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CHRONIC EXTINCTION AND RESTORATION OF CONDITIONED REFLEXES

IV. THE DEPENDENCE OF THE COURSE OF EXTINCTION AND RESTORATION OF CONDITIONED REFLEXES ON THE „HISTORY" OF THE CONDITIONED STIMULUS. (THE PRINCIPLE OF THE PRIMACY OF FIRST TRAINING)

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In the previous papers of this series the following facts concerning the transformation of excitatory into inhibitory conditioned reflexes, and vice versa, were established.

1) The chronic extinction of an alimentary conditioned reflex is a gradual and slow process while its restoration is very prompt (Konorski and Szwejkowska 1950).

2) This difference between the course of both processes is not due to the fact that the extinction and restoration are conducted against the excitatory background (i. e. when the experimental stimulus is applied among positive stimuli), since the same difference is seen when the extinction occurs against the inhibitory background (Szwejkowska 1950).

3) This difference is not due to the fact that the food reinforcement represents for the animal a positive value, since the same

holds when instead of alimentary conditioned reflexes defensive motor conditioned reflexes are used (Konorski and Szwejkowska 1952).

The present paper tries to elucidate the puzzle of this difference in the course of extinction and restoration of conditioned reflexes from the point of view of the history of the conditioned stimulus.

METHOD

The typical method of salivary food conditioned reflexes adopted in this series and described elsewhere (Konorski and Szwejkowska 1950) was used.

All experiments with chronic extinction and restoration of conditioned reflexes were conducted in the same standard manner. An „experimental" stimulus (i. e. stimulus designed to a particular sort of transformation) was applied once in each experimental session, usually in the third or fourth place. A well established and strong positive conditioned stimulus was used as a control stimulus, and it was applied 3—5 times in a session.

The course of experiments in which acute or subacute transformations of conditioned reflexes were performed is described in further text.

RESULTS

The experiments were performed on 3 dogs. As their course was not quite identical we shall consider them separately.

1) „Bekas", a male dog, of the age of 4 years, weight 17 kg.

Series I. Adaptation to the stand and experimental situation, 8 days.

Series II. Elaboration of an alimentary conditioned reflex to the sound of Metronome. 10 experiments, 42 trials.

Series III. Introducing of an unreinforced stimulus, Lamp. While continuing to apply Metronome with reinforcement, a new stimulus — the rythmic lightening of a Lamp — was introduced, this stimulus from the very beginning not being reinforced. It is worth noting that this stimulus, applied for the first time, evoked a salivary reaction which amounted to 40% of the reaction to Metronome. In following trials this reaction rapidly diminished, attaining the mean value of interval salivation, and thereafter decreasing beneath this value. It should also be noted that the application of Lamp, especially if it was given twice or thrice in succession, produced a more or less pronounced inhibitory after-effect. All this goes to show that Lamp has acquired a strong inhibitory character. Altogether this series included 79

experiments, in which Metronome was applied 290 times and Lamp 185 times.

Series IV. Elaboration of a positive conditioned reflex to Lamp. Starting from exp. No. 90 to No. 119, Lamp was applied once daily (usually in the third or fourth trial) with reinforcement. The course of elaboration of the conditioned reflex to this stimulus is shown in Fig. 1 (compared with the elaboration of the conditioned reflex to a new stimulus in this dog, cf. also Fig. 6). It is seen that this process is very slow, and the conditioned reaction to Lamp

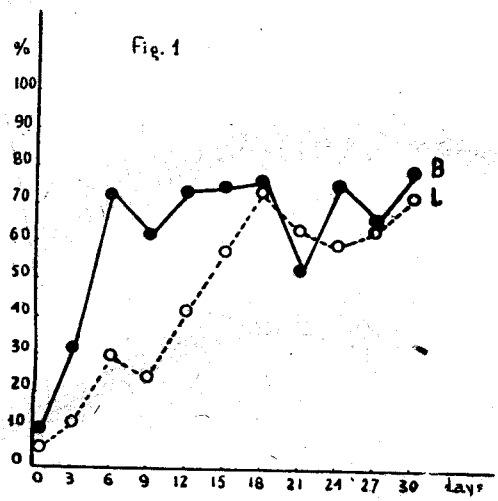

Fig. 1. The elaboration of the conditioned reflex to a primarily inhibitory stimulus (Lamp) and to a new stimulus (Bell) in „Bekas".
Abscissae: experimental sessions. Ordinates: the magnitude of a conditioned reflex in percentage of the magnitude of the reflex to the control stimulus (M). Circles, reflex to Lamp, dots, reflex to Bell. Each point represents mean value of three successive experimental sessions.
The reflex to the inhibitory stimulus grows much slower than that to a new stimulus.

does not reach the value of the conditioned response to Metronome, although the „strength" of both these stimuli (as judged from the evidence obtained in other dogs) is more or less the same.

