Changing Concepts Concerning Physiological Mechanisms of Animal Motor Behaviour

BY

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INTRODUCTORY REMARKS

AT the beginning of this century, when Pavlov undertook bis gigantic research work on the physiology of higher nervous actiyity, hę selected a particular type of response called by him conditional (or in English "conditioned") reflex (hereafter denoted as CR) which he considered a simple and general model of acquired animal behaviour. This type of response is formed when any stimulus is followed a number of times— "is reinforced"—by some particular stimulus eliciting a specific, inborn (unconditioned) effect and consists in the first stimulus starting also to elicit the same effect. The extensive research work carried out over several decades by Pavlov and his co-workers was almost exclusively devoted to the study of alimentary and acid CRs, the salivary effect being used as the main quantitative indicator. Nevertheless, Pavlov was strongly convinced that the results obtained in experiments with these reflexes were representative of *all* kinds of CRs, based on other reinforcing agents, and also that the properties of this type of response are representative for the whole animal acquired behaviour. Although Pavlov was fully aware that the chief part of this behaviour consists of *motor* activity, he deliberately rejected the idea of using motor CRs in his experimental work, judging that they could provide too strong a temptation to anthropomorphic and psychological speculations, which he wished to avoid at all costs. On the basis of their experimental findings, Pavlov and his co-workers attempted to unravel the general mechanisms of the function of the brain in much the same way as, through experimentation on spinal reflexes, his great contemporary Sherrington

attempted to unravel the general mechanisms of the function of the spinal cord.

Pavlov's first assumption, namely that the results obtained on alimentary CRs are valid for all other CRs of the same type, has proved to be right— hence the tremendous applicability of Pavlovian "laws" for research work in this field, especially now that it has been resurrected by combining it with EEG methods. However, the second assumption, claiming that Pavlovian conditioning may stand as a model for the *whole* of the animal's acquired behaviour, is considered now by the majority of students working in this field as incorrect. As far as I know, Miller and I (Miller and Konorski, 1928; Konorski and Miller. 1933) were the first authors to demonstrate that motor behaviour of animals, based on the "reward" and "punishment" principle, is distinct from, and cannot be reduced to Pavlovian CRs. In consequence we attempted to produce a CR model for this type of behaviour, to investigate its properties in the same way as Pavlov's group did in respect to the "classical" CR, and to understand its physiological mechanism.

When we started our analysis of animals' motor behaviour, the extensive research work of American behaviourists dealing with animal motor behaviour was already in progress. However, according to their tradition and scientific attitude they were rather reluctant to enter into a physiological interpretation of their results, and our own papers, published chiefly in Polish and Russian, could have hardly any influence upon their line of investigation. On the other hand, the Pavlovian group did not accept our concepts because they claimed the principal difference between the classical CRs and those reflexes we were working on. In consequence, the systematic studies of the acquired motor behaviour from the physiological point of view had been, as far as I know, not undertaken by other authors. And so, before the war I worked on this problem with Miller quite alone, and after the war a number of younger people joined me in this enterprise. Although the new facts obtained in recent years in our laboratory have changed considerably our previous views, it seems worthwhile to present here the development of our ideas from the very beginning together with their respective experimental documentation. This is the subject of this lecture.

CONDITIONED REFLKXES TYPE II, VERSUS CONDITIONED REFI.EXES

TYPE: I

The thesis claiming that Pavlovian CRs are not sufficient as a model ft the whole acquired animal behaviour can be demonstrated *a priori* by the following consideration. According to the Pavlovian general

scheme, the basic functional role of the CR is that of signalization. This means that besides a relatively limited number (definite for a given species) of biologically significant agents, eliciting particular inborn or unconditioned reflexes (UCR), there is an indefinite number of indifferent stimuli, hitting the organism chiefly through distance-receptors and becoming "signals" of those agents when they happen regularly to precede them. According to this scheme, the efferent side of the reflex arcs is relatively rigid and unchangeable, while the only plastic, variable, and, one should say, *creative* part of the central nervous system is its afferent part.

But is it really so ? Common observation of animals reveals that their individual motor behaviour is far from being rigid and unchangeable, that it evolves greatly during their life, and surely does not reproduce only those patterns of responses which are established in the UCR arcs. As is well known, this behaviour is developed mostly by trial and error, i.e. by fixation of those behavioural patterns which lead to positive effects and elimination of those leading to negative effects. So, while it is quite possible that *autonomic* reactions really follow Pavlovian principles exactly, i.e. may be elicited either by specific stimuli or by their conditioned signals, *motor* reactions on the contrary follow quite different rules and possess quite different properties. Miller's and my first aim was to construct CR experiments in which these characteristics of acquired motor reactions would be manifested.

TABLE I.—FOUR VARIETIES OF TYPE II CONDITIONED REFLEXES

	Experimental setting		Results
1	$(S_e + M)$—food	S_e—no food	$S_e \rightarrow\ M$
2	$(S_e + M)$—acid	S_e—no acid	$S_e \rightarrow \backsim M$
3	S_e —food	$(S_e + M)$—no food	$S_e \rightarrow \backsim M$
4	S_e —acid	$(S_e + M)$—no acid	$S_e \rightarrow\ M$

