EXTINCTION AND DIFFERENTIATION OF CONDITIONED REFLEXES INDUCED AGAINST A BACKGROUND OF UNCONDITIONED STIMULATION

(Analysis of the Mechanism of the Development and Localization of Internal Inhibition During Covering)

B.I. Khodorov

Physiological Laboratory (Head—Prof. L.L. Shik) of the A.V. Vishnevskii Institute of Surgery (Dir.—Active Member AMN SSSR A.A. Vishnevskii) of the AMN SSSR, Moscow
(Presented by Active Member AMN SSSR P.S. Kupalov)
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In a previous paper [9] we showed that a complete and stable motor-defensive conditioned reflex may be induced in dogs not only by the usual combinations of stimuli, but also against a background of unconditioned stimulation, with what is known as covering with intensification. An indifferent stimulus, when repeatedly combined with intensification of an existing current, acquires the power in the first place to intensify sharply the motor-defensive reaction of a dog in response to preceding background electrical stimulation of the skin, and secondly to induce a conditioned reflex when used in isolation.

In order to continue the study of the properties of conditioned reflexes to intensification induced by this means, in the present research we investigated the pattern of development of differentiation and extinction of these reflexes.

EXPERIMENTAL METHOD

Experiments were carried out on three dogs (Dik, Sil'va and Ryzhaya), in which a number of conditioned reflexes were induced before the beginning of the present research by means of the covering with intensification technique. In contrast to the usual methods of covering, with covering with intensification the strength of the acting current was increased intermittently (1.5-2.0 times) in each combination immediately after the addition of the conditioned stimulus to the unconditioned (5 seconds after its start). During the extinction or differentiation of these reflexes, we discontinued the intensification of the acting current in conjuction with the use of the inhibiting stimulus against the background of the unconditioned reflex (i.e., we began to cover by the usual method). The source of current was a rectangular impulse generator (70 cps, duration of impulse 1 msec). To record the limb movements we used Petropavlovskii's "knee-caps", connected pneumatically to a Marey's capsule. The animal's respiration was recorded throughout the experiment.

EXPERIMENTAL RESULTS

Formation of differentiation against a background of unconditioned stimulation. At the beginning of the experiments a conditioned reflex to a tone of 1000 cps was induced in the dog Dik by the covering with intensification technique. We attempted to form differentiation between this stimulus and a tone of 200 cps.

The positive stimulus—a tone of 1000 cps (T-1000)—on each application against a background of electrical stimulation of the skin caused intensification of the dog's motor reaction (Fig. 1a; 33nT-1000, 34nT-1000), and we always accompanied this effect by doubling the strength of the acting current. The same positive effect as with T-1000 was produced in the dog Dik by other conditioned stimuli (bell, M-120, light), also when subjected to covering with intensification (see Fig. 1a and b; tests 1n3, 3nM-120, 3nC).

The first application of the tone of 200 cps (T-200) against a background of electrical stimulation of the skin caused no appreciable change in the unconditioned reflex; in the course of the second covering, in response to T-200 the dog developed a powerful orientational reaction, accompanied by weakening of the unconditioned defensive reflex (see Fig. 1a; 2nT-200). In subsequent experiments this difference between the effects of T-1000 and T-200 became obliterated. Both stimuli gave a positive effect (see Fig. 1b; 40nT-1000 and 6nT-200), in spite of the fact that the action of T-1000 was always reinforced (was accompanied by intensification of the current), whereas the application of T-200 against a background of electrical stimulation of the skin was left unreinforced (the current strength remained unchanged throughout the whole combination).