Series V. Chronic extinction of the conditioned reflex to Lamp. Starting from exp. No. 120 and on, Lamp continued to be applied once daily among the applications of Metronome, but now again unreinforced. The course of this extinction is shown in Fig. 2a. It is seen that the process of extinction occurs rapidly (in

6 experiments the reflex drops to 1/3 of its initial value), but the response to Lamp does not reach its bottom it had before Series IV. While previously the salivation to Lamp amounted only to 3—6% of the salivation to Metronome, now it dropped no lower than to 15—25% of the response to Metronome.

Series VI. Introducing a new conditioned stimulus, Bell. A new excitatory conditioned stimulus — the sound of a bell — was introduced. The elaboration of the conditioned reflex to this stimulus was

Fig. 2

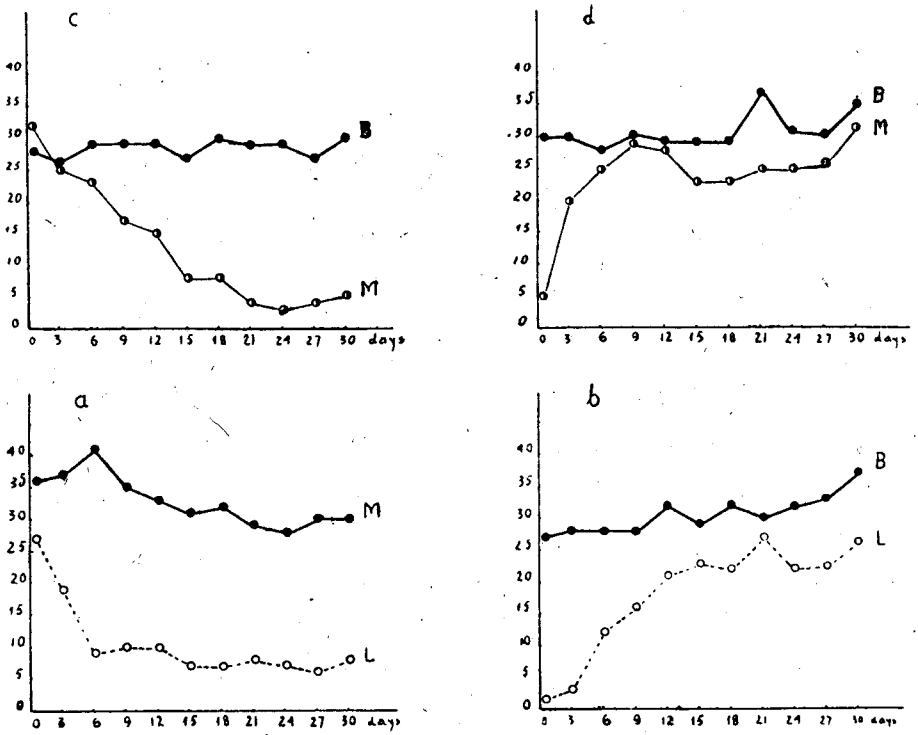

Fig. 2. Chronic extinction and restoration of conditioned reflex to a primarily excitatory stimulus (Metronome) and to a primarily inhibitory stimulus (Lamp) in „Bekas". Abscissae: experimental sessions. Ordinates: magnitude of conditioned reflexes in grades of the manometer. Circles, experimental stimulus, dots, control stimulus. a, extinction of Lamp, Metronome being a control, b restoration of Lamp, Bell being a control. c, extinction of Metronome, Bell being a control. d, restoration of Metronome, Bell being a control. The extinction of the primarily inhibitory stimulus is rapid, its restoration slow, the extinction of the primarily excitatory stimulus is slow, its restoration rapid.

relatively slow (cf. Fig. 1 and 6) but finally it reached the same value as the reflex to Metronome. This series will be discussed later.

Series VII. Chronic extinction of Metronome. The new conditioned stimulus, Bell was now taken as a control and Metronome was submitted to chronic e x t i n c t i o n in a usual way (Fig. 2c). The process of extinction was slow, the reflex to Metronome dropped to 1/3 of its value only after 15 experiments.

Series VIII. Restoration of the reflex to Metronome. After 30 extinction experiments Metronome was again applied w i t h reinforcement (Fig. 2d). The process of restoration was rapid, and in a few days Metronome regained its previous value.

Series IX. Restoration of the reflex to Lamp. Now the last series was performed in which the excitatory reflex to Lamp was re-established, while, as in the previous series, Bell was taken as a control (Fig. 2b). The process of restoration was slow and, as in Series IV, the reflex to Lamp reached only 70% of the control value.

Summary of the course of experiments on „Bekas".

In this dog Metronome was trained from the beginning as an excitatory conditioned stimulus, while Rythmic Lamp was trained from the very beginning as an inhibitory stimulus. It appeared that while the process of extinction of the reflex to Metronome was slow and its recovery rapid, the transformations of the reflexes to Lamp took quite a different course: both the first elaboration of the excitatory conditioned reflex and its restoration after extinction were very slow, while its extinction was more rapid than the extinction of Metronome. The elaboration of the conditioned reflex to a new stimulus, Bell was more rapid than the formation of the conditioned reflex to the primarily inhibitory stimulus, Lamp.