S_e, exteroceptive stimulus

M, movement provoked

$\backsim$ M, antagonistic movement

→, elicits

—, is followed by

Our solution of this problem was as follows (Table I): If in an experimental situation, schematically represented in fig. 1, an exteroceptive stimulus S_e is combined with a movement M produced in any manner (for instance, by passive displacement of the limb) and then reinforced by a positive agent (such as food for the hungry animal, or water for the
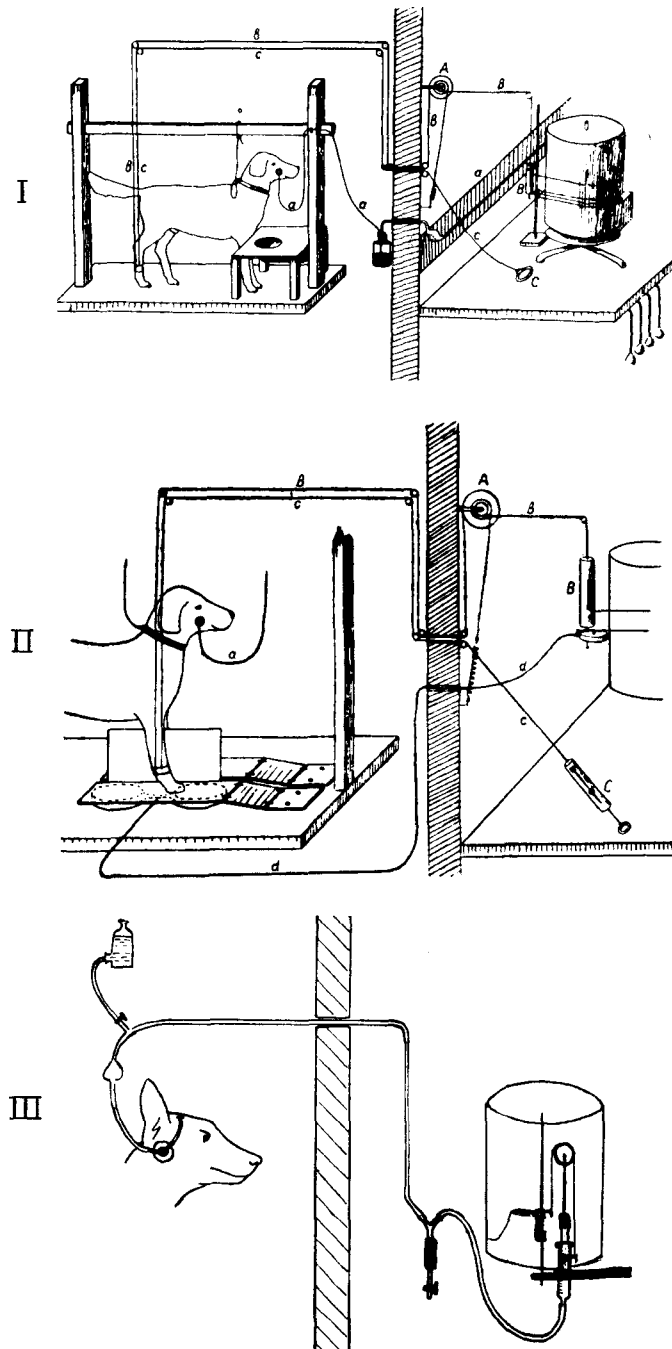
FIG. 1. Legend bottom of facing page.

thirsty animal), while the stimulus applied alone is not reinforced, then after several repetitions of such trials the animal will start to perform the movement M in response to the stimulus S_e (fig. 2a). If however an exteroceptive stimulus S_e is combined with a passive movement M and then reinforced by a harmful agent (such as introduction of acid into the mouth, an electric shock, etc.), while the stimulus alone is not reinforced, then after some repetitions of such trials the animal will perform the antagonistic movement designed as M (fig. 2b).
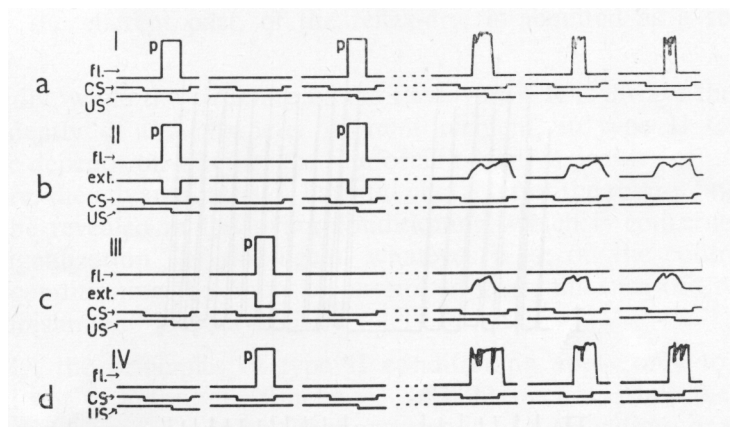

FIG. 2.—Four varieties of type II CR (semi-schematic). On the left, period of elaboration of a reflex; on the right, period of the reflex being established. Explanations: fl, flexion of the leg; p, passive flexion; ext., extension of the leg (as measured by the device shown in fig. 1, II); note that if the leg is flexed the tracing goes down; CS, conditioned stimulus; US, unconditioned stimulus (food in a and c, introduction of acid into the mouth in b and d).

On the contrary, if stimulus S_e presented alone is reinforced by food, while the stimulus accompanied by the movement M is not, the animal will learn to perform the antagonistic movement (fig. 2c). If, however, stimulus Se is reinforced by acid, and is not reinforced when accompanied by the movement M, the animal will learn to perform this movement in response to the application of the stimulus S_e (fig. 2d).

