

MECHANISMS OF LEARNING

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I. INTRODUCTION

Before we proceed to the main topic of this paper it will be useful precisely to determine the scope of problems we shall deal with and the method of their analysis.

First and foremost let us explain the concept of learning. It seems that according to the intentions of the organizers of this symposium learning is to be understood in its broadest sense, including, among others, the simple Pavlovian conditioning. Although we shall show later that perhaps it would be better to restrict somewhat this term and to apply it only to those phenomena which are *commonly* called learning, we shall give here a general definition embracing all the phenomena with which we shall be concerned.

By learning we shall denote a process leading to the lasting changes in the manner in which an organism reacts to a stimulus which are due to the application of this stimulus in definite combinations with other stimuli, and which are not caused by any destructive effects which the applied stimulus might produce.* Such changes we shall also call *plastic changes*, and the property of the system responsible for their formation *plasticity*.

This definition requires some comments. The first concerns the term 'stimulus'. By this term we shall understand any compound of agents acting on the receptive parts of the nervous system (i.e. on receptors, afferent pathways, or directly on nervous centres) and evoking their excitation. Thus the direct stimulation of dorsal roots or of a sensory area of the cortex is a stimulus, while the direct stimulation of the motor cortex or of ventral roots will not be called a stimulus within the above meaning. We shall see later that the term stimulus defined in this manner is perfectly adequate for the description of the various forms of learning discussed in this paper.

Further, the lasting character of plastic changes needs some comment. The point is that in many cases the repetition of a stimulus may lead to such a change in the manner in which an organism reacts to that stimulus which is only transitory. As examples may serve: a diminution of the magnitude of a conditioned alimentary reflex in successive trials as the animal grows more and more satiated; an increase of defensive conditioned reflexes in

* The application of a stimulus alone is also considered as a definite combination.

successive trials due to facilitation; an increase of a motor reaction elicited by direct stimulation of the motor cortex at brief intervals, etc. Such changes are generally based on transitory alterations in the excitability of corresponding centres and, as we assume, they have nothing in common with the learning process. On the other hand, it can be proved that the changes occurring in 'genuine' learning are always lasting. Indeed, if a combination of stimuli (leading to some particular plastic change) is applied even at very long intervals, after a sufficiently great number of trials the change in an animal's reaction will become manifest, which means that previous trials *were* effective in its formation. Similarly, if after the establishment of a definite plastic change the training has been discontinued for a long time and the animal seems to have fully forgotten what it had been taught, it can be proved that the reversibility of the process was only apparent, as the second training necessary for the re-establishment of the plastic change will be shorter than the first.

Finally, the non-destructive character of the applied stimuli must be explained. It is clear that if a stimulus has a destructive effect, the way in which an organism reacts to such a stimulus will change on its repetitive applications, and this change may be, in dependence on the degree of damage, more or less lasting. The most common example of this kind of change is the fatiguability of nervous centres as a result of their repetitive stimulation. In this case the change in the animal's response is usually transitory. On the other hand, if the applied stimulus is a drug (e.g. morphia), the progressive destruction of the stimulated centres may be permanent. Although there are cases in which it is difficult to say whether the given change of animal's reaction arose owing to the true learning process or to such a 'pseudolearning' caused by damage, we think that these two processes must be clearly distinguished.

While accepting this rather wide definition of learning, we must, however, point out that only a small group of phenomena included within it will be discussed in this paper. First, we shall be concerned only with the simplest types of learning, and secondly, we shall trace them only in higher animals.

We pass now to the second term which requires explanation, viz. the term 'mechanism'. It must be stressed that we shall be concerned here only with the *physiological* mechanism of learning. Such a viewpoint is rather unpopular among psychologists concerned with those problems. Although psychologists, especially in America, make abundant use of the Pavlovian conditioned reflex, they tend to deal only with its behaviouristic content, and usually they reject *in toto* Pavlov's physiological theory, regarding it as a needless speculation.

Undoubtedly the reluctance to accept Pavlov's theory is partly due to its unintelligibility and to defects which have often been emphasized and criticized. But it would seem that the inadequacy of Pavlov's theory does not mean that the physiological approach to the learning processes is in itself unsound or impossible. On the contrary, we think that in the study of conditioned reflexes, just as in the study of innate reflexes, the description of their properties and interactions is not the aim of the investigations, but rather a method by which to understand their central mechanisms; in other words, we think that the hypothetical central mechanisms with which we operate here play the same role as the structural formulae in biochemistry, i.e. that of systematizing, integrating and controlling experimental work.

