THE REFLEX TO "TIME" IN THE ARTIFICIAL ELECTRODEFENSIVE REACTIONS OF DOGS

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I.P. Pavlov was led to conclude that "time" could, under certain conditions, act as a conditioned stimulus; this view evolved on the basis of a number of works [9, 13, 14, 25]. The question of time as a conditioned stimulus was studied in numerous subsequent investigations [1-7, 10, 15-17, 19, etc.]. It was established that reflexes to "time" follow the same laws as reflexes to other experimental stimuli used in work with animals.

The majority of authors conducted their experiments with the use of secretory technique; there has not been an adequate amount of work on this important question employing the motor technique. It must, moreover, be mentioned that fairly conflicting references are encountered in the literature [2, 7] concerning the dynamics of the formation of the motor conditioned reflex to "time" in dogs.

All this led us to the study of the appearance and course of the reflex to "time" during the formation of defensive motor reactions in dogs.

EXPERIMENTAL METHOD

A defensive reflex in the form of raising of the right fore-limb was developed in dogs to electrocutaneous reinforcement; if the dog raised its paw in response to the signal and kept it raised for a definite period of time no current was applied to the limb (V.P. Petropavlovskii's technique [22]).

The magnitude of the motor reaction was measured by special meters [23].

The reinforced stimuli consisted of a bell (bl+) and light from a 40-watt electric bulb (lt+); the same stimuli served as differentiation stimuli but were interrupted once per second (bl-, lt-). The number of positive and inhibitory stimuli in an experiment was about equal. A total of 8-9 stimuli was used in an experiment. In one series of experiments these stimuli were used in no particular sequence, in another a stereotyped sequence was adopted; lt-, lt+; bl-, bl+, lt-, bl-, bl+. The pauses between the stimuli were maintained constant -4 minutes - throughout the two series of experiments. The duration of each conditioned stimulus was 25 seconds. The unconditioned stimulus (induction current) was applied on the 10th second of the action of the positive stimulus (bl+, lt+). The experiments were performed during 1953-1955, always during the first half of the day. The experimental material consists of 839 experiments.

Five dogs were used in the experiments: Moriak, Chernysh, Viunok, Sharik, belonging to the strong type of higher nervous activity and Shtorm, whose higher nervous activity was of the weak type.

The type characteristics of all the dogs except Sharik were determined in detail. Sharik was not subjected to special investigations, and his type was judged solely on the basis of the dynamics of conditioned reflex formation and the results of observations of his behavior in the animal house and during experiments.

EXPERIMENTAL RESULTS

As reported earlier [27], the defensive reflexes developed by us first became apparent during the intervals between the stimuli used (intersignal reactions), and only later appeared in response to the direct action of these stimuli. It was shown in the same investigation that during the first few trials the intersignal reactions were distributed almost uniformly throughout the whole interval but soon began to undergo a rearrangement approaching more and more the time of presentation of the next stimulus. Reactions appearing not earlier than 36 seconds prior to presentation of the stimulus are classed as reflexes to "time." It is the characteristics of these reflexes to time that form the subject of the present work.

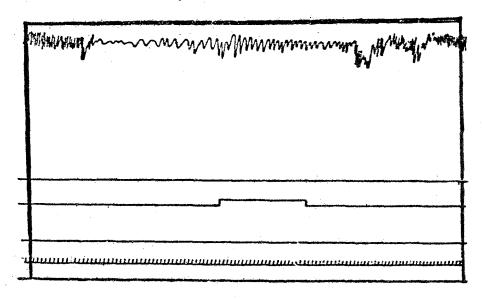


Fig. 1. Change in respiration towards the time of application of the stimulus (inhibitory bell, application No. 9). Dog Shtorm, experiment 4/27/1954. Records from above down: respiration, movement of the paw, conditioned stimulus marker, time marker (1 second).

The conditioned reflex to the time of application of the stimulus manifests itself first of all by a change in respiration (Figure 1) and in some dogs by a vocal reaction (loud barking, squealing, whining) towards the end of the interval. The conditioned reflex in the form of the movement being elaborated appears somewhat later.

In the absence of a definite sequence of positive and inhibitory stimuli during the experiment the reflex to the time of their presentation appears at the end of each pause, i.e., before each stimulus, irrespective of their position in the experiment. The intensity of this reflex, depending on the type characteristics of the dog, may be either the same throughout the experiment, decrease towards the end of the experiment, or undergo irregular changes during the experimental day.

When the sequence of positive and inhibitory stimuli is fixed, definite phases in the establishment of the reflex to "time" can be observed (Table 1).

