DEVELOPMENT OF A STABLE EXCITATORY FOCUS IN THE SPINAL CORD OF WARM-BLOODED ANIMALS

S. A. Skuratova

From the Electrophysiological Laboratory (Head—Doctor of Biological Sciences O. V. Verzilova) Institute of Normal and Pathological Physiology (Director—Active Member of the AMN SSSR V. N. Chernigovskii) AMN SSSR, Moscow

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The mechanism of the formation of stable excitatory foci in the central nervous system is of great importance in describing nervous activity under normal and pathological conditions.

The idea of the dominant, which was put forward by A. A. Ukhtomskii who was influenced by the ideas of N.E. Vvedenskii, has been the subject of much further development by many workers [1-14].

However, until now, many of the questions associated with the conditions and mechanisms of the development of dominant zones in the central nervous system have not been sufficiently studied.

Thus, in the formation of the dominant, not enough is known about the coordinating function of the spinal centers. It is particularly important to study these centers in warm-blooded animals.

The present work deals with the detailed method of formation of a dominant in the spinal cord of the cat, and the prolonged influence of subthreshold, threshold, and suprathreshold stimulation of an afferent nerve.

METHOD

The experiments were carried out on decerebrate cats. Dissections were made of the semitendinosus muscles and peroneal nerves in both hindlimbs, as well as of the ulnar nerves in both front legs.

Stimulation of the central ends of the nerves was effected with an electric current from an induction coil, or from a stimulator working at a frequency of 50 cps. The reflex contractions of the muscles of the antagonists (semitendinosus muscles) were recorded.

The dominant was developed in the flexor center of the hindlimbs by application of subthreshold, threshold, or suprathreshold stimulation of long duration to the peroneal nerve.

Other afferent nerves, including the peroneal nerve of the opposite side and the ulnar nerves of both sides, were stimulated to supply supplementary stimulation for the purpose of revealing the dominant.

At first, the peroneal nerve of one side was stimulated, and the thresholds for the reflex contraction of the semitendinosus muscles of the ipsi- and contralateral sides were determined; after this, the intensity of the stimulation was varied, and the reflex contractions of the same muscles were recorded.

In other tests, the peroneal nerve of one side was stimulated, causing reflex contraction of the semitendinosus of the ipsilateral side, and in addition, the peroneal nerve of the contralcteral side and the ulnar nerves of both sides were also stimulated. In this case, stimulation of the peroneal nerve of the contralateral side normally