The stimulus S_e may be either a sporadic exteroceptive stimulus (auditory, visual, etc., analogous to those used in classical Pavlovian experiments) or it may be a continuous stimulus, for instance the whole experimental

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FIG.1.—Experimental set-up for the study of type II CR (semi-schematic). I. General view of experimental set-up; a, apparatus for recording salivary reactions; b, apparatus for recording flexion of the hind-leg; c, device for producing passive movements. II. Apparatus for recording extension of the fore-leg (d). C, dynamometer measuring the resistance of the animal against lifting its leg. III. The new improved technique for recording salivary reaction developed by Kozak (1957). (I and II taken from Konorski and Miller, 1936.)

situation. Let us see what will happen in this last case. The animal placed in the experimental situation is compelled in one way or another to perform some movement, and whenever this movement appears it is reinforced by food. The situation itself is not reinforced. As a result the animal will start to perform the movement actively in this situation, and after some training it will do so with maximal frequency depending on the duration of intake of food presented after each movement (fig. 3).
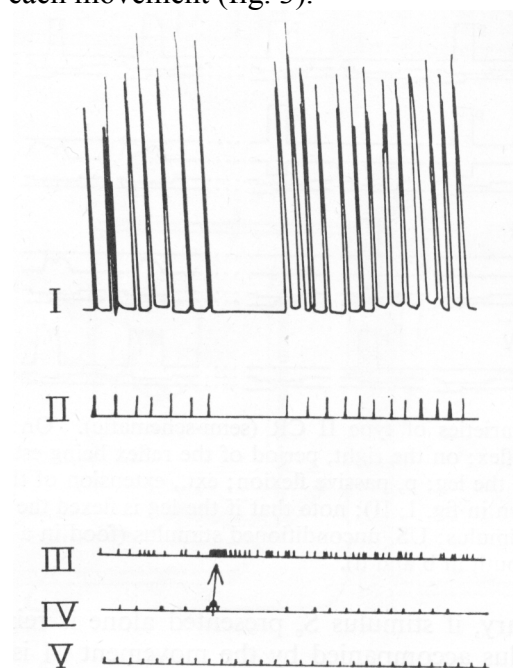

FIG. 3.—CR type 11 (first variety) established to experimental situation. I, active lifting of the fore-leg; If, putting the leg on the platform; III, salivation in drops; IV, presentation of food; V, time (5 sec.). Arrow denotes the moment of presentation of the increased portion of food. (From Konorski and Miller, 1933.)

We have called the type of motor CRs represented in Table I and fig. 2 *conditioned reflexes type II to* distinguish them from Pavlovian CRs. which we called type 1. They were later called instrumental conditioned responses, as opposed to classical conditioned responses, by Hilgard and Marquis (1940), and operant behaviour, as opposed to respondent behaviour, by Skinner (1938). It is easy to see that these four varieties make up simple models of animal motor behaviour and of those types of reactions which have been utilized, usually in more complicated forms, in numerous behaviouristic experiments, beginning with Thorndike.

It can be proved that the physiological mechanism of type II CRs, whatever it is, is different from that of Pavlovian CRs. First, in classical conditioning only the conditioned stimulus (CS) is different from the unconditioned stimulus (UCS) being chosen arbitrarily by the experimenter, while the effect faithfully reproduces the effect of the UCR. On the other hand, in type II conditioning both the stimulus *and* the motor effect are different from those in the UCR. In other words, in type II conditioning not only the afferent part (as in conditioning type I), but also the efferent part, of the reflex-arc, is acquired as a result of training.

Secondly, while the structure of the Pavlovian CR is always the same, independently of the character of reinforcement, in type II CRs the structure depends on whether the reinforcing agent is positive or negative. Therefore, the advantageous or harmful character of the reinforcing agent cannot be revealed in Pavlovian conditioning, which is concerned only with "signalization" of this agent, whatever it is; on the contrary, in type II conditioning the opposite physiological significance of "reward" and "punishment" plays a decisive role.

Thirdly, the principles of type II conditioning apply only to motor acts and not to autonomic functions. In consequence, while the type I conditioned response may be either autonomic (e.g. salivation) or somatic (e.g. flexion of the leg when the reinforcing agent is an electric shock delivered to the paw), the type II conditioned response consists only of *movements.* One should realize that the participation of motor responses, and not autonomic responses, in the type II CRs makes the chief, and maybe the only, *physiological* difference between the somatic and autonomic functions.

ROLE OF PROPRIOCEPTION IN TYPE II CONDITIONING

As mentioned before, the initial provocation of a movement designed for type II conditioning may be accomplished in a variety of ways: it may be elicited as an effect of some unconditioned reflex (Thorndike, 1911); it may be brought about by passive displacement of the limb or the body (Konorski and Miller, 1933); or else it may be produced by stimulation of the sensorimotor cortex by implanted electrodes (Loucks, 1936; Konorski and Lubinska, 1939; Tarnecki, 1960). The common feature of all these procedures is that the movement has been *accomplished,* i.e. that proprioceptive stimulation generated by its performance has been produced. Therefore, the assumption seemed to be reasonable that the *sensation* of the trained movement is an indispensable condition for the elaboration and occurrence of the type II CR. This assumption was corroborated by a general belief, based both on experimental evidence and clinical data, that proprioception (or indeed any other feed-

back. e.g. visual) is indispensable for the performance of so-called "voluntary" movements.

According to this assumption our principles of the formation of type II CRs had to be extended, and should now run ;is follows (Table II).