In my recent monograph (Konorski, 1948) I have made an attempt to present the main data of the physiology of higher nervous activity in a form more intelligible to the contemporary neurophysiologist, and thus to bridge the gap between physiologies of the lower and the higher nervous functions. In the present paper, basing myself partly on the evidence given in that book, I shall try to separate and to define different types of learning, to present their chief properties, and to discuss some problems connected with their structure.

II. MODIFIABILITY OF UNCONDITIONED REFLEXES

One must assume that the simplest form of a plastic change should be the modifiability of innate reflexes due to the mere repetition of the corresponding stimuli. Unfortunately, this type of plastic change is as yet very poorly investigated, and therefore we can give here only fragmentary evidence which may serve as its illustration.

To begin with, there are unconditioned reflexes which tend with their repetition to diminish in strength or, as it is said, to be extinguished. The orientation reflex may serve as a classic example of these reflexes; it is evoked by new and unusual stimuli which in themselves possess no specific significance for the organism.

It is easy to see that even with very rarely spaced repetitions, an orientation reflex gradually diminishes, which means that this process is not due to the fatigue of the centres involved.

In the Pavlov school the opinion prevails that the extinction of the orientation reflex is a cortical process, and that in decorticate animals this reflex is as stable as other unconditioned reflexes. The experiments of Lebedinskaia & Rosenthal (1935) seem to refute this opinion. In their dog, which was almost completely decorticated, the orientation reaction to an auditory stimulus was totally extinguished after eighty-eight applications

of the stimulus at brief intervals. Of course this effect could be ascribed to fatigue. But the next day the reflex disappeared after only twelve repetitions, which fact, if it is not accidental, must be ascribed to the learning process. Unfortunately, this series of experiments has been discontinued and we do not know what would have been the further course of the extinction.

The problem arises whether the orientation reflex is the only unconditioned reflex possessing the property of being extinguished on its simple repetitions, and especially whether this property is manifested also in some specific reflexes, such as, for example, the defensive reflex of rats to the smell of a cat (Griffith, 1920). As yet we have no evidence on which to base an answer to this question.

The next question, also so far unsolved, is whether unconditioned reflexes exist which on repetition undergo a lasting increase in strength. It is well known, for instance, that when the introduction of acid into the mouth of a dog is repeated day after day, the salivary reflex gradually grows stronger and its latent period diminishes. But it may be that this procedure, being obviously very unusual for the animal, evokes a strong orientation reflex which at first inhibits the specific reaction to the acid and then gradually subsides. So this whole problem too awaits its more extensive elaboration.

To end this section it must once more be emphasized that the problem discussed here concerns only the modifiability of a reflex caused by its repetitive elicitation and not by its being combined with other reflexes. It is clear that if a stimulus evoking an unconditioned reflex is conditioned to another reflex, then its own response can be either increased or diminished according to whether the two reflexes are allied or antagonistic. So in this sense every reflex can be said to be modifiable, but such modifiability depends on quite a different central mechanism.

III. CONDITIONED REFLEX OF THE FIRST TYPE

While, as we have seen, the problem of the modifiability of unconditioned reflexes as the effect of their repetition has, as yet, been worked out rather unsatisfactorily, another plastic phenomenon commonly called the conditioned reflex (and which we shall call here conditioned reflex of the first type) has been studied far more thoroughly. This is because the great physiological school of Pavlov was engaged in its study during nearly 40 years, and to-day it is being investigated in many other laboratories.

One great merit of Pavlov is that from the immense chaos and complexity of the acquired activity of the organism he separated out some simple and, maybe, elementary phenomenon, reproduced it in a pure form in laboratory

conditions, and made it a basis for further extensive investigation. If Pavlov's idea was really sound and his conditioned reflex *is* actually an elementary phenomenon of acquired behaviour, then his method should be accepted as a most valuable instrument for the analysis of animal behaviour. But if it is not so, and if the principle of reflex does not show the proper way to the understanding of cortical activity, then a great deal of the vast experimental material accumulated in this field may appear to be useless, and the science of conditioned reflexes will lose much of its value and significance.