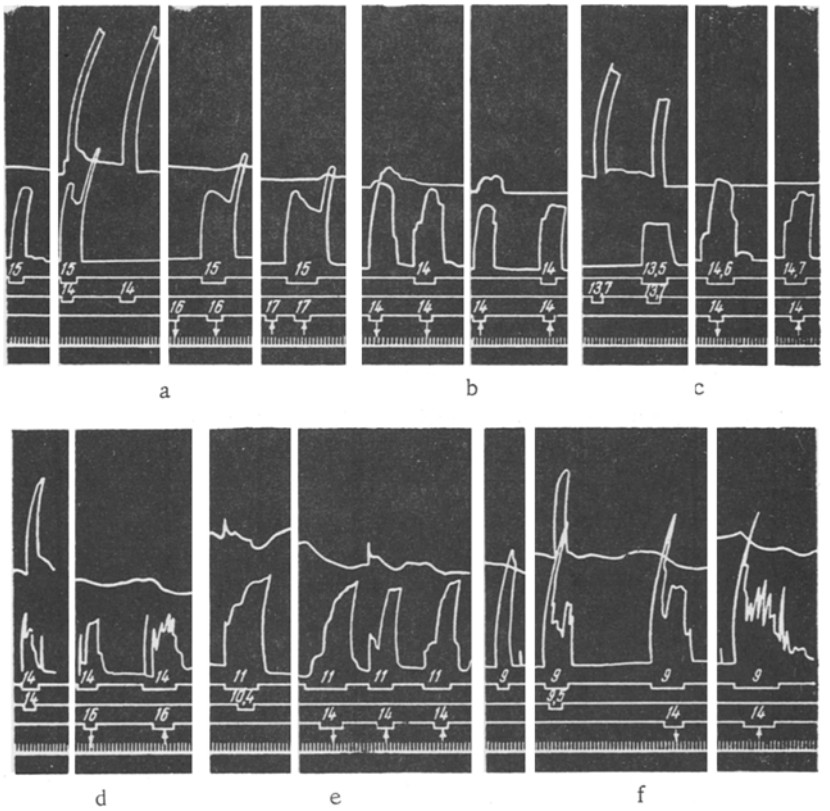

Fig. 1 Development of a dominant zone in the flexor center of the spinal cord of the cat in response to prolonged subthreshold stimulation of the ipsilateral peroneal nerve. a) Initial condition; b) 1 hour after the onset of subthreshold stimulation; c) After 1 hour 30 minutes of subthreshold stimulation; d) after 3 hours of subthershold stimulation; e) 40 minutes after the end of subthreshold stimulation; f) 4 hours 10 minutes after the end of subthreshold stimulation. Curves, from above downwards: contraction of ipsilateral semitendinosus, stimulation of the ipsilateral peroneal; stimulation of the contralateral peroneal; stimulation of the ipsilateral ulnar nerve ↑ , and contralateral ulnar nerve ↓, time marker (seconds). The figures show the strength of the stimulus current in terms of the centimeter scale of the induction coil.

caused an inhibition of the reflex contraction of the ipsilateral semitendinosus muscle (reciprocal inhibition), while stimulation of the ulnar nerve either had no effect, or else inhibited reflex contraction of the semitendinosi. After these test, nervous stimulation was applied to bring about the formation of a dominant. After avery 15-25 minutes, the stimuli were interrupted, and the test described above applied.

The criterion for the formation of a dominant in the flexor center of the spinal cord, was the appearance of an increase in the reflex contraction of the semitendinosi in response to stimulation of other afferent nerves (peroneal nerve of the contralateral side, and ulnar nerves of both sides).

RESULTS

In the first group of experiments, the dominant was developed in the flexor center of the hindlimbs by a long-maintained application of subthreshold stimulation (2-3 cm below threshold) of the peroneal nerve. The effect of these subthreshold stimuli, was to cause first an increase and then a decrease in the excitability and in the amplitude of contraction of the muscle.

As the dominant in the flexor center of the spinal cord developed, the inhibition of the flexor reflex by stimulation of the "test" nerves (peroneal nerve of the contralateral side and ulnar nerves of both sides) was first reduced, and then when the dominant had fully developed in the center of excitation of these nerves, instead of an inhibition, there was an increase in the amplitude of the flexor reflex.

As can be seen from the myograms (Fig. 1 a), recorded before the action of the subthreshold stimulation, the "supplementary stimulation of the afferent nerves, superimposed on the reflex contraction of the semitendinosus muscle, inhibited these contractions.

Stimulation of the same nerves separately, when the muscles were not otherwise stimulated to contract, produced no contraction of the ipsilateral semitendinosus. The myogram (Fig. 1,b), recorded 1 hour after the onset of subthreshold stimulation, shows that the "supplementary" stimulation of the ulnar nerves of both sides, separately, caused the ipsilateral semitendinosus to contract, while stimulation of the same nerves during reflex contraction of the semitendinosus caused an increase in the flexor reflex.

