

ON THE STUDY OF MOTOR DEFENSE CONDITIONED REFLEXES

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The method of motor defense conditioned reflexes is widely used in modern physiology laboratories. It was first employed by V. P. Protopopov [10], and was later radically improved by other authors. As shown by subsequent work (mainly that of V. P. Petropavlovskii [8] and L. S. Gambaryan [4]), the main essential defect of Protopopov's method was that despite all the animal's response activity, it could not escape the painful stimulus: the flow of current through the paw. The result was that chaotic movements and lifting of the paw between signals developed, which often led to neurotic conditions. Taking this fact into account, V. P. Petropavlovskii introduced a substantial change in the method. In his modification, the current was automatically turned off as soon as the dog lifted its paw to a definite preassigned height, and was automatically turned on when the paw was below this level.

In using Petropavlovskii's method we came to a point where it was necessary to compare conditioned reflex activity in different dogs and in each dog individually during different periods of investigation. Which motor responses should be regarded as greater and better responses and which as smaller and worse? The question arose as to the proper criteria for evaluating and comparing motor conditioned reflexes.

Motor responses studied by Protopopov's method can in general only be evaluated from the quantitative standpoint (over-all description of motor activity), since the animal's response does not free it from the painful stimulus – i.e., does not perform its adaptive role. In Petropavlovskii's method, besides the quantitative characteristics of the reflex, it is also possible to evaluate its biological quality (its adequateness), which in itself is of fundamental importance in evaluating higher nervous activity, as has been repeatedly emphasized in the writings of E. Sh. Airapet'yants [1, 2], P. K. Anokhin [3], and others.

But in published reports to date there is no single system of evaluation, no single scale which would combine the quantitative and qualitative indices of the motor

conditioned reflex and at the same time reflect gradations in these indices. Thus, comparison of different motor reflexes and complete evaluation of these reflexes have been impeded.

With this as a starting point, we have employed a scale from zero to seven in our work, for recording both quantitative and qualitative indices of the motor defense conditioned reflex. Our chief criterion in evaluating this reflex was the history of its development in the animal. Here we took into consideration I. P. Pavlov's statement that as the defense reaction develops it changes in a definite sequence: from its lowest primitive form to the most "expedient" form [6]. In fact, despite all the differences which we have observed in different animals in the process of developing conditioned reflexes by Petropavlovskii's method (disappearance or, on the other hand, prolongation of some phases, etc.), there is a similarity in the main sequence of stages: At first, as we all know, frequent phasic jerks are observed, which assume an increasingly well defined tonic form from one trial to the next. The chaotic, "inexpedient" reaction gradually becomes an "expedient" (under the given conditions) tonic conditioned reflex.

A special analysis of this complex motor reaction [11] has shown that when lifting is phasic, an ordinary conditioned reflex develops in response to the conditioned signal, and when lifting is tonic, a conditioned-conditioned reflex develops. For this reason, phasic lifting, even with a large amplitude of movement, must evidently be rated lower as being less complex and less complete than sharply defined tonic lifting, even though the latter is of small amplitude. In addition, the adequateness of the reflex – i.e., its ability to protect the organism from "threatening danger" (under these conditions – raising the paw to the level at which the current is cut off) – as a qualitative index of conditioned reflex activity is a fundamental and deciding factor in evaluating the reflex, and we have attempted to reflect this in the following scale.

Seven-point scale (characteristics of motor defense conditioned reflex)

Rank	Height and character of motor reaction
0	No lifting
1	Shifting from one foot to the other and back
2	Low, phasic (i.e., not sustained) lifting
3	High phasic lifting
4	Low, tonic (i.e., sustained) lifting
5	Inadequate tonic lifting
6	Adequate, well-defined tonic lifting
7	Above adequate level, well-defined tonic lifting

Each rank corresponds approximately to a definite stage in the development of the conditioned reflex; a higher rank corresponds to a more complete, more adequate conditioned reflex. We are aware that this scale is still far from the desired degree of perfection. But as an attempt to give a simultaneous account and comparison of the quantitative and qualitative aspects of the conditioned motor reaction, it has been used with success in our work.

In recent years, valuable improvements have been made in the method of conditioned motor defense reflexes [4, 9, 12, etc.]. All the authors in question have devoted most of their attention either to the system for giving the unconditioned stimulus, or to the response activity of the animal, or to the recording system, whereas the system for signalling – i.e., for giving the conditioned stimulus – has remained almost unchanged since the time of Protopopov's first work.

In the alimentary, acid, and other methods the conditioned stimulus is necessarily turned off together with the unconditioned stimulus; if not, as is well known, it begins to lose its significance as a signal, and extinctive inhibition develops. In Petropavlovskii's method, the conditioned stimulus continues to act after the current stops flowing to the paw.* Thus, the conditioned stimulus over a period of several seconds is first a signal of the current (while the paw is down), and then a "signal of the absence of current" – i.e., a signal that intentionally should not be reinforced with the electric current so long as the paw is lifted above the adequate level.