Taking into consideration the vast experimental evidence accumulated in this field both by Russian and American authors we can formulate the general principle of first-type conditioning in the following way:

If two stimuli s_1 and s_2 are applied in overlapping sequence, the stimulus s_1 being antecedent, then, with repetition of such combination, a plastic change in the nervous system is formed, consisting in the stimulus s_1 acquiring the ability to elicit the response of the same kind as the stimulus s_2 . Bearing in mind the general meaning given to the term 'stimulus' in §1, we may apply this definition not only to the typical cases of conditioning, in which stimuli s_1 and s_2 act on receptors, but also to all other cases, in which one of these stimuli (or both) acts with the omission of receptors. For instance, stimulus s_1 may be applied directly to a receptive area of the cortex (Loucks, 1938), or it may be not an actual external agent but its 'trace' left in the nervous system after this agent has been removed (cf. Pavlov, 1927, p. 39); similarly, stimulus s_2 may be applied to the dorsal roots (Loucks & Gannt, 1938), or it may be a drug affecting directly nervous centres, etc.

The above definition gives only the necessary but not the sufficient condition for the establishment of the conditioned reflex. The actual course of conditioning greatly depends on physiological relations between stimuli s_1 and s_2 and their relative physiological 'strength'. If the two stimuli give rise to allied responses, the conditioned reflex is set up promptly and is strong; when they are antagonistic, the conditioned reflex is established with difficulty and is rather weak (Konorski, 1948, chapter VII, §3). When stimulus s_2 elicits a very weak response which is, moreover, antagonistic to the one evoked by stimulus s_1 , the conditioned reflex may fail to be established at all, since the response to s_2 is fully inhibited by the reflex evoked by s_1 . This is the reason why in conditioned reflex practice it is the rule to use stimuli evoking a strong reaction (such as presentation of food, introduction of acid into the mouth of the animal, electric shock, etc.) as reinforcing stimuli (s_2), while the so-called 'neutral' stimuli (auditory, visual and tactile) usually serve as conditioned stimuli (s_1), as they produce

a very feeble proper reaction and are neither antagonistic nor allied to other reflexes. An alternative explanation of why this is the best way of establishing conditioned reflexes will be given in the last section.

In our definition we have introduced two statements which need a more detailed examination.

The first is the assumption that the 'direction' of conditioning is determined by the sequence of the stimuli applied, i.e. that the antecedent stimulus is always conditioned and the subsequent stimulus is conditioning. This assumption is based on the vast experimental evidence collected both in Russia (cf. Konorski, 1948, p. 19) and in America (cf. Hilgard & Marquis, 1940, p. 174). It goes to show that if a 'neutral' stimulus is preceded by an unconditioned stimulus the conditioned reflex to the neutral stimulus either fails to be established at all or is insignificant and evanescent. It has been claimed that 'backward conditioning' (as it is called) *can* be successfully elaborated (Shnirman, 1925; Switzer, 1930; Neždanova, 1940), but as the experiments yielding the negative result are abundant and unequivocal while those yielding the positive result contain some possibilities of error,* we deem that the hypothesis concerning the sequence of stimuli in the process of conditioning is well substantiated.

The second assumption put forward in our definition is that, in order that conditioning might be set up, the reinforcing stimulus (s_2) must be a stimulus in the proper sense (see §1). In other words, according to this assumption it is impossible to form a conditioned reflex, if a 'reinforcing agent' acts directly on efferent parts of the nervous system and produces a reaction which is not mediated by nervous centres.

This assumption is based both on theoretical considerations and on experimental evidence.

As to the former, we have many reasons for believing that the process of conditioning takes place in the midst of the central nervous system between its 'entrance gate' and its 'way out', where various factors reaching the system from outside meet to interact and associate. If a reaction is produced by the stimulation of efferent parts of the nervous system in or beyond its 'way out', it cannot become a conditioned reaction, since it does not interact with other incoming stimulations. Speaking freely, we can say that the 'creative' part of the nervous system lies somewhere between the receptive and the executive sets of neurons.

