

# SUMMATION OF EXCITATIONS DURING UNCONDITIONED REINFORCEMENT OF A CONDITIONED REFLEX

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We have shown previously [5] that, as a rule, an unconditioned defensive motor reflex is increased by application of the conditioned stimulus which it is used to reinforce. The effect is particularly well shown when threshold ("weak") or suprathreshold ("medium") electrical cutaneous stimulation is used for the unconditioned reinforcement. A strong unconditioned reflex shows little or no increase when the conditioned stimulus is applied. From these results we concluded that at the moment of unconditioned reinforcement there is a summation of conditioned and unconditioned excitations.

However, in the experiments referred to, the conditioned reflexes were usually brought about by "strong" or "medium" electrical cutaneous stimulation and a weak threshold or subthreshold stimulus was applied only in certain special cases. This method did not exclude the possibility that the increase of the weak unconditioned reflex by the conditioned reflex might be brought about not only by summation of excitations but also by repeated application of a strong electrical stimulus forming a response pattern (stereotype) in which there was a strong response to the reinforcing stimulus: the weak current used instead of the strong might in this way evoke the stereotype.

In order to test this hypothesis special experiments were carried out in which the strength of the unconditioned reinforcement was changed for long periods. With this arrangement, the results were the same as those obtained previously [5], which confirmed our view of the summation of the conditioned and unconditioned excitations during the combined application of the conditioned and the electrical cutaneous stimuli.

## METHOD

The experiments were carried out on two dogs (Rusty and Silva) from March to May, 1958. The Bekhterev-Protopopov method involving the defensive response to electrical stimulation was used. The

stimulus consisted of 1-msec square waves applied at a frequency of 70 cps to the right hind leg. Limb movements were recorded using Petropavlovskii knee-caps connected pneumatically to a Marie's capsule, while respiration was recorded using corrugated tubing similarly connected.

At the start of the experiment, in Rusty we developed a stereotype of responses to stimuli applied in the following order: bell, metronome (M-120), differentiation to the metronome (M-60), interrupted light, and bell. All these stimuli except the bell acted for 10 sec, during the last 2 sec of which electrical reinforcement was given. The bell sounded for 30 sec, during which time electrical cutaneous reinforcement was given from the 8th to the 10th and from the 28th to the 30th seconds so that the conditioned reflex showed two maxima, one toward the beginning and one at the end of the period of application of the conditioned stimulus.

At the start of the experiments the thresholds for the reflexes were determined and an appropriate strength of electrical cutaneous reinforcement selected (in the figures, these test are shown at the start of each kymogram). Tests of the isolated action of the unconditioned stimulus were carried out subsequently for the usual set of reflexes.

## RESULTS

The initial state of the conditioned reflexes in Rusty is shown in Fig. 1. In this experiment for reinforcement we used a suprathreshold electrical reinforcement of 30 v, and the effect of this stimulus by itself is shown at the start of the trace. It can be seen that during the action of the bell (279) the current caused a far stronger motor reaction than when applied by itself.

The electrical stimulus (13 v) was then again given three times in succession, and in all cases the animal reacted by a very feeble withdrawal of the foot. At the end of the experiment (Fig. 1), a stimulus