2) „Dudek", a male dog, age 3 years, weight 12 kg.

As the course of experiments performed on this dog was similar to those performed on „Bekas", we shall report them more concisely. Here, too, after the elaboration of a positive conditioned reflex (to Bell) a new stimulus (Whistle) was introduced and it was applied without reinforcement. After a lapse of time it became a strong inhibitory stimulus. Then, conditioned reflexes to two new stimuli (Lamp and Metronome) were established. Finally, in the last series of experiments Whistle was transformed into an excitatory conditioned stimulus.

The course of the formation of conditioned reflexes to Metronome and Whistle is represented in Fig. 3. It shows that in spite of the quite equal „strength" of both these stimuli the conditioned reflex to Metronome is formed much more rapidly and attains much higher value than the reflex to Whistle.

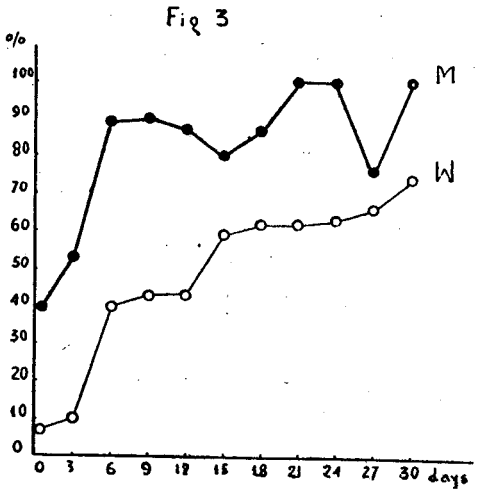

Fig. 3. The elaboration of the conditioned reflex to a primarily inhibitory stimulus (Whistle) and to a new stimulus (Metronome) in „Dudek". Abscissae: experimental sessions. Ordinates: the magnitude of conditioned reflex in percentage of the reflex to the control stimulus (Bell). Circles, the reflex to Whistle, dots, the reflex to Metronome.

3) „Romus", a male dog, age 3 years, weight 18 kg.

As the course of experiments conducted on this dog was somewhat different from that performed on „Bekas" and „Dudek" we shall report them in more detail.

Series I. Adaptation to the experimental situation — 4 days.

Series II. Elaboration of a conditioned reflex to Metronome. 28 experimental sessions, 124 trials.

Series III. Introduction of a new stimulus, Bell, applied without reinforcement. There were 48 experiments, 84 applications of Bell, 200 applications of Metronome. Alike in „Bekas" and „Dudek" the unreinforced stimulus evoked at the beginning of its application a quite significant salivary reaction (ca. 50% of salivation to Metronome), which gradually subsided. It also produced a marked inhibitory after-effect.

Series IV. Introduction of two new stimuli with reinforcement. This was a long series of experiments in which, in addition to the old conditioned stimuli (Metronome — excitatory, Bell inhibitory), two new stimuli (Whistle and Rhythmic Light) were introduced. Conditioned reflexes to these stimuli were formed with great difficulty, and they never attained the value of the reflex to Metronome. Moreover, the dog became very restless, the reflexes were more and more irregular and all symptoms of an experimental neurosis were mainfest. On the assumption that the new stimuli were responsible for the disturbance in conditioned reflex activity they were

Table I.

Acute elaboration of conditioned reflexes to a new stimulus (Bub) and to the inhibitory stimulus (Bell)

Elaboration of conditioned reflex to Bub.

No. of trial \ No. of exp.	168	169	170	171	172	189	190	
1	37*	35	43	34	30	43	43	
2	8	45	51	36	37	34	44	
3	33	46	54	40	38	36	40	
4	28	54	46	48	37	28	38	
5	32	54	48	39	37	41	35	
6	35	45	45	40	37	37	28	
Sum of 6 trials	153	279	287	237	216	219	228	1619

Elaboration of conditioned reflex to Bell

No. of trial \ No. of exp.	178	179	180	181	182	192	193	
1	31*	15	32	25	22	23	30	
2	4	23	36	35	41	38	34	
3	24	23	34	30	38	31	34	
4	30	26	36	33	30	29	24	
5	32	21	27	24	26	30	33	
6	20	22	31	26	26	27	36	
Sum of trials	141	130	196	173	183	178	191	1192

* The conditioned reflex to the control stimulus (M).

withdrawn and only Metronome continued to be applied. In fact, this measure restored the normal state in a few days: conditioned reflex activity became again regular, the reflexes became high, and the animal was quietened down.