This standpoint is also well substantiated by many experimental data. In particular, Gannt and his associates were greatly concerned with the

* One of these possibilities consists in the fact that application of an unconditioned stimulus not preceded by a conditioned 'signal' leads to the elaboration of a strong conditioned reflex to the experimental environment and 'to time'. Therefore in these conditions the appraising of the conditioned effect of a tested stimulus is very uncertain.

problem of which parts of the nervous system are essential for conditioning (cf. Gantt, 1937). Loucks (1935) has shown that conditioning was impossible when the 'reinforcing' agent directly stimulated the motor cortex. Similarly, it has been found that such reactions as gastric secretion to histamine, or adrenaline hyperglycaemia, cannot become conditioned reactions (Katzenelbogen, Loucks & Gantt, 1939; Gantt, Katzenelbogen & Loucks, 1937), since they are produced by the direct action of these drugs on peripheral organs. On the contrary, the effect of morphia (consisting in salivation, vomiting, etc.) can be easily made a conditioned reaction, since it is mediated by nervous centres.

The above general principle, according to which only those activities can become conditioned which occur through the mediation of the central nervous system, may be very useful in determining the mechanism of action on the organism of various agents. Suppose we have an agent *A* (which may be the peroral or parenteral application of a drug or a chemical, the direct stimulation of a nervous structure, etc.) that produces a number of effects a_1 , a_2 , a_3 , etc. In order to establish which of these effects have peripheral and which central origin we attempt to set up a conditioned reflex using the agent *A* as reinforcement. Those effects which will enter into the conditioned reaction are undoubtedly mediated by the centres, while those which will be missing are probably peripheral. Thus the conditioning procedure may serve as a 'sieve' to select reactions of different origin.

To take an example let us turn to the experiments by Masserman (1943). This author has demonstrated that the 'sham rage' which is produced in cats by the direct stimulation of the hypothalamus by means of chronically implanted electrodes cannot become a conditioned reaction; in other words, we can hundreds of times 'reinforce' an indifferent stimulus by the stimulation of the hypothalamus, and the indifferent stimulus will not evoke the corresponding response. Similarly, the author observed that 'sham rage' does not in the least interfere with other, antagonistic activities of the animal; the cat can simultaneously continue to lap milk, clean its fur, respond to petting, etc., in spite of vigorous outward manifestation of rage. All this goes to show that stimulation here affects only the purely executive centres and not the structures involved in the production of the rage itself. It is worth pointing out, however, that the general conclusion of the author, according to which 'there is little or no basis for the thesis that the hypothalamus governs or even mediates the emotional experiences themselves' (p. 56), is not convincing. According to the evidence recently provided by Hess (1947), we can obtain a 'genuine' rage in the animal if, not the efferent fibres emerging from, but the afferent fibres leading to, the hypothalamus

are stimulated. It would be extremely interesting to examine whether in the latter case conditioning of the rage reaction could be more successful than in Masserman's experiments.

In the light of these considerations rather unexpected results seem to have been obtained by Bykov (1944), who claims to have obtained a conditioned acceleration of the heart rate (p. 47) and a conditioned contraction of the spleen (p. 60), using as reinforcing agent an adrenaline injection. We have hitherto believed that both these reactions to adrenaline are of peripheral origin, and consequently their conditioning should be impossible. Bykov's results seem to indicate that our belief has been erroneous and that the mechanism of these effects must be quite different. Unfortunately, the author stating the above facts leaves them without any further analysis.

To end this section we should like to discuss one further question which very often causes misunderstandings. According to our definition the conditioned response of the first type comprises only those elements which are present in the corresponding unconditioned reflex. It is not necessary that *all* elements of the unconditioned reflex should be represented in the conditioned reflex and that their intensity should be the same. It is, however, essential that the conditioned response should not contain any foreign elements. We mention this because many authors stress the fact that very often a conditioned response is *qualitatively* different from the unconditioned reaction. A commonplace example of this is a motor behaviour which accompanies the conditioned alimentary reaction. It consists in an attentive fixation on the place whence the food appears and in 'expectation pose', while the unconditioned response consists in the seizing of food, in biting it, chewing and swallowing. Of course, there is nothing in common between these two reactions.

From our standpoint such facts do not in the least testify against the existence of Pavlovian conditioned reflexes, nor do they refute our definition, but they indicate that in the repertory of acquired animal reactions there are responses which do not occur according to the classic Pavlovian scheme. With such responses we shall be concerned in later sections.