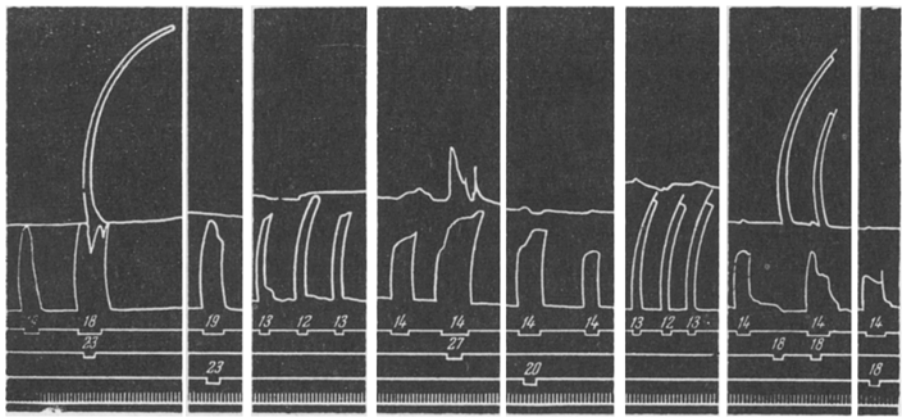

Fig. 2. Formation of a dominant in the flexor center of the spinal cord of the cat in response to prolonged threshold stimulation of the ipsilateral peroneal nerve. a,b) Initial condition; c) 20 minutes after onset of subthreshold stimulation; d) 1 hour after the onset of threshold stimulation; e) 3 hours after the onset of threshold stimulation. Traces as in Fig. 1.

During the time occupied by these changes, spontaneous rhythmic movements of the front and hindlimbs were observed quite often, in the form of automatic walking movements.

As can be seen from the next myogram (Fig. 1,c), the effect of a further 1 hour 30 minutes of subthreshold stimulation was to cause almost complete failure of inhibition of reflex contraction of the semitendinosus on stimulating the peroneal nerve of the contralateral side, while there was still, a more clearly shown increase in the reflex contraction of the muscle in response to the " supplementary" stimulation of the ulnar nerves of both sides.

When the dominant had become fully established in the flexor center, there was a complete elimination of the normal reciprocal relations between the centers of the antagonist muscles. Here, stimulation of the peroneal nerve of the contralateral side, applied during reflex contraction of the ipsilateral semitendinosus, caused an increase and not an inhibition of the flexor reflex.

The myogram (Fig. 1,d) recorded 3 hours after the onset of subthreshold stimulation, shows that stimulation of the peroneal nerve of the contralateral side during reflex contraction of the semitendinosus, causes no inhibition, but rather increases the strength of the reflex.

Stimulation of both ulnar nerves during reflex contraction increases the reflex considerably.

We were able, in these experiments, to observe the stability and inertia of the dominant focus, i.e., the

dominant was preserved for a considerable time, even after the cessation of the stimulus which originally caused it to be established.

The myogram (Fig. 1,e), recorded 40 minutes after the end of subthershold stimulation, shows a marked increased in the reflex contractions of the semitendinosus muscle, in response to the action of the "supplementary" stimulation of the contralateral peroneal and both ulnar nerves.

In Fig. 1,e , it can also be seen that there is an associated inhibition in the antagonist center during the formation of the dominant in the flexor center. Here , stimulation of the contralateral peroneal during contraction of the ipsilateral semitendinosus muscle, not only caused no contraction of the corresponding muscle, but on the contrary, caused it to be inhibited, while the reflex contraction of the ipsilateral semitendinosus was increased. "Supplementary"stimulation of the ulnar nerves caused an increase in the strength of the flexor reflex.

The next myogram (Fig.1,f) , was recorded 4 hours 10 minutes after the end of the subthreshold stimulation which led to the formation of the dominant. It can be seen that the "supplementary" stimulation of the contralateral peroneal again caused an inhibition of the reflex contractions of the semitendinosus, while stimulation of both ulnar nerves increased the reflex contraction of the muscle, thus indicating the great inertia of the dominant.