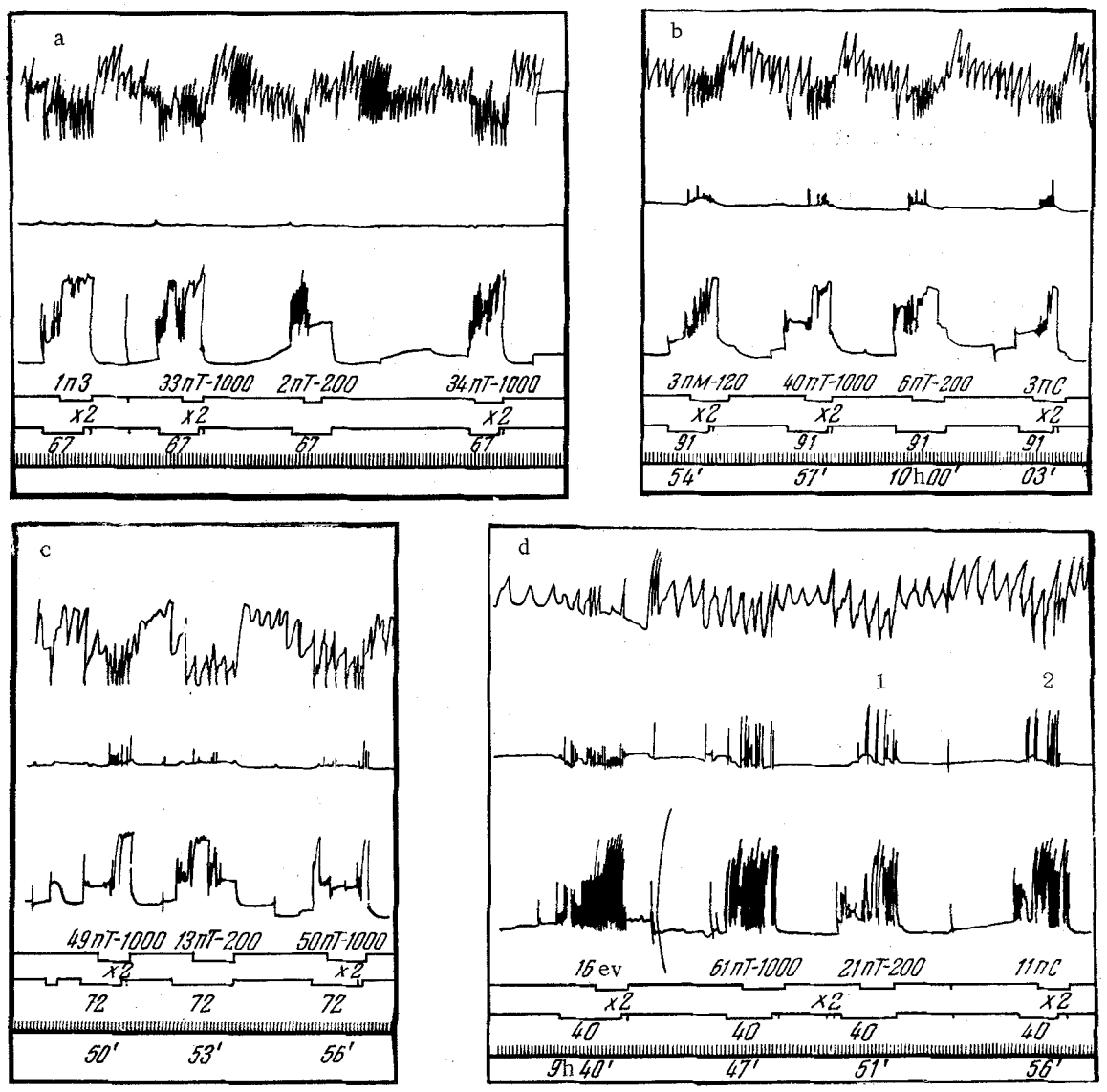

Fig. 1. Differentiation of stimuli against a background of unconditioned stimulation. First experiments. Tone of 1000 cps (T-1000), applied against a background of unconditioned stimulation, is always accompanied by intensification of the acting current; the tone of 200 cps is applied without intensification. The dog Dik. a) Experiment 208 (November 30, 1958); b) experiment 210 (October 3, 1958); c) experiment 214 (October 21, 1958); d) experiment 219 (November 11, 1958). Significance of the curves (from above, down): Pneumogram; movement of the left (unstimulated) hindlimb; movement of the right hindlimb (stimulated by the current); marker of conditioned stimulation; marker of unconditioned stimulation; time marker (1 second). 1) Vocal reaction 2) voice.

The first signs of differentiation between the stimuli appeared after the 12th absence of reinforcement of the 200 cps tone (T-200). In test 13nT-200 (Fig. 1c) this stimulus caused an obvious weakening of the unconditioned reflex instead of an intensification. The immediately ensuing reflex to the positive tone of 1000 cps showed successive inhibition (50nT-1000). The inhibitory action of T-200, however, was unstable and after a short time it again gave way to a positive action (Fig. 1d; 21nT-200). Only after 32 nonreinforcements did the inhibitory effects of T-200 begin to acquire a more stable character, and, in some cases, moreover, after application of the differential stimulus, successive inhibition of the reflex to the positive tone also developed (Fig. 2a; 33nT-200, 67nT-1000).

A further ten nonreinforcements were required for the differentiation to be stable and concentrated. The final results of these experiments are shown in Fig. 2b.