Table 1 shows that during the first few experiments (Groups I and II) a conditioned motor reflex appears before each stimulus, both positive and inhibitory. However, the conditioned reactions preceding the differentiation stimuli begin gradually to diminish in magnitude as compared with reflexes appearing before the positive stimuli (Groups III and VI) and become completely inhibited on reinforcement of the systematic arrangement. Subsequently the conditioned reflexes to the time of presentation of positive stimuli also begin to be inhibited; they are observed mostly at the beginning of the experiment only.

In experiments with a constant stereotyped pattern of stimuli a remarkable mobility of the conditioned reflex to the time of their presentation was noted. In individual experiments the constant 4-minute intervals were intentionally replaced by 1-, 2-, 6- and 7-minute ones and in all these experiments it was observed that

TABLE 1

Change in the Reflex to Time of Presentation of Successive Stimuli With Reinforcement of the Stereotyped Pattern (Mean values of groups of 10 experiments) Dog Chernysh

	1	-	Sequenc	e of stim	uli in the	experimen	t			
**		2	3		5	6	7	8		
Groups of ten exper-	stereotyped pattern of stimuli									
iments	(t-)	it+	(b1-)	b1+	(lt -)	lt+	(bl -)	bl+		
1	Ī	108 1	109 3	84.1	59.9	31.5	40.8	34.1		
11		892.4	700.1	914.1	679.4	404.0	283.0	295 2		
111	_	556.2	261.9	402.0	117.8	320.1	67.6	255.2		
IV		156.8	23.9	255.2	78.0	145.6	0	71.5		
V	_	67.4	24.6	52.1	9.1	45.8	0	40.0		
Vi	—	66.1	5.4	79.5	14.6	0	0	0		
VII		75.5	0	86.6	1 0	1.4	0	7.6		

the dog was able to switch over to the new time relationships in the course of a single experiment,

In this variant of the experimental procedure the stimulus used was summated and consisted not only of the distant stimulation but also of the constancy of the time of its presentation. This created optimal conditions for a more definite formation of cortical functional mosaic with the appearance of definite positive and inhibitory foci, positive and inhibitory "positions" in the experiment.

TABLE 2

The Influence of Intervals Between Stimuli on Conditioned Reflexes to Time

Pauses between	Reflexes during the pauses			
stimuli in	preceding application of			
minutes	stimu li			
	positive	inhibitory		
	(average value during the experiment)			
1	221			
2	652	0		
4	180	0		
6	514	86		
7	78	0		

Marked stability of elaborated systematic arrangement was noted in all the experiments with alteration in the pauses between the stimuli but preservation of their sequence: the reaction during the intervals appeared, as a rule, only before the positive stimuli. This arrangement was not impaired when the constant 4-minute intervals were replaced either by equal or by unequal intervals (2, 4, 6, 1, 3, 7, 5 minutes) in the course of the experiment (Table 2).

In the latter case the reactions in the intervals reflected, understandably, the sequence of presentation of the stimuli rather than the conditioned time.

The magnitude of the reflex to "time" was different in the experiments with and without a stereotyped pattern. This was judged by the formation of delayed inhibition, on the grounds of the common features in the mechanism

of the formation of delay and reflex to "time" (Pavlov). Thus, in the presence of a stereotyped pattern of stimuli no delaying inhibition could be achieved (257 combinations), whereas in experiments with variable significance of each 4-minute interval of time delay developed very rapidly—after 12 combinations. Evidently, excitation elicited constantly by time as a conditioned stimulus was of considerable strength in the former case and hindered the development of the inhibitory process. The facts described below are probably associated with delaying inhibition.

At the beginning of the experiments all the dogs showed the following curious picture: having raised the paw during the first few seconds of the action of the positive conditioned stimulus, the dog lowered the paw on the 10th second (towards the moment of its reinforcement by the current) i.e., produced a reaction opposite to the signal significance of the stimulus (Figure 2). This fact was observed during reactions both to the auditoryand light-positive conditioned stimuli, but in the case of the bell, inhibition towards the moment of application of the unconditioned stimulus appeared earlier than in the case of the light, and disappeared later. Chernysh,

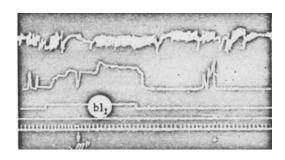


Fig. 2. Inhibition of conditioned reaction on the 10th second of stimulus action. Dog Chernysh, experiment 5/27/1954. Records the same as in Figure 1.4) time of presentation of unconditioned stimulus.

for example, lowered the paw towards the moment of the usual reinforcement of the bell by electric current (10th second) for the first time during the 2nd experimental day and this reaction persisted for 10 days. The reflex to light, on the other hand, was inhibited on the 10th second beginning with the 4th day (with the given stimulus) and disappeared by the 7th day. Later such a picture was only observed when the experimental conditions were very difficult. It would appear that during the early stages, when the proprioceptive stimulation had not yet become a signal, the pain character of the unconditioned reinforcement determined the overpowering character of the conditioned stimulus at the moment of application of the unconditioned stimulus - transient "overswing" inhibition then appeared: the dog, having raised its paw to the signal, lowered it on the 10th second (time of application of current).