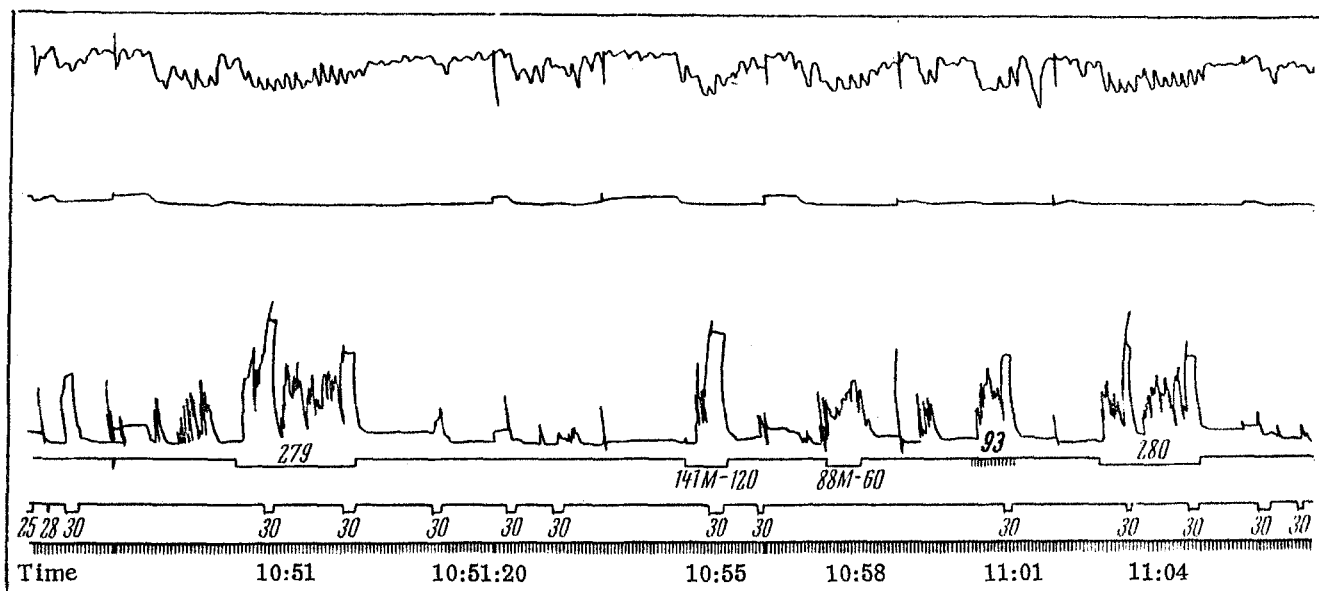


Fig. 1. Motor responses to unconditioned electrical cutaneous stimulus applied either by itself or together with a conditioned stimulus. Experiment on the dog Rusty (No. 105). Initial level of conditioned reflexes. Curves from top to bottom: pneumogram (inspiration downward), movement of the left hind limb, movement of the right (stimulated) limb; conditioned stimulus marker, unconditioned stimulus marker, time marker (...). Numbers on fourth line represent the number (in order) of the conditioned stimulus applied: no letters) bell; M-120) metronome positive; M-60) differentiation; number (bold type) interrupted light. Numbers below fifth line: stimulus voltage in scale divisions of stimulator.

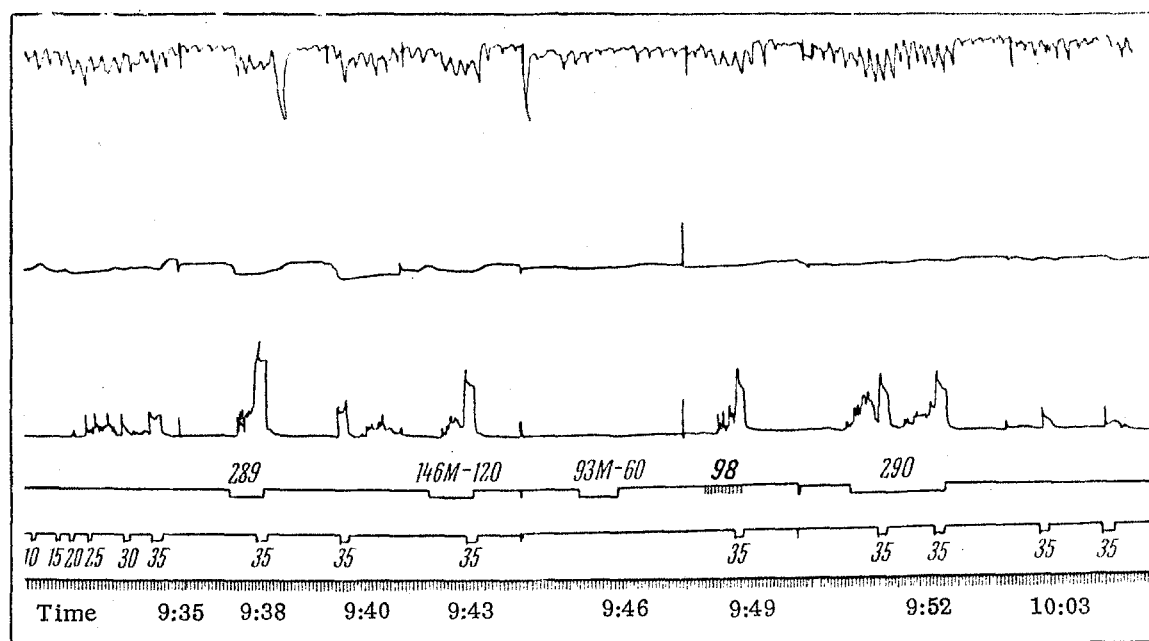


Fig. 2. Summation of weak conditioned and unconditioned reflexes. Continuation of experiments on Rusty (No. 110). Indications as in Fig. 1.