Meanwhile, the conditioned stimulus for the defense reaction is not so harmless an agent for the animal that it may easily and quickly change its biological significance. Thus, as Pavlov noted, "the conditioned stimulus is a pure substitute, a pure surrogate for the unconditioned stimulus. In a conditioned elementary reflex, the animal may lick a flashing light bulb, may, so to speak, catch a sound itself in its mouth and eat it, licking its lips and making chewing sounds with its teeth as though it were dealing with food itself" [7]. In our own experiments with defense reflexes, we have also observed this.

For this reason, the most adequate defense reaction for the animal will be that reaction which delivers it

both from the action of the disturbing factor itself and from the signal of the disturbing factor. (In this respect, the general idea introduced by Petropavlovskii in improving Protopopov's method, though correct as far as it went, proved logically incomplete, and its embodiment in the method was also incomplete.)

Guided by this basic proposition, we employed a system in which, when the paw was lifted to the adequate level, the dog turned off not only the unconditioned stimulus but also the conditioned stimulus. Under these circumstances the animal not only protects itself from the disturbing agent, but also removes the signal for this disturbance. When the signal for the current is turned off, a supplementary conditioned stimulus – an illuminated translucent shield – is automatically turned on; it continues to signal as long as the paw remains "under the current" i.e., as long as it is possible for the dog to receive a shock if it lowers its "working limb." If, during this period, the paw is lowered beyond the adequate level, the unconditioned stimulus and the ordinary conditioned stimulus are turned on at the same time that the translucent shield is turned off. The total period of signalling – i.e., the total time of application of the ordinary and supplementary conditioned stimuli – lasts twenty seconds; the current is turned on five seconds after the ordinary conditioned stimulus is turned on. As is shown by the experiments described below, this type of system helps the animal develop conditioned reflexes, and creates more natural experimental conditions.

EXPERIMENTAL METHODS AND RESULTS

We performed the first series of experiments on six dogs in an acoustically deadened room, by Petropavlovskii's method. The voltage applied to the paw from the induction coil was about 30 v, and the current was approximately 15 ma. The motor and respiratory components of the response were recorded with a kymograph. The following conditioned stimuli were used: a bell, a buzzer (differential stimulus), a Pavlov-type tactile stimulator, and a light. Although a large number of trials were made (considerably more than a hundred), we observed more or less clearly defined conditioned reflexes (corresponding to the sixth rank on our scale) in only one dog – and even with this dog we often observed very strong jerking movements in response to the conditioned stimulus, and in the intervals between signals we noted prolonged, large-amplitude lifting of the paw. In the other five dogs, the conditioned reflexes were chaotic and unstable and sometimes disappeared; in the intervals there was barking, and the dogs were

* Strictly speaking, the conditioned signal is still reinforced even in this position (by kinesthetic stimulation from the lifted paw [5, 11, etc.]). But in this case reinforcement is qualitatively different from reinforcement by electric current, about which we shall have more to say.

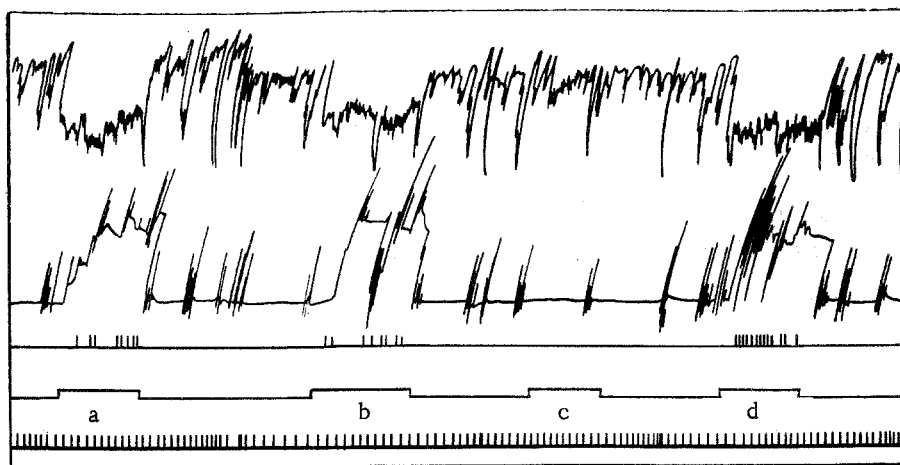


Fig. 1. Motor defense conditioned reflexes, developed by V. P. Petropavlovskii's method. Dog: Ryzhii. Experiment 97 (March 28, 1958). The starting conditioned stimulus – the signal of the current – is applied throughout the entire run. Curves (top to bottom): respiratory movements; lifting of paw; unconditioned stimulus; conditioned stimulus; time (2 seconds). a) Bell (+); b) Tactile stimulator (+); c) Buzzer (-); d) Light (+).