TABLE II.—INTERRELATION BETWEEN TYPE I AND TYPE II CONDITIONED REFLEXES

	Experimental setting		CR type I	CR type II
1	(S_e+S_M)—food $\downarrow$ saliva	S_e—no food	(S_e+S_M) $\downarrow$ saliva	S_e $\downarrow$ M
2	(S_e+S_M)—acid $\downarrow$ saliva	S_e—no acid	(S_e+S_M) $\downarrow$ saliva	S_e $\downarrow$ $\backsim$ M
3	S_e—food $\downarrow$ saliva	(S_e+S_M)—no food	S_c $\downarrow$ saliva	S_e $\downarrow$ $\backsim$ M
4	S_e—acid $\downarrow$ saliva	(S_e+S_M)—no acid	S_e $\downarrow$ saliva	S_e $\downarrow$ M

S_e, exteroceptive stimulus

S_M, proprioceptive stimulus

M, movement provoked

$\backsim$ M, antagonistic movement

$\rightarrow$, elicits

—, is followed by

(1) When a compound composed of the exteroceptive stimulus S_e. and proprioceptive stimulus S_M generated by the movement M is reinforced by a positive agent, e.g. *food.* eliciting unconditioned salivary reaction, while the stimulus S_e applied alone is not, then on the one hand, according to the principles of Pavlovian conditioning. CR type I is formed to the compound $S_e + S_M$ which will now produce a conditioned salivation, while stimulus S_e alone will be differentiated, but on the other hand CR type 11 will he established consisting in stimulus S_e evoking now the movement M.

(2) When the compound $S_e + S_M$ is reinforced by a negative agent such as introduction of *acid* into the animal's mouth, eliciting also unconditioned salivation, while stimulus S_e alone is not, then the CR type I will be formed to the compound S_e+S_M, which will now produce salivation as in the preceding case, but on the other hand CR type II will be established, consisting in stimulus S_e evoking a movement antagonistic to movement M.

(3) When stimulus S_e applied alone is reinforced by *food,* but the compound S_e+S_M is not, then on the classical conditioning level the differentiation between S_e and S_e+S_M will occur, stimulus S_M becoming the so-called conditioning inhibitor, and on the type II conditioning level stimulus S_e will evoke the movement antagonistic to M.

(4) When. however, stimulus S_e is reinforced by *acid,* while the compound S_e+S_M is not, then on the classical conditioning level the same response will occur as in case 3, but on the type II conditioning level stimulus S_e will evoke the movement M.

To generalize these principles one may say that when a proprioceptive stimulus becomes the indispensable complement to a conditioned compound stimulus signalling a positive reinforcement, or to an inhibitory compound stimulus signalling the lack of negative reinforcement, the movement generating this proprioceptive stimulus is elicited by the other component of the compound; on the other hand, when a proprioceptive stimulus becomes the indispensable complement to a conditioned compound stimulus signalling a negative reinforcement, or to an inhibitory compound stimulus signalling the lack of positive reinforcement, the movement antagonistic to that generated by the proprioceptive stimulus is elicited by the other component of the compound.   Many data supporting this conception were gathered by us in the course of our studies concerning type II CRs. Here we shall discuss only some of them, concerning the first variety of these reflexes.

Let us begin with the simplest case, namely elaboration of a type II CR to the experimental situation (cf. fig. 3). Here the situation alone (S_e) is not reinforced by food, but when it is complemented by the proprioceptive stimulus S_M, generated for instance by passive flexion of the leg. the reinforcement is presented. After a number of such trials we may observe that stimulus S_M begins to elicit salivation and turning towards the food tray, i.e. the type 1 conditioned reaction. At approximately the same time the flexion of the leg begins to appear actively in that situation (Konorski and Miller, 1936).

More complicated is the case in which a type II CR is elaborated to a sporadic stimulus (Konorski and Miller, 1933, 1936).   Let us suppose that we begin our experiments by applying only the compound S_e+S_M (S_M being provided by the passive flexion of the leg) and reinforcing this compound by food. After a number of such trials we observe the following state of affairs: (1) to stimulus S_e the animal salivates and turns towards the food tray; (2) the same occurs in response to the passive flexion produced alone; (3) the animal begins to perform the movement M actively, but does so only in intertrial intervals and never to stimulus S_e

This picture is, in terms of our concept, easy to understand. When the compound stimulus S_e+S_M is reinforced by food, both S_e and S_M become CSi "on their own account." In consequence of stimulus S_M becoming a CS in the experimental situation, movement M is performed actively in this situation. Since stimulus S_e is itself a signal of food and evokes a direct alimentary reaction, movement M is inhibited in the presence of this stimulus.

And so we see that simple combination of S_e with S_M reinforced by food does not lead to the elaboration of the type II CR $S_e \rightarrow M$. In order to achieve this aim one must apply also from time to time stimulus S_e alone without reinforcement, i.e. to inhibit partially the type I CR to this stimulus and to make stimulus S_M a necessary complement to the compound CS. After applying this measure the movement M begins to appear more and more regularly in the presence of stimulus S_e, and this
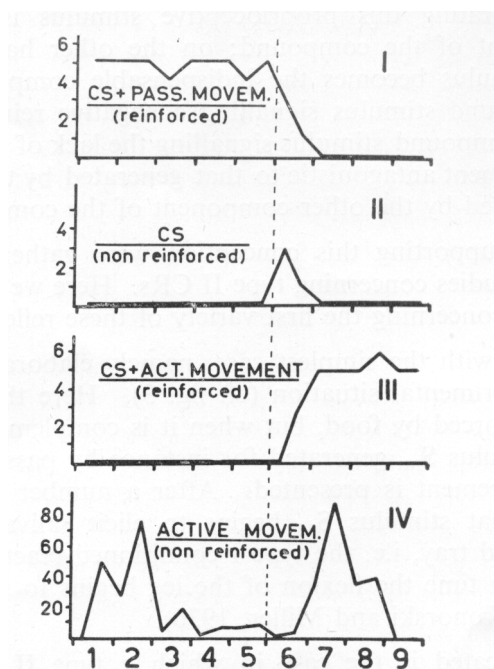