Series V. The comparison of elaboration of the conditioned reflex to a new stimulus and to the inhibitory stimulus, Bell. When the normal conditioned reflex activity was fixed, a new stimulus (the sound of bubbling of water) was introduced. It was applied 6 times daily during 5 successive experimental sessions without any other stimuli intervening. Thereafter it was withdrawn, and a number of control experiments with Metronome followed. After that, Bell was applied w i t h r e i n f o r c e m e n t in just the same way

Protocol No. 1. „Romus". Exp. No. 194, 16/7/51.

No. of trial	Min.	C. s.	Its isol period	C. r.	Reinf.	Remarks.
1	2′	Bub.	20″	44	Food	Vivid alim. reaction to Bub.
2	6′	Bub.	20″	41	Food	The same.
3	10′	Bell	20″	33	Food	Very poor alim. reaction to Bell, eats rather slowly and as it were „cautiously"
4	14′	Bell	20″	31	Food	The same. After eating restless.
5	18′	M	20″	39	Food	Very vivid alim. reaction to M, eats without interruptions.
6	22′	M	20″	42	Food	The same.

as Bubbling. The comparison of the formation of the conditioned reflex to Bubbling and Bell is shown in Table I. It will be seen that there is a great difference between the two processes. The reflex to Bubbling is formed promptly and soon achieves high value. The elaboration of the reflex to Bell is more irregular and remains much below that to Bubbling and Metronome. The series ended with an experiment in which all three stimuli were given (see protocol No. 1). It is seen that although Bell is applied in the „best" place (i. e. in which conditioned reflexes are usually the greatest) it gives the weakest conditioned reaction, while the reaction to Bubbling and to Metronome is much stronger.

Series VI. Subacute extinction of Bell and Metronome.

After a series of experiments in which both Metronome and Bell were applied with reinforcement, and the two reflexes were more or less equalized, the extinction of the reflex to Bell and to

Metronome was carried out. The extinction of Bell was conducted in a following way. Each experiment consisted of 7—9 trials. At first Metronome, with reinforcement, was applied several times, then three applications of the unreinforced Bell followed, and finally several applications of Metronome terminated the experiment. In such a way 10 experimental sessions were conducted. After a lapse of time in which Metronome and Bubbling was used a similar series with the extinction of Metronome was performed, Bubbling being used as a control. The comparison of the two series is represented in Fig. 4. It is easy to observe that the process of extinction of the reflex to Bell is much more rapid than that to Metronome.

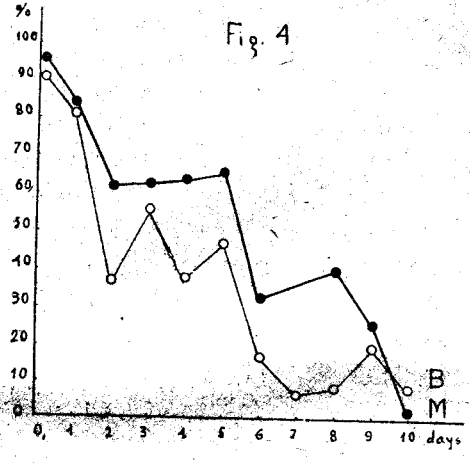

Fig. 4

Fig. 4. Subacute extinction of the conditioned reflex to a primarily inhibitory stimulus (Bell) and to a primarily excitatory stimulus (Metronome) in „Romus". Abscissae: experimental sessions. Ordinates: magnitudes of conditioned reflexes in percentage of the reflex to a control stimulus. Circles, the reflex to Bell, dots the reflex to Metronome. Each point represents the mean value of the reflex of a given day (3 trials).

The extinction of the reflex to Bell is more rapid than that to Metronome.

Summary of the experiments on „Romus".

In „Romus" as in „Bekas" and „Dudek" one stimulus (Metronome) was trained from the beginning of experiments as an excitatory conditioned stimulus and another stimulus (Bell) as an inhibitory conditioned stimulus. The properties of the Bell were investigated. It was established that: 1° its „acute" transformation into a positive conditioned stimulus (by applying this stimulus exclusively, time after time) was slower and more incomplete than the formation

of the conditioned stimulus from a new stimulus; 2^0 its „subacute" extinction (by applying it again without reinforcement each day several times in succession) was more rapid than the similar extinction of the normal positive stimulus (Metronome). It was also observed that the elaboration of conditioned reflexes to new stimuli, just after an intensive training of the inhibitory conditioned reflex to Bell, was rather difficult and produced a temporary experimental neurosis in the dog.

DISCUSSION

Kosteneckaya (1949) has first established the following facts. If a dog is trained in such a way that from the very beginning of the conditioned reflex training the food is given without any signalling stimuli, and various „indifferent" stimuli are applied in intervals between food presentations, then these stimuli adopt a strong inhibitory character, and moreover, this first inhibitory training leaves its marked impression on the whole later conditioned reflex activity. So, it was shown that conditioned reflexes to new stimuli are elaborated with much greater difficulty than they are elaborated normally, that they remain weak and irregular, and improve only after the inhibitory stimuli are withdrawn.