IV. INHIBITORY CONDITIONED REFLEX OF THE FIRST TYPE

If after the elaboration of a conditioned reflex we cease to reinforce it by the unconditioned stimulus, the conditioned response gradually disappears. As is well known, Pavlov demonstrated that this process is due to a special kind of inhibition which he called internal inhibition.

In the above-quoted monograph (Konorski, 1948, chapter IX, §I), on the basis of our own experimental data as well as on data of other authors,

we came to the conclusion that if a neutral stimulus s_1 is applied in the reverse overlapping sequence with an unconditioned stimulus s_2 , i.e. when it precedes and signals the end rather than the beginning of the action of this stimulus, then an inhibitory conditioned reflex to stimulus s_1 is established, and this kind of inhibition is a typical Pavlovian internal inhibition. It is easy to grasp that this experimental situation is exactly reverse to that which takes place when stimulus s_1 signals the beginning of the stimulus s_2 and which gives rise to the formation of an excitatory conditioned reflex to stimulus s_1 . So we see that the inhibitory conditioned reflex of the first type has exactly the same general 'formula' as the excitatory reflex, the only difference between them being that in the case of the excitatory reflex the reinforcement consists in the onset of the unconditioned stimulus, while in the case of the inhibitory reflex it consists in the cessation of that stimulus.

This new kind of internal inhibition may be called *simple* or *original* inhibition, since other kinds of internal inhibition (extinction, differentiation, etc.) can be easily derived from it. Indeed, when a conditioned stimulus s_1 is applied without reinforcement it evokes an excitation of the unconditioned centre which immediately ceases, when this centre is not subsequently excited by its proper stimulus. In consequence, stimulus s_1 becomes now a signal of the cessation of excitation in the unconditioned centre, and as a result the inhibitory conditioned reflex is formed to it.

V. CONDITIONED REFLEXES OF THE SECOND TYPE

If we assumed for the moment that Pavlovian conditioned reflexes (both excitatory and inhibitory) were the basis of *all* acquired behaviour of the animal, then this behaviour should be described in the following way.

The foundation of all behaviour would consist of a limited number of unconditioned responses, which could be elicited not only by their specific stimuli, but also, thanks to conditioning, by their 'signals', i.e. by neutral stimuli which happened to coincide in time with the former ones. Thus the plasticity would be ascribed only to the receptive side of the nervous system, while the executive side would be constant and unmodifiable and would comprise only such responses as are founded in the unconditioned reflex arcs.

If we take into consideration the whole of animal behaviour and especially the motor activity, we shall observe at once that it cannot be confined in this scheme. For we know very well that the motor activity is not less modifiable than the receptive activity, that it also changes as the effect of the animal's individual experience, and cannot in the least be reduced to the mere compounds of unconditioned responses. Therefore, besides the

Pavlovian conditioned reflexes there must be other mechanisms of plasticity which would account for these other forms of acquired behaviour.

In 1928 we succeeded in separating out a new form of conditioned reflex, different from the Pavlovian conditioned reflex, which we called the 'conditioned reflex of the second type' (Miller & Konorski, 1928). On the basis of our experimental work concerning this type of reflex (vide Konorski, 1948, chapter XI) the principles of its elaboration can be generally formulated as follows:

If we subject to conditioning procedure of the first type (i.e. reinforce by an unconditioned stimulus) a compound of stimuli consisting of an exteroceptive and a proprioceptive stimulus, in which the proprioceptive stimulus constitutes an indispensable complement to the conditioned compound, then the exteroceptive stimulus begins to evoke either the movement generating the proprioceptive stimulus or the movement antagonistic to it, which depends (1) on whether the conditioned reflex, first type, to the compound is excitatory or inhibitory, and (2) on whether the reinforcing stimulus is positive or negative. By positive unconditioned stimuli we denote such agents as food, an individual of other sex, etc., and by negative unconditioned stimuli we denote such agents as the introduction of acid into the animal's mouth, the electric shock, etc.*

Thus we obtain four varieties of conditioned reflexes, second type. They are as follows, (s denotes an exteroceptive stimulus, s_r proprioceptive stimulus, r corresponding movement, $\sim r$ antagonistic movement, \rightarrow evokes):