FIG. 4. -The course of elaboration of type II CR (first variety) to sporadic stimulus. Abscissae, experimental sessions; ordinates, numbers of particular types of trials as indicated in the graphs. Note that in the first stage of experiments (on the left of broken line) only the compound of stimulus and passive movement reinforced by food is applied (I). Active movements appear only in intervals (IV), but not to the stimulus (III); these movements not being reinforced gradually disappear. In the next stage (on the right of broken line) CS without passive movement and without reinforcement is also applied (III. This leads to the formation of type 11 CR to CS (III); active movements in intervals temporarily reappear, but not being reinforced they again disappear (IV). (From Konorski and Miller, 1936.)

movement performed at intervals is gradually extinguished. So the type II CR $S_e \rightarrow M$ is eventually established (fig. 4, cf. also fig. 7b).

A further group of facts supporting our hypothesis is brought out in experiments dealing with inhibition of type II CRs. If we extinguish a reflex $S_e \rightarrow M$ by non-reinforcement, we observe that motor (type II) and salivary (type I) reaction disappear more or less simultaneously (fig. 5). The same occurs during differentiation. A stimulus similar to
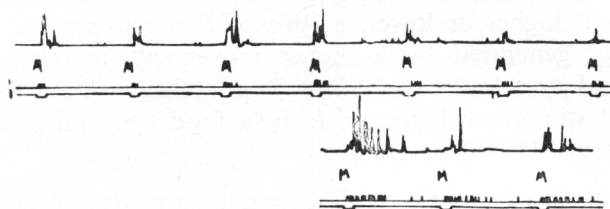

FIG.5.—Extinction of type II CR (first variety) to a sporadic stimulus. From top to bottom: record of motor reaction of the foreleg, salivation, CS. The beginning of extinction is represented on the lower graph. Note that first applications of the unreinforced CS produce abundant salivation and repeated movements of the leg. Gradually both the salivary and the motor reaction decrease more or less (but not quite) in parallel. (From Konorski and Miller, I936).
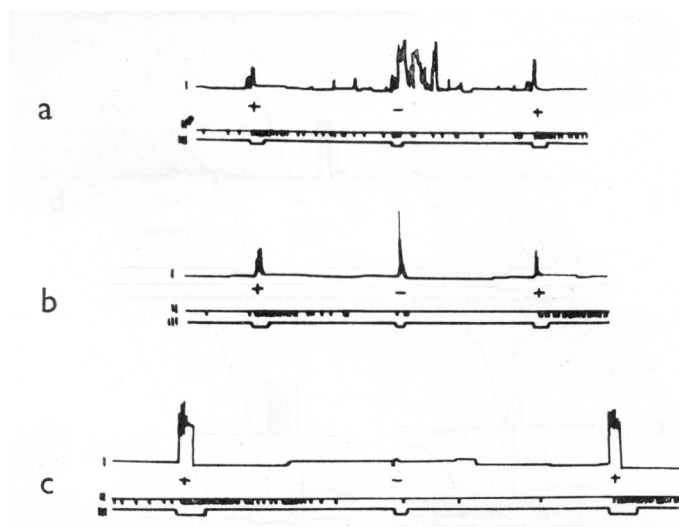

FIG. 6.—Differentiation of type II CR. Fragments of records of three experiments of a series are shown, in which CS in the first and the third trial is reinforced and the stimulus similar to CS in the middle trial is not reinforced. In each graph from top to bottom: record of movements of the fore-leg, salivation, CS positive or inhibitory. a, 2nd application of differentiated stimulus: abundant salivary reaction and vigorous movements of the leg; b, 9th application of differentiated stimulus: only one movement of the leg and moderate salivation; c, 47th application of differentiated stimulus: no movement and nearly no salivation, (From Konorski and Miller, 1936.)

the CS originally elicits both motor and salivary reaction, but not being reinforced stops doing so after approximately the same number of trials (fig. 6). This again may be explained as meaning that the movement M stops appearing when the type I CR to the compound S_eS_M is inhibited.

To give a last example: Having a conditioned compound stimulus S_e+S_M, we may differentiate not only stimulus S_{e1} from stimulus S_{e2} (as shown before), but also stimulus S_{M1} from a similar stimulus S_{M2}. In this way we are able to *shape* the motor response according to our will. making it higher or lower, of this or that pattern, etc. Indeed, if stimulus S_{M1}, generated by a higher movement, is reinforced, while S_{M2} generated by a lower movement, is not, then we have to expect that only the first stimulus will remain to be a food CS, and in consequence only movement Ml will be executed.

If one looks retrospectively at all these data. and also takes into account some new results obtained later in our laboratory, one sees that not all the facts fit so neatly into the postulated theory, as advocated in the above paragraphs.   For instance, now and again we observed some obvious discrepancies between the salivary and motor reactions; in some cases the trained movement was performed by the animal, but was not accompanied by salivation (fig. 7d), while in others, on the
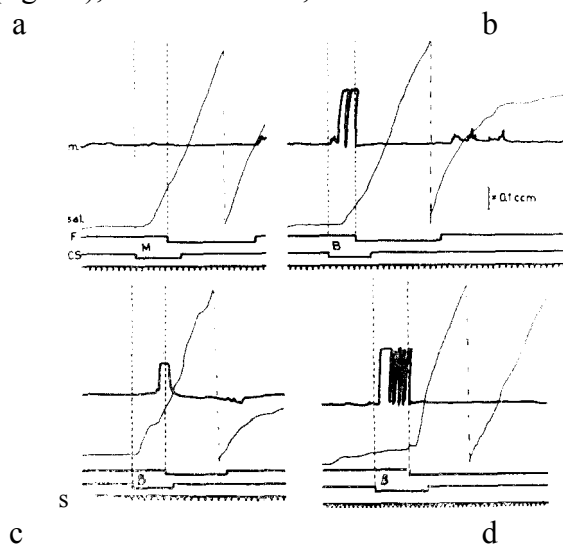