These findings were fully confirmed in our laboratory. In one of our dogs (unpublished experiments of W. Kozak) the preliminary training was just the same as in Kosteneckaya's experiments, and afterwards it was observed that the elaboration of all conditioned reflexes in this dog occurred with exceeding difficulty, and they remained always relatively weak in comparison with the unconditioned reflex (cf. Fonberg 1952).

In this series of experiments the procedure was somewhat different. First, the conditioned alimentary reflex to a given stimulus (say, stimulus A) was normally established, and then another stimulus (say, stimulus B) of the same or another analyser was introduced, and it was for a long period applied without reinforcement. It was demonstrated that the stimulus B has acquired quite different properties than the stimulus A. While stimulus A behaved much in the same way as those stimuli we dealt with in our previous papers (Konorski and Szwejkowska 1950, Szwejkowska 1950), viz. the process of its extinction was protracted and its restoration was prompt and complete, stimulus B could be transformed into a positive conditioned stimulus with great difficulty, its effect remained weaker,

than the effect of stimulus A, and its extinction occurred relatively rapidly, while its restoration was very protracted. And so, the problem put forward in our previous papers, why there is such a distinct difference between the rate of extinction and restoration of conditioned reflexes, seems now to be elucidated. It is shown to depend on the previous „history" of the stimulus. If this stimulus has been, from the very beginning of its conditioned reflex „career", applied with reinforcement, then it is difficult to transform it into an inhibitory stimulus, while it is very easy to restore its previous excitatory character. When, on the contrary, the first training of a given stimulus has been inhibitory, then its properties are quite reverse; now it is difficult to transform it into an excitatory stimulus, while it is easy to render it again inhibitory. We shall call this principle „the principle of the primacy of first training".

Many experimental data obtained in Pavlov's laboratories concerning various forms of transformation of excitatory conditioned reflexes into inhibitory, and vice versa, may be adduced to support this principle.

A number of authors (Rikman, cit. after Pavlov 1940, p. 302 ff, Pawłow, 1951, str. 254, Jakovleva 1938, 1944, Maiorov 1938, Timofeeva 1948, and others) have found that a well established differential inhibitory stimulus as a rule can be transformed with a great difficulty into an excitatory conditioned stimulus. Such a stimulus, even after many reinforced trials, gives much smaller conditioned responses, compared to a control excitatory stimulus; furthermore, these responses are often irregular, and sometimes a more or less pronounced disturbance of the conditioned reflex activity (experimental neurosis) results from its application (Rikman). Moreover, even in those cases, when after being transformed it has reached the same effect as the control stimulus, its „latent" inhibitory properties may be shown by submitting it to the acute extinction with the subsequent restoration; its extinction occurs much faster, while its restoration occurs much slower, than the respective processes of the control stimulus (Iakovleva 1944). All this goes to indicate that differential inhibitory stimuli must be classed as belonging rather to the group of our B stimuli than to the group of our A stimuli. In fact, such stimuli are generally from the very beginning of their application being given without reinforcement, and so their first training is inhibitory.

But it must be stressed that the more „similar" is a differentiated stimulus to its excitatory counterpart (i. e. the greater is generalisation to be overcome), the more excitatory elements it carries along from the beginning of its training, and consequently cannot be regarded as 100% inhibitory as are regarded those stimuli that are quite unlike their excitatory counterparts. In order to illustrate this point we shall adduce the following series of experiments.

In one of our dogs the Bell (S_1) was an excitatory conditioned stimulus. To this a differentiation was established by two stimuli: another Bell (S_2), very similar to the first one, and the sound of a Buzzer (S_3), rather unsimilar to S_1. Both these stimuli were applied the same number of times, and after the inhibitory reflexes had been firmly established, they both started to be reinforced by food. The course of the formation of inhibitory and then excitatory conditioned reflexes to these stimuli is represented in Fig. 5. We see that stimulus S_2 exhibits at the beginning a strong generalization to stimulus S_1, and the course of its transformation into a positive