- (1) *If the compound $s + s_r$ is reinforced by a positive unconditioned stimulus, stimulus s alone not being reinforced, then stimulus s begins to evoke the movement r ($s \rightarrow r$).*
- (2) *If the compound $s + s_r$ is not reinforced by a positive unconditioned stimulus, while stimulus s alone is reinforced, then stimulus s begins to evoke the movement antagonistic to r ($s \rightarrow \sim r$).*
- (3) *If the compound $s + s_r$ is not reinforced by a negative unconditioned stimulus, while stimulus s alone is reinforced, then stimulus s begins to evoke the movement r ($s \rightarrow r$).*
- (4) *If the compound $s + s_r$ is reinforced by a negative unconditioned stimulus, while stimulus s alone is not reinforced, then stimulus s begins to evoke the movement antagonistic to r ($s \rightarrow \sim r$).*

For the investigation of conditioned reflexes of the second type a method had to be devised in which:

- (1) both the exteroceptive stimuli and the reinforcing agents are easily applicable and discernible,
- (2) the motor responses are simple, easily elicitable, observable and measurable,

* I.e. the exteroceptive stimulus alone is differentiated from the compound (see below).

(3) and in addition to the registering of the conditioned reflexes of the second type the registering of the reflexes of the first type is possible.

It seems that an appropriate method which fulfils the above conditions is as follows: (1) as the experimental animal we take a dog with the Pavlovian salivary fistula; (2) as exteroceptive stimuli we use the so-called 'neutral' stimuli commonly applied in conditioning technique; (3) proprioceptive stimuli are supplied by the lifting of one of the dog's limbs; (4) the presentation of food is used as a positive unconditioned stimulus, while the introduction of acid into the mouth or air-puff into the ear is used as negative unconditioned stimuli; (5) both the flexion movements and the extension movements are recorded on the kymograph; (6) raising the limb can be produced either mechanically (passive flexion), or by electric shock applied to the dog's foot, or even through electric stimulation of the motor cortex by means of chronically implanted electrodes (Loucks, 1935; Konorski & Lubińska, 1939).

The above definition requires several comments. The most important concerns the proprioception.

According to the definition, in order that any movement may become the effect of a conditioned reflex, second type, the proprioceptive stimulus generated by its performance must become a conditioned signal of a certain unconditioned stimulus. Therefore, if a given movement is not accompanied by any reception, as happens, for instance, in the case of de-afferentation of the limb, the flexion of this limb cannot become a conditioned stimulus of the first type, and consequently the animal is unable to learn to perform this movement as the effect of the second type conditioning, unless the proprioception can be substituted by other stimuli, e.g. visual, as is the case with people suffering from *tabes dorsalis*. Similarly, if in producing a passive movement we exercise too strong a pressure on the dog's limb (or in a reflex flexion we use too strong a current), then the weak proprioceptive stimuli are overshadowed by the strong exteroceptive ones (cf. Pavlov, 1927, p. 141); consequently the conditioned reflex, first type, cannot be established to the proprioceptive stimuli, and as the result the conditioned reflex of the second type, consisting in raising the leg, also cannot be formed.

On the other hand, the problem arises whether all the movements accompanied by proprioception, or, more generally, all activities which are 'felt' can become conditioned responses of the second type. As to the autonomic activities there is no doubt whatever that they cannot. If we evoke the erection in a dog (or for that matter in man) and reinforce it, say, by food, we shall not teach the animal to 'perform' erection, as we should teach him to perform a movement. We are not able to turn pale or to blush

purposely (i.e. in order to reach some positive aim or to avoid some negative result) in the same way as we are able to move our limbs, although both these effects are accompanied by sensation.

But when we turn to the motor activity the matter is not so clear. If, for instance, we try in a dog to set up a conditioned reflex of the second type consisting in raising the foreleg, the training is easy and prompt. But to teach dogs in the same way to lift their hindlegs is more difficult, and I have seen dogs (though not many) which were not able to perform this movement as the effect of second type conditioning. Instead, they performed some indefinite reaction with their rump, lifted both hindlegs, etc., but there was no isolated flexion of one leg, which movement was taught to them. Whether this inability is due to the lack of exact proprioception connected with this movement (the animal does not 'know' which movement is to be performed), or to the imperfection of the central motor apparatus, is difficult to say. It seems that this problem deserves a detailed comparative investigation, in which the elaboration of various conditioned reflexes of the second type in different species should be accompanied by corresponding histological and direct physiological studies of the motor cortex.

