappearance of the dominant (see Figs. 1; 9, 10 and 2, 9). After removal of the novocain the dominant disappeared, and the reappearance of reciprocal inhibition could be observed (Fig. 1, 11), i.e., the same effect as was produced by passage of a constant current in the descending direction.

Hence, the application of novocain to a segment of the nerve between the polarizing and stimulating electrodes abolished the effect brought about by the constant current. Since in these experimental conditions the nerve remained connected to the central nervous system, the change in the state of the centers during polarization of the sensory nerve could not be attributed to the spread of loops of current along the nerve trunk. It might be suggested that the change in the functional state of the spinal centers during the action of a constant current on the afferent nerve is associated with the development of a weak stream of impulses in some of the afferent nerve fibers which could not be detected by the recording system used. However, the fact that a change in the direction of the weak constant current used for polarization led to reversal of the changes in reflex excitability does not support this hypothesis. The explanation which seems most probable at the present time is therefore the mechanism of electronic and perielectrotonic transmission of influences from the afferent fibers to the corresponding nerve centers (synapses and nerve cells).

SUMMARY

Experiments were performed on frogs (Rana ridibunda). Polarization of the sensitive saphenous nerve by subliminal constant current changes the functional state of the spinal cord centers. Constant ascending current (the cathode is located nearer to the spinal cord) induces a dominant state in the corresponding flexor center. Constant descending current (the anode is located nearer to the spinal cord) depresses the dominant which appeared earlier and enhances the reciprocal inhibition. Application of 2% novocain solution to the area of the afferent nerve between the polarizing and stimulating electrodes eliminates the effects caused by the action of the constant current.

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