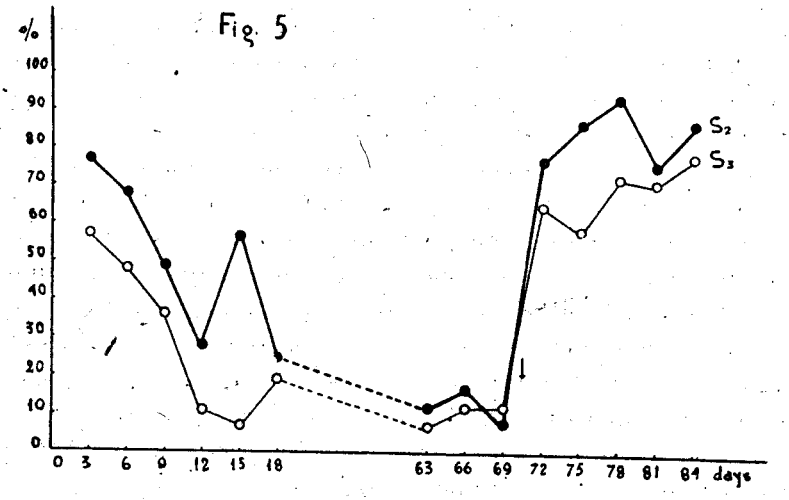

Fig. 5. The elaboration of an inhibitory conditioned reflex and its transformation into an excitatory conditioned reflex to a more (S_2) and less (S_3) similar stimulus in respect to the primarily conditioned stimulus (S_1) in „Nepek". Abscissae: experimental sessions. Ordinates: magnitudes of the reflex in percentage of the reflex to control stimulus. Circles, the reflex to S_3, dots, the reflex to S_2. At arrow S_2 and S_3 start to be reinforced. The inhibition of the reflex to S_3 is more rapid than that of the reflex to S_2, while its restoration is slower and more incomplete.

stimulus is very prompt. In other words it comes closer to our A group. In contrast to it, the stimulus S_3 exhibits much a lesser generalization to stimulus S_1, consequently it is more inhibitory since the beginning of training than S_2, and therefore its transformation into an excitatory stimulus is more difficult and incomplete. In other words it comes closer to our B group. Thus, various differentiated inhibitory stimuli may be placed in between the A and B groups, closer to the one or the other, according to the subtleness, resp. coarseness of differentiation.

Similarly, it is well known that if a stimulus is for a long time reinforced in an ordinary manner (i. e. after 20—30 sec. from its outset), and thus a short-delayed reflex to it is well established, then it is very difficult, and sometimes practically impossible, to transform it, by protracting its isolated action to 2—3 min., into a long-delayed reflex. But if a stimulus is trained with a delayed reinforcement from the beginning of its practice, then a delayed reflex is formed relatively easily, and in this case it is difficult, and may be even impossible, to transform it into a normal reflex by moving the time of reinforcement closer to the beginning of the conditioned stimulus (Pavlovian Wednesdays 1949, I p. 120, 129, III p. 378 etc., Frolov cf. after Pavlov 1940 p. 229, Pawłow 1951 str. 193, Jakovleva 1944, Timofeeva 1948 and others). Experimental neuroses may result from such transformations (Timofeeva 1948).

Furthermore it must be emphasized that the nature of the first training determines not only the properties of that stimulus to which it is applied, but extends partially to the whole of the conditioned reflex activity of the dog, influencing also the properties of other stimuli submitted to other forms of training. So, in all dogs of our first group, as reported in previous papers of this series, the first training was purely excitatory, and no permanent inhibitory reflexes were formed at all. In consequence not only the restoration of all extinguished conditioned reflexes proceeded in them very rapidly, but also all conditioned reflexes to new stimuli developed very readily, and after a few reinforcements they achieved the same magnitude as the old and well established reflexes. In contradistinction to this group, we noticed that our second group of dogs, in which after the first excitatory training (to stimulus A) the inhibitory training (to stimulus B) was carried out, displayed quite different properties. Conditioned reflexes to new stimuli (elaborated after the inhibitory training) grew much slower than in the first group, and

often did not achieve maximal values. Similar facts were reported by Kosteneckaya (1949).

Accordingly, in Fig. 6 three curves of elaboration of new conditioned reflexes are shown.

Curve I represents the mean rate (taken from 2 series of experiments) of the elaboration of conditioned reflexes to new stimuli in those dogs which have been hitherto submitted almost exclusively

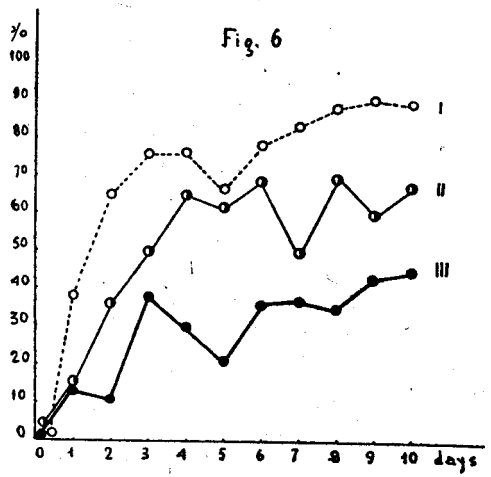

Fig. 6

Fig. 6. The elaboration of conditioned reflexes to new and to inhibitory stimuli in various series of experiments. Abscissae: experimental sessions. Ordinates: magnitudes of conditioned reflexes in percentage of control stimuli. Further explanation in text.

to an excitatory conditioned reflex training (these dogs served in experiments reported in our previous papers of this series, Konorski and Szwejkowska 1950, Szwejkowska 1950).