FIG. 7.—Various interrelations of type II and type I conditioned responses. In each graph from top to bottom: motor reaction, salivation (according to W. Kozak's method), food presentation, CS, time in sec. a, type 1 CR to metronome; b, c, d, type II CRs to buzzer. Note that in b salivation begins only after the initiation of movement (normal case), while in c salivation begins earlier than the movement, and in d strong motor reaction is not accompanied by salivation, which begins only after the presentation of food. (From experiments of S. Soltysik.)

contrary, salivation occurred already in response to stimulus Se and well preceded the appearance of the movement (fig. 7c).

Nevertheless the strong explanatory power of our concept left us in no doubt that it was true, the more so that it was in full agreement with the generally accepted and intuitive view claiming that proprioception *is* indispensable for voluntary movements. In fact, we believed that the essence of the so-called voluntary character of somatic movements is due to the fact that they are connected with *sensation,* in contradistinction to the autonomic reactions, such as secretion, or contraction of smooth muscles, which as a rule are not.

Perhaps the strong belief in the correctness of this concept has restrained us from making a decisive and most direct test, namely proving that deafferentiation of the limb taking part in the trained movement would really lead to its abolition. We thought that there was enough evidence in the literature that it is so. and that special experiments to this effect were not needed. Therefore, when Jankowska undertook such experiments in our laboratory, 1 had no doubt whatsoever as to their issue.

EXPERIMENTS WITH DEAFFERENTIATION OF THE EFFECTOR OF

TYPE II CONDITIONED REFLEX

The first series of experiments performed by Jankowska (1959) on cats and rats ran as follows.   The animal was placed in the experimental cage, and a piece of cotton-wool was put into its right ear. In response to this stimulus the animal performed scratch movements with its right hind-leg, each movement being immediately reinforced by food. After a number of such trials it was observed that scratch responses were followed by turning the head towards the source of food, i.e. the type I CR was established to a stimulus generated by scratching. At the same time putting the cotton wool into the ear became superfluous, since the animal started to perform the scratch movements (usually in a more or less simplified form) spontaneously after having been brought to the experimental cage. When this type II CR had been firmly established, the right hind-leg was differentiated by cutting the dorsal roots from L_1-L_4 to S_4 in cats and from Th_{12} to L_6 in rats. The result was that as soon as the animal recovered from the operation and was placed in the experimental cage, it began to perform the conditioned scratch movements in more or less the same fashion as before operation. These movements had no tendency to disappear with the lapse of time.

Our first idea after obtaining these results was that perhaps our concept of the mechanism of the type II CR is correct only as far as its *elaboration* is concerned. We thought, however, that after the reflex has been established it may not need further proprioceptive feedback, since the

necessary intercentral connexions with the corresponding motor centres had been already formed.

Since, as is well known, the unconditioned scratch reflex does not need proprioception of the limb for its occurrence, it was possible to test this assumption quite easily. The hind-leg of the cats was differentiated *before* the CR training; then by means of putting cotton-wool into the ear the scratch reflex, of course much less precise than in normal animals, was elicited, and each such pseudo-scratching was reinforced by food. After several days of such a training the animals learnt easily to perform the analogous movements instrumentally just as they did in normal conditions. Similar results were obtained in rats. So this assumption turned out to be wrong.

However unexpected these results were, we consoled ourselves by another supposition: perhaps the conditioned scratch reflex, being established from the unconditioned scratch reflex, has some particular properties, for instance that it is based not on proprioception of the movement but on the conditioned sensitization of the skin receptive field. Therefore, it was necessary to repeat such experiments in dogs in a typical experimental set-up used in studies of type II CRs, resorting to passive flexion as means of elaborating these reflexes.

These decisive experiments were undertaken by Gorska and Jankowska (1960, 1961). They trained dogs to lift either the fore-leg or the hind-leg in response to given sporadic stimuli, in some animals by means of food reinforcement (first variety of type II CRs), in others by means of avoidance technique (fourth variety). When the reflexes were firmly established, differentiation (from L_1-L_3 to S_4-Coc_1) of the respective limb was accomplished.

The results obtained in all the dogs were quite unequivocal. Although in the general behaviour of the animal the differentiated leg was practically useless, in the experimental situation the animals were able to perform the trained movement with the affected leg (fig. 8, Plate XVIII). This reflex did not vanish with the lapse of time, although some changes in the pattern of the movement used to occur in connexion with the increase of the extension tonus in distal joints.

The last type of experiment, though performed so far on only one animal by Tarnecki (unpublished), was the following: After deafferentation of the left fore-leg of a cat, chronic electrodes were implanted on the right motor cortex corresponding to the fore-leg area. Then in the experimental situation the cortex was stimulated, the movement of the fore-leg elicited and each time reinforced by food. Very soon the animal learnt to perform this movement instrumentally, so that electric stimulation was withdrawn (fig. 9).

One would ask of course why is it that in experiments of our laboratory the trained movements of the deafferentated limb appeared so regularly, and even, to some extent, skilfully, while in experiments of old authors, for instance those of Mott and Sherrington (1895), the "voluntary" movements of such a limb were hardly performed at all. It is not difficult to provide a reasonable answer to this question.