of this strength was almost without effect, as the animal had become adapted to it. Nevertheless, in all tests with the metronome (141 M-120), light (93) and bell (280), the unconditioned stimulus caused a strong motor reaction.

From experiment 109 onward, only a weak electrical cutaneous stimulus was used as reinforcement. A gradual reduction in the strength of the unconditioned reinforcement led to a corresponding weakening of the

conditioned reflexes to all stimuli. In spite of this result, the use of weak electrical stimulation together with the conditioned stimulus caused an increased effect in all cases (Fig. 2).

In the succeeding experiments, from No. 114 onward, a stronger unconditioned reinforcement was applied, and this led to the rapid restoration of the conditioned reflexes. However, in this case the application of a stimulus of moderate strength together

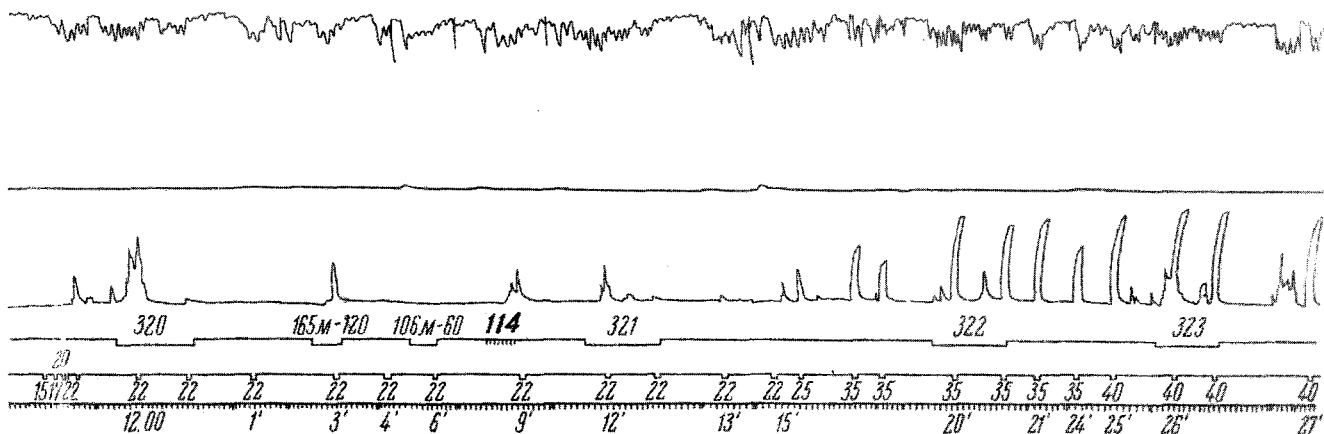


Fig. 3. Change of response with transition from a weak to a strong unconditioned reinforcement. Continuation of experiments on Rusty (No. 123). Indications as in Fig. 1.

with the conditioned stimulus caused an increased effect, while a still stronger unconditioned stimulation caused approximately the same strength of motor response whether given separately or combined with the conditioned stimulus.

Similar results were also obtained in experiments Nos. 116-119.

In the next set of experiments, the results were obtained first, as before, by greatly reducing the strength of the unconditioned reinforcement, and then suddenly increasing it to a high value.

The first tests with the weak reinforcement were used in experiment No. 119, and it was continued from then on. Reduction in the strength of reinforcement in experiments Nos. 120-123 caused a return to the reduced values of the conditioned reflexes. However, when combined with weak or even imperceptible conditioned effects, the unconditioned stimulus regularly evoked a stronger motor response than it did when given alone.

The results of the final experiment of this series are shown in Fig. 3. At the start of the experiment, all conditioned reflexes were reinforced by a weak shock of 22 v. Although after the first few applications, this stimulus changed from being threshold to being subthreshold so that when given alone it caused no overt response, when given together with the conditioned stimuli it continued to cause a definite reflex response (165 M-120, 321). By contrast, when the differentiated metronome stimulus (106 M-60) was used, an electrical cutaneous stimulation of this strength was completely ineffective.