The same relationships, but opposite in sign, were noted also during the formation of the inhibitory reflex: during the first 10 seconds of the action of the differentiation stimulus there was an inhibitory reaction; on the 10th second (moment of reinforcement bl+) a positive reaction occurred either in the form of a single raising of the paw (Figure 3a) or in the form of a tonic reaction (Figure 3b,c); later this manifestation was only discernible in the change of the pneumogram.

Thus, in both cases, the adequate reaction on the 10th second passed into a reaction opposite to the signal significance of the stimuli.

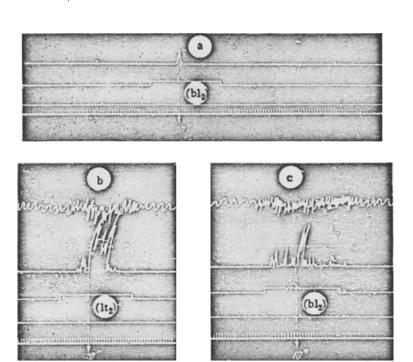


Fig. 3. Disinhibition of the motor reaction on the 10th second of the action of the differentiation stimulus in the dog V'iunok: a) experiment 5/10/1954; b, c) experiment 5/17/1954. Records are the same as in Figure 1. In trace a) respiration was not recorded.

It seems to us that these experiments indicate that not only the time of application of the stimulus possesses strong signal properties [18] but also the time of application of the reinforcement of this stimulus (under our experimental conditions) acquires a distinctive signal role. This is particularly vividly demonstrated by the appearance of a motor conditioned reaction on the 10th second of the action of the inhibitory (differentiation) stimulus; the reflex to the time of reinforcement of the positive stimulus proved to be generalized to auditory stimuli, and to a greater extent than the reflex to the signal stimulus: the dog distinguished continuous sound from an interrupted one and only on the 10th second reacted similarly to both. This phenomenon should, evidently, be regarded as a peculiar manifestation of the reflex to "time." Alongside the reflex to the time of the presentation of successive conditioned stimulus are flex to the time of presentation of the unconditioned stimulus also develops in the cases described.

While the signal role of time from the beginning of the action of a positive stimulus to the moment of its reinforcement has long been known from work on trace and delayed food reflexes [8, 11, 12, 22], the fact that the increase in the stimulating process at this moment could also be transferred to the inhibitory stimulus was new to us and particularly interesting.

The present investigation leads to the following conclusions.

The reflex to "time" is revealed first in the vocal and respiratory components and only later in the motor component of the conditioned defensive reaction being elaborated. As training of the conditioned motor reflex to positive and inhibitory stimuli proceeds, a gradual concentration of the stimulating process towards the moment of presentation of the conditioned stimulus occurs: a) with constant pauses, but in the absence of a definite sequence of stimuli, the conditioned reflex to the time of their presentation occurs before each successive stimulus irrespective of its signal significance (positive, inhibitory); b) with constant pauses and a fixed sequence of positive and inhibitory stimuli the reflex to "time" (with reinforced stereotyped pattern) appears only before the positive stimuli.

The conditioned reflex to the time of presentation of positive conditioned stimuli hinders the development of delaying inhibition. During the formation of motor defensive reflexes with 10-second lags a conditioned reflex to the time of application of the unconditioned reflex is observed in the first few combinations. It is expressed in inhibition of the respiratory and motor reflexes on the 10th second of the action of the positive stimulus. The conditioned defensive reflex to the time of reinforcement of the stimulus which is positive during the first few combinations occurs also during the reaction to the inhibitory stimulus: disinhibition is seen on the 10th second of the action of the differentiation stimulus; it is expressed in the form of a transient or prolonged motor reaction. As the positive and inhibitory reflexes are strengthened the reflex to the time of application of the unconditioned reflex is extinguished and becomes only infrequently discernible in the respiratory component. This reflex becomes prominent under difficult experimental conditions. The conditioned reflex to "time" observed by us during the formation of artificial motor reflexes arises as the result of constant coincidence of given segments of time with a definite functional state of the cortical cells regularly evoked by the action of the stimuli used.