So-called "voluntary" movements of the animals are, according to our view, nothing else but "natural" type II CRs displayed in certain conditions. These reflexes, in contradistinction to the "artificial" ones established in experimental practice, are usually *ambidextrous,* i.e. they can be performed with the same skill with both right or left limb. For instance, when a cat has to draw in food from outside the cage, and uses preferably the right fore-leg for this aim, it will immediately switch to the left one if by some means the right leg is immobilized or its movements are ineffective. On the contrary, when the animal has been "artificially" trained to perform a movement with a given leg (as is the case in our usual CR procedure), non-reinforcement of this movement never leads to attempts to perform the same movement with the symmetrical leg. The same is seen after unilateral ablation of the sensorimotor cortex. After operation all the "natural" movements are performed almost exclusively with the unaffected limb, as if the affected one were paralysed (Jankowska and Gorska, 1960). On the other hand, all "artificial" trained movements are executed only with the same leg as before, however hard it is for the animal to use the paretic limb for this purpose (Stepien *et al.,* 1961).

And so it is quite understandable that in the case of deafferentation we encounter the same state of affairs: since for many "purposeful" natural motor acts the affected limb becomes useless, the animal immediately starts to perform them only with the normal one, while all the movements specially trained to be performed only with one limb are still executed after deafferentation.

How are all these results to be explained?

First, one may suppose that after deafferentation the animal performs the trained movement under the guidance of vision instead of proprioception, even if the hind-leg and not the fore-leg is used. But this was ruled out by obscuring the animal's eyes.

Then it may be supposed that the sensations from the whole body may play a role of the feedback sufficient for the performance of this movement. Indeed, when the animal lifts its leg, the whole balance of the body is changed, the pressure of other feet on the ground is increased, and so on. This assumption, however, although not quite disproved, seems to be improbable for the following reasons. Even if in a normal

animal the sensation of a particular movement *is* provided by the whole body, undoubtedly the most important part of the feedback is supplied by the proprioception of the movement itself. Therefore, after deafferentation of the limb some reorganization of the whole structure of sensation should take place, as is the case, for instance, when the animal or man is deprived of one receptor and has to learn to utilize another one for the same aim. In consequence, in such a case we should expect that the motor CR would deteriorate after operation, and then gradually recover when other receptors were involved. But here rather the contrary is true, namely, the movement is present *from the very beginning* and its alteration occurs afterwards with the development of the rigidity of the limb. Therefore, we have to admit that peripheral feedback is not indispensable for the execution of a simple voluntary movement, i.e. for the display of the type II CR.

If so it seems that two possible explanations of the facts obtained may be offered. One would preserve in principle our old concept of the mechanism of type II conditioning, however in a modified form. We have good anatomical evidence to suppose that besides the peripheral feedback mediated by afferents and informing the brain about the *execution* of movements, there may exist also a central, abridged feedback informing the brain that the movement has been *initiated,* i.e. that messages have been sent forth from the respective motor centres. One of such abridged loops is formed by collaterals sent off from the pyramidal tracts to the gracilis and cuneate nuclei and hence back to the sensory cortex (Kuypers, 1960). Another loop is formed by pathways leaving the motor-premotor cortex, running through the pons to the cortex of the cerebellum, hence to the dentate nucleus, then through brachia conjunctiva to the ventrolateral nucleus of the thalamus and back to the precentral cortex. Therefore, a problem of first importance arises—whether these loops, or some others too, play a decisive role in the elaboration and maintenance of type II CRs in those cases in which their effects consist of simple and unitary movements. This problem is now being studied in our laboratory.

If the supposition put forward above proves to be wrong, there remains a last possibility that the proprioceptive feedback, either in its full or abridged form, is not needed at all for the formation and maintenance of type II CRs. To put it more clearly, according to this view the type II CR is supposed to be formed not *because* the proprioceptive stimulus has become a type I CS, but on the contrary, a type I CR to this stimulus is formed and maintained because the movement is being performed and reinforced. In such a case, the conditioned connexions responsible for the type II CR would run directly from other centres involved in conditioning to the motor centres representing the highest control of a

given motor act. The important consequence of this view is that a *true* passive movement without any reflex component could not be a source of type II CR, and that in our usual experimental procedure conditioning was possible because pulling the leg upwards elicited Sherringtonian "shortening reflexes."

Both hypotheses outlined above do not in the least put in doubt the important role played by proprioception in all motor behaviour. First, this behaviour usually consists of chains of reflexes in which proprioceptive links are indispensable. It is clear then that after a removal of these links the given sequence of movements is rendered impossible. Secondly, all refinements of movements, giving them a skilful character, are again due to proprioception, and therefore are lost after deafferentation. But it should be noticed that the above role played by proprioception in the performance of motor acts is exactly the same whether these acts are conditioned or unconditioned. In this connexion it is worth stressing that the instrumental scratch reflex was changed and simplified after deafferentation in exactly the same way as was the unconditioned scratch reflex.

SUMMARY

To summarize these considerations we should fully accept the concept that proprioception plays an important role in motor acts, either innate or acquired, as a large source of stimuli eliciting these acts or adjusting them properly in the course of their execution. However, we cannot attribute to proprioception any special role connected with *execution* of the learnt movements. As a rule, these movements are established in response to other modalities of stimuli, and neither the feedback of their "starting state" nor of their course is needed for their performance.

It is clear that only now, after the realization of the true scope of the involvement of proprioception in learning and performance of "voluntary" movements the proper investigation of the physiological mechanism of their control may begin. This should be an important subject of future investigation.