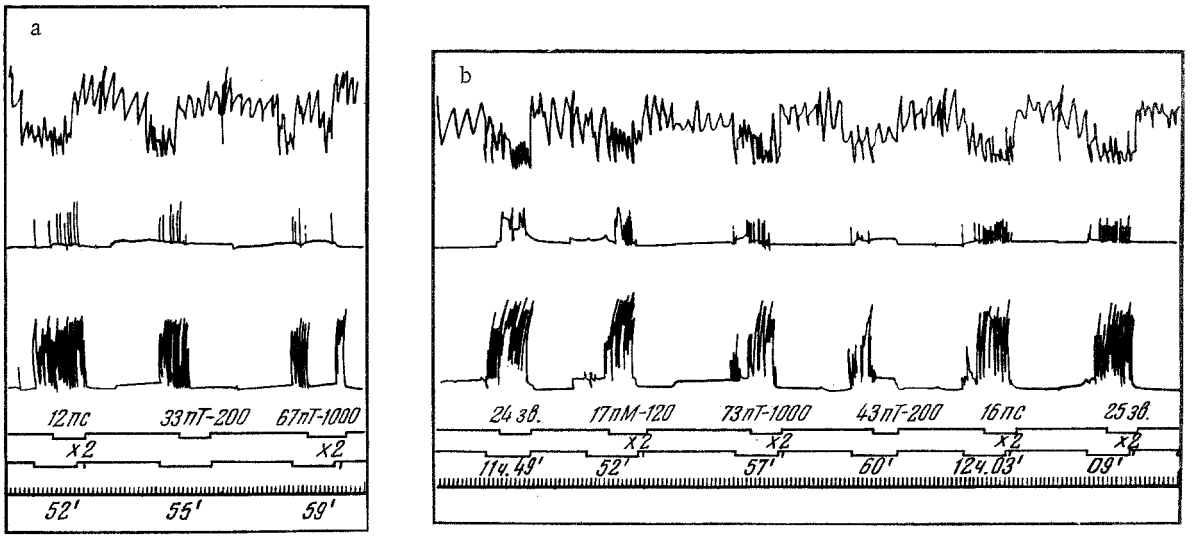

Fig. 2. Complete differentiation of stimuli against a background of unconditioned stimulation. Continuation of experiments on the dog Dik. a) Experiment 221 (November 13, 1958); b) experiment 225 (November 19, 1958). Significance of the curves the same as in Fig. 1.