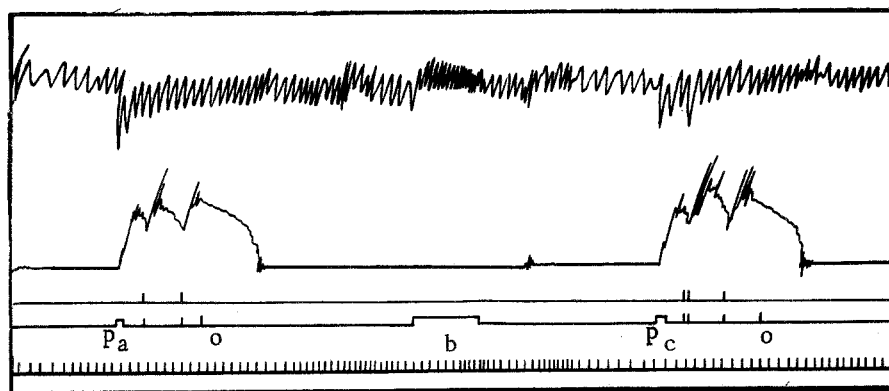


Fig. 2. Motor defense conditioned reflexes, developed by our new modification of the method. Dog: Dik. Experiment 23 (January 3, 1959). The starting conditioned stimulus – the signal of the current – is turned off by the animal itself. There is no special marker for the action of the stop-signal (illuminated translucent shield) on the kymograph record; it turns on at the instant the starting conditioned stimulus is turned off, and vice versa. Significance of records same as in Fig. 1. p-period of delay of conditioned reflex (adequate level); o-instant when experimenter turned off all stimuli, terminating run. a) Bell (+); b) Buzzer (-); c) Light (+).

constantly excited throughout the entire experiment (Fig. 1).

We performed a second series of experiments on three dogs, using our new variation of the method. The over-all experimental conditions remained the same, but the conditioned reflexes, as a rule, were marked by a high degree of definition and adequateness, and the animals behaved much more calmly during experiments (Fig. 2).

Thus, our Pavlovian guiding principle concerning the biological significance of conditioned reflex activity,

together with an experimental comparison of the two versions of Petropavlovskii's method, has led us to prefer the version that we are proposing. Besides the advantages indicated, with our modification it is possible to determine the delay period of the adequate conditioned reflex – i.e. the time from the moment when the conditioned stimulus (the signal of the current) is turned on to the moment when the paw is raised to the adequate level – with quite a high degree of accuracy (to 0.1–0.2 seconds). Since this lifting of the paw coincides precisely with the turning off of the conditioned stimulus (which is also

marked on the kymograph record), the delay period is readily measured with calipers (see Fig. 2, distance p). In this way the technical difficulty of precisely determining the delay period, which Petropavlovskii himself noted with regret, is greatly reduced.

In motor defense conditioned reflexes, one interesting and important feature should be emphasized, which pertains to the specific role of the conditioned stimulus after the paw is lifted to the adequate level. In an actual display of a previously developed conditioned reflex, two qualitatively different periods can be observed: 1) When the conditioned stimulus is turned on, it signals the approach of the current – it evokes a conditioned lifting of the paw; 2) the paw is lifted above the adequate level – now the conditioned stimulus is no longer the signal of the current, since the current was turned off earlier by the animal itself. Therefore, during the second period, the biological role of the conditioned signal is qualitatively different from what it was during the first period.

The same can be said of the organism's response activity and over-all condition. This is evidenced not only by the behavior of the animal (for example, a momentary quieting of the excited animal after the paw is lifted), but also by the autonomic component of the conditioned reflex (see the record of respiratory movements in Fig. 2). The defense conditioned stimulus evokes a sharp, deep inspiration, which has been observed repeatedly by many authors. When the paw is lifted, respiration gradually returns to normal. † Whereas, during the first period, the conditioned stimulus sets the defense apparatus in motion, as it were (in particular, local movement of the stimulated limb ensues), in the second period, on the other hand, the conditioned signal arrests this movement at the height of lifting – the animal freezes, so to speak, in an unnatural pose. Therefore, in contrast to ordinary starting signals, the conditioned stimulus that is applied after the paw is lifted plays a correcting role. It might be called a stop-signal.

Thus, in our experiment, states of the animal that are qualitatively different biologically are signalled by different stimuli. Besides what we have said above, this allows us to study the characteristics of motor defense conditioned reflexes more fully.

SUMMARY

A modification of Petropavlovskii's method of studying motor defense conditioned reflexes is suggested. A seven-point scale is employed for better evaluation

of conditioned-reflex activity, taking into consideration the relationship between the quantitative and qualitative indices of the conditioned motor reaction, and for comparison in graphic form of the results of experiments by the same motor method. To create more natural experimental conditions for the animal, the author suggests a system in which the animal, by raising its paw, turns off both the unconditioned and conditioned stimuli, and simultaneously turns on an illuminated translucent shield, which plays the role of a correcting signal.

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† It is noteworthy that when the ordinary conditioned stimulus continues to be applied after the paw is raised, respiration shows either a limited tendency or none whatever to return to normal (see Fig. 1). But if the signal of the current is turned off when the paw is raised, respiration quickly returns to normal (see Fig. 2).