Curve II represents the mean rate (taken from 5 series of experiments) of the elaboration of conditioned reflexes to new stimuli in those dogs which were submitted at the beginning of experiments to both excitatory and inhibitory training (the respective series of experiments were reported in the present paper, cf. Fig. 1 and 3)

Curve III represents the mean rate (taken from 2 series of experiments) of the elaboration of conditioned reflexes to those stimuli which were trained from the very beginning as inhibitory conditioned stimuli (cf. Fig. 1 and 3).

It is seen that while the elaboration of conditioned reflexes according to curve I proceeds very rapidly, and the elaboration of

conditioned reflexes according to curve III develops very slowly, the curve II takes the medium course, being not so rapid as in the first instance and not so slow as in the third. Generally speaking (as Kosteneckaya has pointed out) the more excitatory conditioned reflexes are already formed and the less inhibitory stimuli are applied, the more rapid is the elaboration of new conditioned reflexes.

Incidentally it should be pointed out that all three curves represented in Fig. 6 exhibit a marked collapse on the fifth day of elaboration of conditioned reflex. We are signalling this fact without going into its further comment.

To sum up we can say that the properties of a given stimulus depend first of all on its individual training; however, they are also affected by the training of all other stimuli in the animal.

But it should not be thought that the properties of a stimulus acquired in its first training are quite unalterable and that this stimulus preserves its primary character irrespectively of its later fate. The fate of the primarily inhibitory stimulus — Rythmic Lamp — in „Bekas" is in this respect very instructive. The salivation to this stimulus after its first inhibitory training was almost nil. But after a monthly excitatory training this stimulus being re-extinguished did not attain such a low level as before, and it continued to elicit a slight salivation which persisted even after many trials (cf. Fig. 2a). Thus, not only the first training left its permanent imprint on the character of the stimulus (which was amply discussed above), but the second training succeeded to modify somewhat its character, and this modification was also enduring and could be traced during succeeding trainings. Similar results were obtained by Iakovleva (1938) and Timofeeva (1948).

The problem arises whether the above formulated principle, stressing the primacy of the first training for the properties of a given stimulus, is restricted only to the transformations of excitatory reflexes into inhibitory ones, and vice versa, or whether it has a more general application. Undoubtedly there is a body of evidence to show that its application is in fact more general and that it bears also upon transformations of heterogeneous conditioned reflexes.

A striking example may be taken from „Pavlovian Wednesdays" (1949 I p. 313) in which an interesting experiment by Rikman is reported. This author elaborated a defensive conditioned reflex (an electric shock to the leg being used as reinforcement) to a musical tone, and then trasformed it into a conditioned alimentary reflex.

This transformation was very difficult for the dog and was accomplished within a year, after hundreds of trials. But it sufficed to apply another musical tone only once but reinforced by an electric shock to completely abolish the alimentary conditioned reflex to the previous tone and restore the defensive reflex.

Another example is presented by Frideman's experiments (Pavlov 1940 p. 227, Pawłow 1951, p. 193). This author transformed a conditioned alimentary reflex into a defensive acid conditioned reflex. „The complete replacement of the one conditioned reflex by the other required about 30 reinforcements by the new unconditioned stimulus. After a considerable practice of the conditioned reflexes to acid the conditioned stimuli were once more transformed back again into alimentary ones; the transformation occurred rapidly, and only a few reinforcements were needed. This indicates that the original alimentary connection was still preserved in spite of the establishment of a new connection with the reflex to acid".

We may also refer to our own experiments (Konorski and Wyrwicka 1950) in which the transformation of the classical alimentary conditioned reflex (of the first type) into a motor alimentary conditioned reflex (of the second type) was much more difficult than the elaboration of such a reflex to a quite new stimulus.

All this goes to show that the principle of the primacy of first training has a general application and is valid, *mutatis mutandis*, in respect to all types of transformations of conditioned reflexes. It is not difficult to indicate very many instances from the life of animals, as well as of man, where the operation of this principle may be easily found.

The important question is: what may be the physiological mechanism through which this principle works? If we accept after Pavlov that the elaboration of conditioned reflexes is founded on the acquisition of new connexions in the cortex (so called „temporal connexions"), then why is it that the first connexions that a definite stimulus forms with some other stimulus are much „stronger" than new connexions formed by the stimulus, and why is it that those first connexions determine to a large extent its later properties?

Of course, our knowledge of this subject is insufficient to give a full and unequivocal answer to this question. But tentatively we may guess that the following mechanism may be involved here. When a given „indifferent" stimulus is combined with an unconditioned stimulus, there are no substantial obstacles for the respective

„temporal connexions" to be formed between the relevant cortical „centres". But when the established conditioned reflex to that stimulus is transformed into an antagonistic reflex (e. g. an excitatory reflex into an inhibitory one, or an alimentary reflex into a defensive reflex), then the acquired character of the stimulus and the reaction it produces prevents the new connexions with the antagonistic centre to be formed, and this makes the process of such transformation much more protracted than it would be, if this very kind of training were conducted at first.