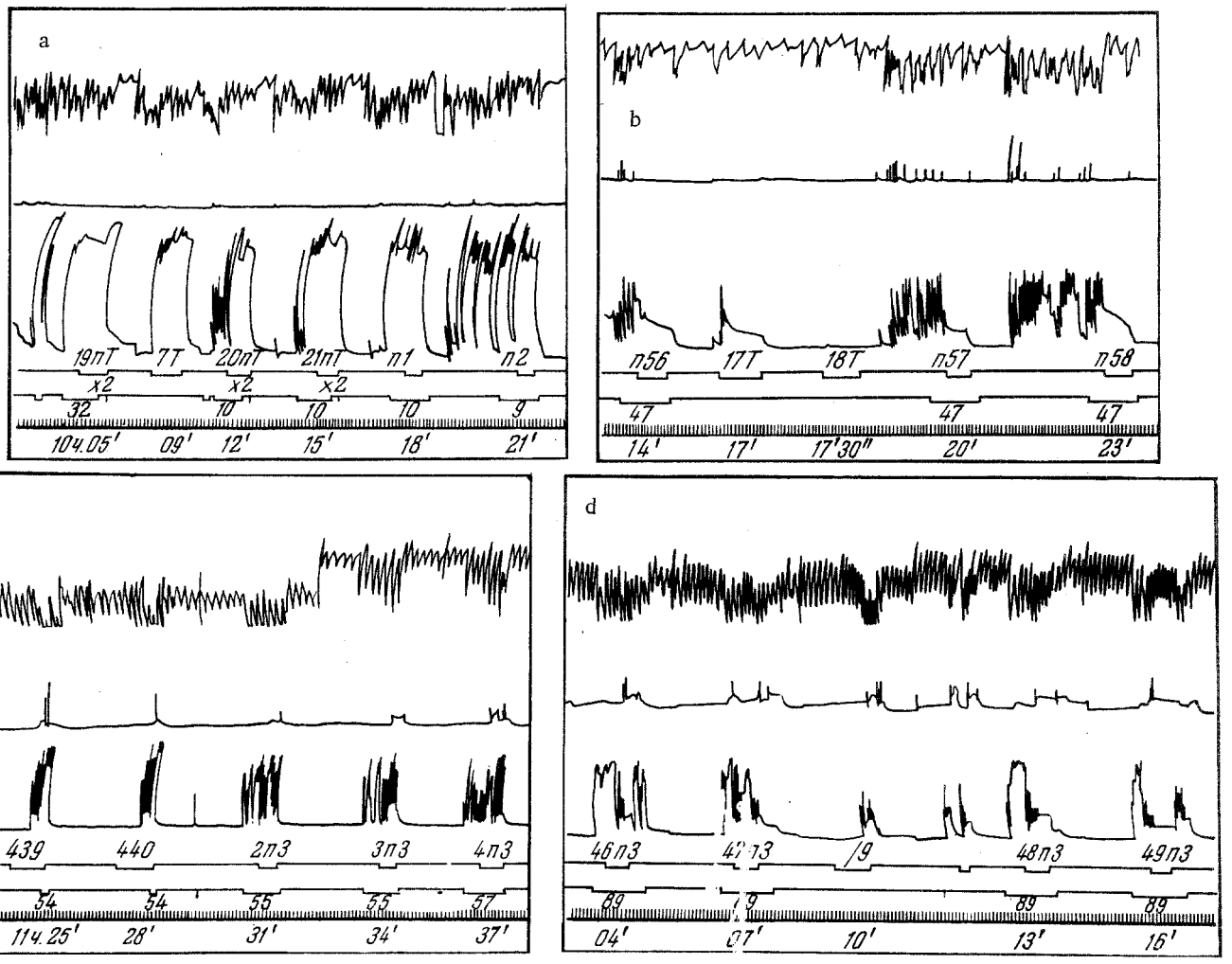

Fig. 3. Extinction of a conditioned reflex against a background of unconditioned stimulation. a) The dog Sil'va, experiment 160 (September 25, 1958); b) the same dog, experiment 167 (September 19, 1958); c,d) the dog Dik, experiment 194 (July 8, 1958) and experiment 198 (July 8, 1958). Significance of the curves as in Fig. 1.

It will be seen that all the positive stimuli—the bell (24), metronome (17nM-120), the tone (73nT-1000), light (16nC) and bell (25)—caused an obvious strengthening of the defensive reaction of the dog, and of both its motor and respiratory components. In contrast to this, the application of the differential stimulus (43nT-200) resulted in sharp inhibition of the unconditioned reflex, in spite of the contining electrical stimulation of the skin.

Extinction of the conditioned reflex to intensification. We obtained the same results in principle by extinction of the conditioned reflexes against a background of unconditioned stimulation as in the experiments to induce differentiation. In the dog Sil'va, before extinction, the positive stimulus—the tone, constantly accompanied by intensification of the acting current—always caused an increase in the strength of the unconditioned reflex. The dog responded to the isolated application of this stimulus with a strong conditioned defensive reaction (Fig. 3a; 7T). After 21nT (see Fig. 3a) we ceased to reinforce the positive effects of the tone by intensification of the current (n1, n2 and so on), i.e., we changed over to the ordinary method of covering. At first this led to a gradual weakening of these effects, and later to their distortion: addition of the tone to the electrical stimulation of the skin began to cause obvious inhibition of the unconditioned reflex (Fig. 3b; n56, n57, n58). It is interesting that these inhibitory effects appeared before the covered stimulus completely lost its power to give rise to a conditioned motor reaction when acting in isolation (see Fig. 3b; 17T). Complete inhibition of the conditioned reaction took place only after 80 "coverings" without intensification. We obtained a similar effect in experiments on the dog Ryzhaya.

The results described above are of interest from several points of view. Firstly, they show that during conditioned stimulation the cerebral cortex retains the ability not only to detect the action of an indifferent or a signal stimulus [1, 6, 7], but also to differentiate between these stimuli (cf. [3]). Secondly, the fact that the unconditioned reflex is inhibited under the influence of an added differential or extinctive stimulus is an important piece of evidence in the doubtful and often debated problem of the spatial localization of internal inhibition. It becomes clear that this inhibition is not localized at the "point" of the conditioned stimulus, nor in the intermediate elements of the conditioned reflex arc, but evidently in those of its links which are directly connected with the performance of the unconditioned reflex; it is probable that the reticular formation of the brain stem takes part in the production of this inhibitory effect [10]. Finally, the results obtained are important in the understanding of the mechanisms of inhibition during covering of conditioned reflexes induced by the usual method. We must dwell on this problem in rather more detail.