In the same experiment (see Fig. 3) the effect was tried of giving a strong unconditioned reinforcement, for which purpose the voltage was raised from 22 to 35 v, after which it was given together with the bell 322 at 40 v. It can be seen from the figure that the rapid transition from the weak to the strong unconditioned reinforcement did not destroy the summa-

tion of the conditioned and unconditioned excitations (Test 323).

Similar results were obtained in experiments on Silva. Gradual change in the strength of the unconditioned reinforcement led to a corresponding change in the strength of the conditioned reflex. However, during the whole of the period of investigation, the effects of threshold and suprathreshold unconditioned stimulation given together with the conditioned stimulus showed a marked increase, and only in the case of the strong unconditioned reflex was there no change.

Thus, in these experiments the results obtained agreed entirely with those of our previous experiments [5], in which the strength of the electrical cutaneous stimulation was varied only in special tests selected from among the usual combination of stimuli.

The consistency of the results obtained indicates that the increase in the strength of the unconditioned reflex under the influence of the conditioned stimulation does represent a genuine summation of excitations in the defensive center and is not the result of the formation of a set pattern (stereotype) of responses of the animal to the electrical stimulation.

The results of this and of the previous investigation [5] show that the summation of the conditioned and unconditioned reflexes during the combined application of the stimuli is very similar to that occurring in the so-called "united" reflexes [6].

In our experiments, the combined conditioned and unconditioned reflexes produced an effect which in many cases considerably exceeded the arithmetic sum of each taken separately; on average, the value of the reflexes was approximately equal to their sum, and finally the combination of two strong or of a strong and weak reflex produced an effect which was equal to or slightly greater than the value of a single strong reflex response. The explanation may be that the conditioned and unconditioned stimuli converge onto the same cortical cells in the area representing the uncon-

ditioned reflex, onto the same cells of the reticular formation of the brain stem, and finally on the same motoneurons of the spinal cord. For this reason, summation of such convergent stimuli ought to obey the same laws as do excitations in nervous centers, i.e., there ought to be facilitation and occlusion [10].\*

The mechanism of interaction of excitation both in the spinal cord, where it was discovered, and also in the subcortical and cortical structures and particularly in the reticular formation has been demonstrated recently by direct electrophysiological means.

It must be realized however that in the interaction of a conditioned and unconditioned reflex there may be complications from many factors associated both with the complexity of the interaction between the different elements of the conditioned reflex arc [1, 2, 7, 8] and with the summation of the excitation in cortical and subcortical cells which may be taking part in some rhythmical activity [9].

In our experiments no cases were found where the conditioned reflex was reduced by application of the conditioned stimulus. Should such effects be found, it would appear to us that they could be caused by the development of a strong orienting reaction at the moment of applying the conditioned stimulus.

Our results as well as those obtained using the feeding method [3, 4] show that the function of a conditioned stimulus is not confined to its signalling action. Besides signalling danger and putting into action at the appropriate time a defensive movement, the conditioned stimulus is also able to increase the strength of the unconditioned response to the direct action of the harmful agent. This effect is of consider-

able biological importance in cases where the conditioned motor response itself does not get the animal out of danger. The Protopopov method which we have used may be said to reproduce experimentally this situation which may occur naturally.

Thus during the unconditioned reinforcement of a conditioned reflex, the two stimuli combine, and according to their physiological effectiveness they may do so to show either occlusion or facilitation.

## SUMMARY

After conditioned motor defensive reflexes had been developed in dogs using Protopopov's method, a comparison was made of the effects produced by unconditioned electrical cutaneous stimuli given either separately or together with conditioned stimulus. The strength of the unconditioned reinforcement ranged from threshold to submaximal values. It was shown that during unconditioned reinforcement there is a summation of the conditioned and unconditioned reflexes, two weak reflexes usually giving an effect which is greater than the sum of the separate values, while two moderate reflexes give a result which is almost equal to the summed effect. A strong and a weak or two strong reflexes give an effect which is equal to or slightly greater than the value of the strong reflex. The results obtained show that in the summation there may be either facilitation or occlusion.

\* As in original — Publisher's note.

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