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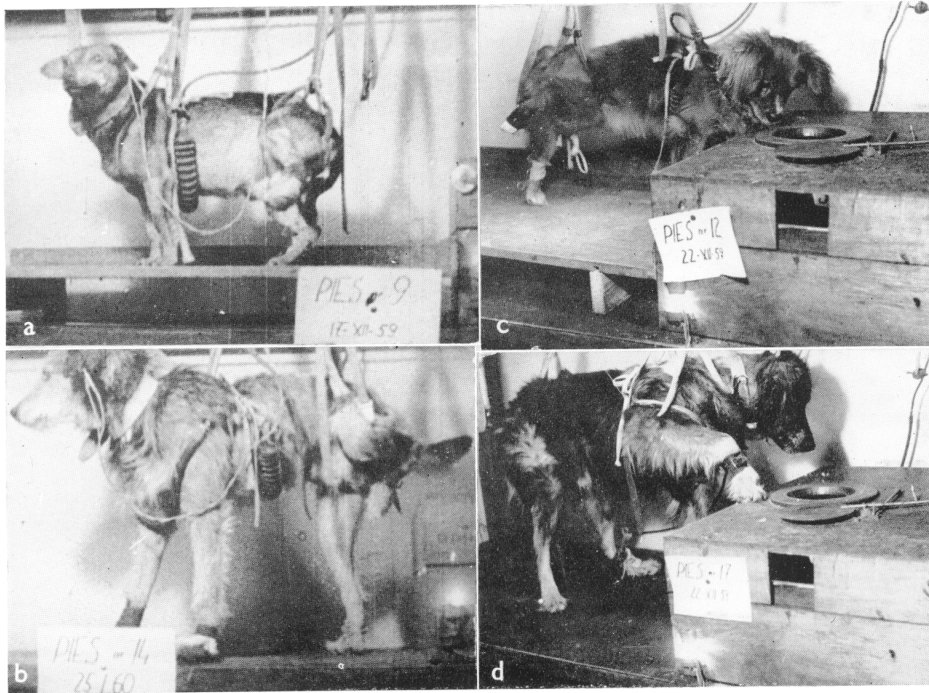THORNDIKE, E. L. (1911) "Animal Intelligence; Experimental Studies." 297 p.
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Fig. 8.—Performance of learned movement after deafferentation of the limb in dogs. a, lifting of the left hind-leg: conditioned avoidance reflex; b, the same; c, lifting of the right hind-leg: conditioned alimentary reflex (the distal part of the leg was resected because of trophic changes); d, putting the right fore-leg on the food tray: conditioned avoidance reflex.
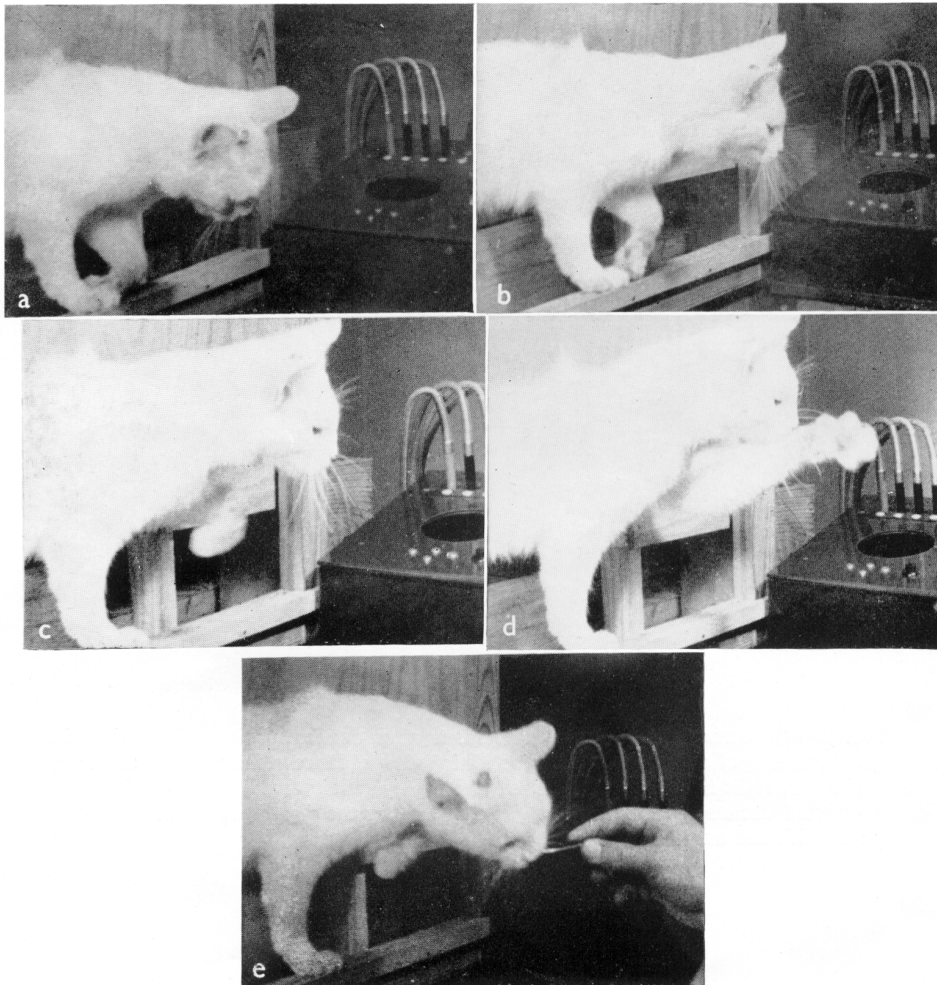
FIG. 9.—The performance of the learned movement by deafferentated left fore-leg in cat. a, resting posture; b, c, d, gradual lifting of the leg; e, presentation of food.

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