We have seen above that the temporary nervous connection formed by the method of covering with intensification is invariably inhibited on the change-over to ordinary covering. The reason for the development of internal inhibition in this case is clear: The positive conditioned effects caused by signal stimuli against a background of an unconditioned reflex cease to be reinforced by a corresponding intensification of the acting current during ordinary covering, and are thus extinguished as nonreinforced. As is easily shown, however, similar relationships also arise during repeated covering of a conditioned stimulus, brought about in the ordinary way. The use of such a conditioned agent against a background of electrical stimulation of the skin in most cases also caused intensification of the unconditioned reflex [2, 6], and the strength of the acting current is not increased under these circumstances. The effect of the conditioned stimulus thus remains unreinforced, and this must inevitably lead to its inhibition [8]. The experiments described below appear to us to confirm this supposition.

The pattern of inhibition developing in covering of a conditioned reflex produced in the usual manner. This series of experiments was carried out on the dogs Dik, Sil'va and Ryzhaya before the use of covering with intensification was begun in these animals. In the usual combinations a bell acted in isolation for 8 seconds, and then to it was added electrical stimulation of the skin for 2 seconds, after which both stimuli were discontinued stimultaneously. During covering, the bell was added to the unconditioned reflex 5 seconds after its onset.

In Fig. 3c we show the results of the first experiment on the dog Dik. We began to cover the conditioned reflex to a bell (tests 439 and 440) with unconditioned stimulation. At first each application of the bell against the background of action of the current (2n3 and later) resulted in an obvious strengthening of the unconditioned defensive reflex—an increase in the frequency and strength of flexion of the stimulated limb, the appearance of movements in the opposite hindlimb, some increase in the strength and rate of respiration and, in some cases, a vocal reaction—the whining or barking of the dog. Later, however, as the covering was repeated, these positive effects began to weaken gradually, and then to undergo distortion—instead of strengthening, the bell caused an obvious weakening of the unconditioned defensive reflex (see Fig. 3d). Particularly indicative in this respect were those combinations in which the conditioned stimulus, applied against the background of the unconditioned reflex, was discontinued a few seconds before the cessation of action of the current: after stopping the bell, the unconditioned motor reaction often was again intensified (tests 46n3, 49n3). As in the experiments considered above (see Fig. 3b) the inhibitory effects of the bell also developed before this stimulus had completely lost its ability to induce a conditioned reaction when applied in isolation (see Fig. 3d; test 9). Complete inhibition of the temporary connection took place only after 51 coverings. We subsequently restored

the conditioned reflex to the bell by renewing its ordinary reinforcements with the electric current. When applied against a background of unconditioned stimulation, the bell was once more capable of causing intensification of the motor defensive reaction of the dog. We obtained analogous results in experiments on the dogs Sil'va and Ryzhaya.

The pattern of development of inhibition during covering of a conditioned reflex induced in the usual manner was thus similar to the pattern of extinction of the temporary connection formed by covering with intensification. This is evidence of a common mechanism of the phenomena under investigation.

We consider that the results described in this paper, taken as a whole, confirm our previous hypothesis of the role of the gradient of unconditioned stimulation in the the mechanism of formation and consolidation of a temporary nervous connection [7, 9]. A temporary connection arises and is consolidated only if the action of the conditioned stimulus is combined with the unconditioned stimulus at the moment of its appearance or sudden intensification. A connection is not formed or, if it is formed, it is inevitably inhibited as soon as the action of the conditioned stimulus ceases to be reinforced by the appearance or the intensification of the unconditioned stimulation.

SUMMARY

Positive conditioned reflexes may be elaborated not only be the usual combination of stimuli, but also if the indifferent agent is applied repeatedly against the background of preexisting unconditioned electrical skin stimulation; each repeated application of this agent was accompanied by intensification of the acting electric current. Differentiation may be formed to the positive "reflex to intensification" if another stimulus, also used against the background of an unconditioned reflex, is not accompanied by intensified current. In this case the differentiating agent begins to exercise a considerable inhibitory effect upon the unconditioned defense reflex. Analogous effects were also observed after repeated applications of the usual conditioned stimulus against the background of an unconditioned reflex. This leads to the conclusion that a combination of the action of a conditioned reflex with a change in the strength of unconditioned stimulation is of decisive significance for the formation and reinforcement of the already elaborated association.

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