SUMMARY

Experimental investigation of reflex to the time of presentation of defensive signal stimuli (sound and light) was carried out by V.P. Petropavlovskii's method. Experiments were performed on 5 dogs over a period of 3 years. It was established that the reflex to "time" was revealed at first in the vocal and respiratory components and only then in the motor component of the conditioned reaction (the raising of the right forepaw).

In the absence of a definite sequence of signal stimulations, but with fixed intervals between them, the conditioned reflex to the time of their presentation appeared irrespective of the position of the stimuli in the experiment. With fixed sequence of the positive and inhibitory stimuli the reflex to "time" appeared only before the positive stimuli.

It was established that not only the time of presentation of the stimulus had a signal action, but also time of the reinforcement (current) acted as a signal.

LITERATURE CITED

[1] E.A. Asratian, Trudy Fiziol, Labor, im I.P. Pavlova (Leningrad-Moscow, 1938), 8, 1-15.

- [2] O.P. Bolotina, Trudy Inst. Fiziol. Im. I.P. Pavlova (Leningrad, 1952), 1, 29-34.
- [3] F.D. Vasilenko, Trudy Fiziol. Labor. im. I.P. Pavlova (Leningrad-Moscow, 1932), 4, 310-317.
- [4] E.G. Vatsuro, ibid. 1948, 13, 5-29.
- [5] L.G. Voronin, Fiziol. Zhur. SSSR 34, 333-338 (1948).
- [6] L.G. Voronin, Zhur. Vysshei Nerv. Defatel. 1, 213-222 (1951).
- [7] L.S. Gambarian, Trudy Inst. Fiziol. im. I.P. Pavlova (Leningrad, 1952), 1, 73-84.
- [8] F.S. Grossman, Material Concerning Trace Conditioned Salivary Reflexes,* Thesis (St. Petersburg, 1909).
- [9] V.S. Deriabin, Further Data on the Physiology of Time as a Conditioned Stimulus for Salivary Glands,* Thesis (St. Petersburg, 1916).
 - [10] A.S. Dmitriev and A.M. Kochigina, Uspekhi Sovremennoi Biol. 15, 1, 31-51 (1955).
 - [11] V.M. Dobrovol'skii, Trace Food Reflexes, Thesis (St. Petersburg, 1911).
- [12] I.V. Zavadskii, Material Concerning Inhibition and Disinhibition of Conditioned Reflexes, Thesis (St. Petersburg, 1908).
- [13] G.P. Zelenyi, Material Concerning the Reaction to Auditory Stimuli in the Dog, Thesis (St. Petersburg, 1907).
 - [14] K.N. Krzhyshkovskii, Trudy O-va. Russkikh Vrachei v St. Petersburg (St. Petersburg, 1908), 267-329.
 - [15] P.S. Kupalov, Trudy Fiziol. Labor. im I.P. Pavlova (Leningrad-Moscow, 1929), 3, 2-3.
 - [16] P.S. Kupalov, Arkh. Biol. Nauk SSSR 31, 4, 301-309 (1931).
 - [17] P.S. Kupalov, Trudy Fiziol. Labor. im I.P. Pavlova (Leningrad-Moscow, 1933), 5, 335-406.
 - [18] P.S. Kupalov and B.N. Lukov, Arkh. Biol. Nauk SSSR 33, 5-6, 665-677 (1933).
 - [19] F.P. Maiorov, Trudy Fiziol. Labor. im I.P. Pavlova (Leningrad-Moscow, 1933), 5, 255-320.
 - [20] I.P. Pavlov, Collected Works (Moscow-Leningrad, 1947), vol. 4.
 - [21] I.P. Pavlov, ibid (1949), vol. 3.
 - [22] V.P. Petropavlovskii, Fiziol. Zhur. SSSR 17, 2, 70 (1934).
 - [23] I.P. Pimenov, A Special Group of Conditioned Reflexes, Thesis (St. Petersburg, 1907).
 - [24] G.V. Skipin and A.S. Sharov, Zhur. Vysshei Nerv. Deiatel. 5, 2 (1955).
- [25] M.M. Stukova, Further Material Concerning the Physiology of Time as a Conditioned Stimulus for Salivary Glands, Thesis (St. Petersburg, 1914).
 - [26] I.P. Feokritova, Time as a Conditioned Stimulus for Salivary Glands (St. Petersburg, 1912).
- [27] G.I. Shirkova, Collected Transactions of the Institute of Higher Nervous Activity. AN SSSR, ser. physiol. (Moscow, 1956), 2, 75-89.

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