By applying "test" stimuli to various nerves during the formation of the dominant zone in the spinal cord, the power of the dominant zone to attract and to summate, at first, excitation arising from stimulation of afferent nerves associated with distant reflex arcs (ulnar nerves of both sides), and then, excitation arising in centers of afferent nerves associated with the reflex arc of the antagonist reflex (contralateral peroneal nerve) can be demonstrated.

More prolonged action of subthreshold test stimuli fails to cause an increase in reflex contraction. In this case, parabiotic changes may develop, and the dominant may pass into a state of inhibition . Stimulation of the contralateral peroneal during reflex contraction of the semitendinosus again induces reciprocal inhibition.

In the second experiment, a dominant was developed in response to the prolonged action of threshold and suprathreshold stimulation (2-3 cm of the induction coil scale above threshold).

During the development of the dominant by this means, phases were noted which resembled those found using subthershold stimulation.

With the threshold and suprathreshold stimuli, the dominant developed more rapidly, but was less stable. Parabiotic stages and the transition of the dominant to a state of inhibition occurred more rapidly in the latter case.

The myogram of Fig.2, a, recorded before the action of threshold stimulation, shows that stimulation of the contralateral peroneal during contraction of the ipsilateral semitendinosus inhibited reflex causes contraction of that muscle.

Stimulation of the ulnar nerve during reflex contraction, produced no effect. Increase in the strength of the stimulus (Fig. 2,b) caused an increase in the amplitude of reflex contraction, showing that there was no parabiotic stage. The drawing clearly shows, that with greater stimulation (12 cm on the induction coil) reflex contraction of the muscle was greater than with a weaker stimulation (13 cm on the coil).

The myogram of Fig. 2, c, recorded 20 minutes after the onset of the threshold stimulation, shows that stimuli applied to the contralateral peroneal nerve and ulnar nerves of both sides cause an increase in the contraction of the semitendinosus, thus indicating the formation of a dominant. But 1 hour after the onset of the action of the threshold stimulation, parabiotic stages occurred in this experiment.

Fig. 2, d shows the equalizing stage of parabiosis which then continues into the paradoxical phase.

When the threshold stimulation was continued, the dominant changed over into a condition of inhibition. The myogram of Fig. 2,e , recorded 3 hours after the onset of the threshold stimulation, shows a reduction in the reflex contraction of the muscle.

Stimulation of the contralateral peroneal and both ulnar nerves now causes an inhibition of the reflex contraction of the semitendinosus.

Consequently, during the development of a dominant focus in the flexor center of the spinal cord under

the influence of stimulation of an afferent nerve, many different phases occur, associated with change in the ability of the center to summate, and these phases are a) first an increase, and then a decrease in reflex excitability and in amplitude of contraction of the semitendinosus; b) reduction, and then complete disappearance of reciprocal inhibition; c) reflex contraction of the semitendinosus followed by an increased contraction in response to stimulating afferent nerves of remote reflex arcs (ulnar nerves of both limbs); d)spontaneous rhythmical movements of the front and hindlimb reproducing automatic walking movements; e) increase in the reflex contractions of the semitendinosus under the influence of stimulation of an afferent nerve reflex arc of an antagonist reflex (contralateral peroneal nerve), thus indicating distortion of the reciprocal relations between the centers of antagonists; f) development of parabiotic stages and the transition of the dominant into a condition of inhibition.

SUMMARY

Experiments were performed on decerebrate cats. The author studied the development of a dominant focus in the flexor center of the spinal cord in the action of subthreshold, threshold and suprathreshold excitations of the afferent nerve.

Experiments proved that in its development the dominant passes through a number of phases connected with the changes in the summation power of the center. After removal of the stimulations provoking the appearance of the dominant, the latter may continue for a long time (up to 4 hours), which demostrates its inertia. In response to threshold and suprathreshold stimulation of a definite intensity the dominant appears earlier, but is less stable. During futher stimulation it easily changes into inhibition, with development of parabiotic stages.

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** See English translation