According to Pavlov's principle of „stratification" of conditioned connexions (Pavlovian Wednesdays, I p. 296, 313, II p. 494, 527, III p. 378), which states that freshly elaborated connexions do not annihilate the old ones but are, so to say, „superimposed" on them, the old connexions survive the antagonistic training and, as soon as this training is discontinued and the old training is resumed, they easily outbalance the new and weak connexions, and so the old reflex is restored.

It remains to consider why is it that a particular training of one stimulus not only determines the properties of that stimulus but is also partly manifested in the properties of other stimuli subjected to different forms of training. The answer to this question must be sought in the integrative character of the conditioned reflex activity. According to it no particular stimuli presented to the animal are independent from one another, but are in some sense interconnected and generalized, forming a whole in which any component puts its share. And so, quite different is the „attitude" of a dog in whom every stimulus hitherto applied in the experimental situation was always reinforced by food, and the „attitude" of another dog, who from the very beginning of its training has learned that there are not only stimuli that announce food but also other stimuli that announce nothing.

Both in our experiments and in experiments of other authors it was often observed that difficult forms of training, such as the transformation of a „purely" inhibitory conditioned reflex into an excitatory conditioned reflex, or the extinction of a firmly established excitatory conditioned reflex, result in more or less severe disturbance of conditioned reflex activity: the dog becomes restless, refutes to take food in the experimental situation, conditioned reflexes are weak and irregular, etc. This fact is easy to understand, if

we take into account that the reinforcement of a strongly inhibitory stimulus leads to a severe „conflict" between the excitatory and the inhibitory processes, which, as is well known from the investigations of Pavlov's school, is the main source of experimental neuroses.

SUMMARY

1. When an „indifferent" stimulus is subjected, from the very beginning of its application, to the inhibitory training in respect to a given reflex (i. e. if this stimulus is applied without reinforcement in a situation in which a definite unconditioned reflex is elicited), then it is much more difficult to transform it thereafter into an excitatory conditioned stimulus than it would be if this stimulus were subjected from the beginning to the excitatory training.

2. The extinction of such a stimulus (after it has been made an excitatory conditioned stimulus) occurs more rapidly than the extinction of those stimuli which are excitatory from the beginning of their training, whereas its restoration is more protracted.

3. When in addition to excitatory conditioned reflexes subsequent inhibitory reflexes are established, then excitatory conditioned reflexes to n e w stimuli are not formed so easily as in the case when the dog is subjected only to the excitatory training.

4. On the basis of these facts „a principle of the primacy of first training" is formulated and its general validity is emphasized.

5. The possible physiological mechanism of this principle is discussed.

REFERENCES

FONBERG E. 1952 — Przewlekła nerwica doświadczalna u psa z dominującymi zaburzeniami ruchowymi (in print).

JAKOVLEVA V. A. 1938 — Opredelenije podviznosti nervnych processov sobaki putem dvuchkratnoj peredelki uslovnogo razdrazitela. Trudy Fiziol. Lab. akad. I. P. Pavlova. *8*, 32.

JAKOVLEVA V. V. 1944 — Issledovanije podviznosti nervnych processov sobaki tipa sangvinika. Trudy Fiziol. Lab. akad. I. P. Pavlova. *11*, 81.

KONORSKI J. and SZWEJKOWSKA G. 1950 — Chronic Extinction and Restoration of Conditioned Reflexes. I. Extinction against the excitatory background. Acta Biol. Exper. *15*, 155.

KONORSKI J. and SZWEJKOWSKA G. 1952 — Chronic Extinction and Restoration of Conditioned Reflexes. III. Defensive motor reflexes. Acta Biol. Exper. *16*, 91.

KONORSKI J. and WYRWICKA W. 1950 — Researches into Conditioned Reflexes of the second type. I. Transformation of conditioned reflexes of the first type into conditioned reflexes of the second type. Acta Biol. Exper. *15*, 193.

KOSTENECKAJA N. A. 1949 — Obrazovanije tormoznych uslovnych refleksov na indifferentnyje razdraziteli. Trudy Fiziol. Lab. akad. I. P. Pavlova. *15*, 124.

MAIOROV F. P. 1938 — Inertnost' tormoznogo processa u sobaki sil'nogo uravnovesennogo tipa. Trudy Fiziol. Lab. akad. I. P. Pavlova. *8*, 139.

PAVLOV I. P. 1940 — Conditioned Reflexes. Oxford.

PAWŁOW I. P. 1951 — Wykłady o czynności mózgu. Warszawa.

PAVLOVSKIJE SREDY (Pavlovian Wednesdays) 1949. Moskva.

SZWEJKOWSKA G. 1950 — Chronic Extinction and Restoration of Conditioned Reflexes. II. Extinction against an inhibitory background. Acta Biol. Exper. *15*, 171.

TIMOFEEVA T. A. 1948 — Vlijanije obratnych peredelok na tormoznyj process. Trudy Fiziol. Lab. akad. I. P. Pavlova *13*, 154.