The second comment to our definition of the conditioned reflex, second type, concerns its reinforcement. According to some authors (first and foremost Pavlov, 1941; and Guthrie, 1935), the motor behaviour of animals is based simply on the 'association' set up between an exteroceptive stimulus and a movement. As an example the usual teaching of a dog to raise the foreleg to the command, or to come to a call, is given. It is said that no reinforcement is required to teach the animal these tricks.

Such conclusions are based on inexact observations. When we teach a dog to 'give his paw' we usually apply positive reinforcement, e.g. petting when the movement is performed, as well as negative reinforcement, e.g. light strokes when it is not performed. We have been able to prove over and over again that if such an experiment is conducted in proper conditions (the dog on a stand, the experimenter outside the room) the simple combination of a stimulus with a passive flexion repeated hundreds of times leads to no 'association' of the stimulus with the movement (the problem of the so-called latent learning will be discussed later). The same negative result was obtained by Loucks (1935) who combined an exteroceptive stimulus with a movement elicited by stimulation of the motor cortex. Moreover, one needs only to extinguish a conditioned reflex of the second type (first variety) by not reinforcing it by food to see that the 'association' between the stimulus and the movement does not depend at all on their simple coincidence.

Finally, our third comment concerns the role played by the proprio-

ceptive component in the conditioned compound stimulus. We have said that for a conditioned reflex, second type, to be established a proprioceptive stimulus must be a necessary complement to the conditioned compound, i.e. it must be an indispensable condition (in the given situation) to obtain food or to avoid a noxious stimulus.

When an alimentary conditioned reflex of the second type is elaborated to the experimental environment, i.e. when we simply raise the dog's leg in a given situation and reinforce this by food, then the above condition is obviously fulfilled; for the external stimulus (the experimental environment) alone is not reinforced, while the raising of the leg in this environment is. But if we wish to elaborate a conditioned reflex of the second type to a sporadic stimulus, it is not sufficient simply to combine the stimulus with the passive flexion and to reinforce this compound by food, for in this case the movement is not made a necessary condition for obtaining food. To achieve our aim we must teach the dog that the external stimulus alone does not lead to food, which we can do either by applying this stimulus alone without reinforcement, or by protracting its duration till the dog performs the movement trained. Generally speaking, a conditioned reflex of the second type comes into being only when the compound of external and proprioceptive stimuli is *differentiated* from the external stimulus alone. According to whether the compound is reinforced and the exteroceptive stimulus alone is not or vice versa, and whether the reinforcing agent is positive or negative, we obtain the four varieties of these reflexes, as above specified.

It is evident that the mechanism of the second type conditioning accounts for a great part of animal motor behaviour, viz. for that type of behaviour which arises when the animal learns to *perform* some action if this action is rewarded (first variety), or if it leads to avoiding or escaping the punishment (third variety), or to *refrain* from an action if it is punished (fourth variety), or leads to deprivation of or missing a reward (second variety). This is precisely that type of behaviour which was first subjected to scientific analysis by Thorndike and now forms the foundation for the great majority of behaviourist studies. It is commonly called 'habit', and its acquisition is called 'learning' in a narrower and more usual sense of the word. Indeed, the sentence 'a dog has learnt to raise his leg to metronome' sounds quite natural, but the sentence 'a dog has learnt to salivate to metronome' makes a rather awkward impression.

It is beyond the scope of this paper to show how the common methods of learning used in animal psychology, such as maze learning, trial-and-error learning, and so on, can be explained by the principle of the second type conditioning, as this task would involve a more detailed discussion of the

properties of this type. But we ought to summarize briefly the views of certain American psychologists concerning the idea of the diversity of the two types of conditioning.

It seems that as soon as Pavlov's work had penetrated to America the first reaction was to identify the Pavlovian conditioned reflexes with habits. One representative of this view was Watson (1924), who believed that conditioned reflexes are elements of habits, and that a complex habit, if analysed, can be shown to consist of conditioned reflexes. As a matter of fact the views of Pavlov and Guthrie quoted above are not very far from this standpoint.

However, approximately since the 1930's more and more authors have been disposed to believe that there *is* a profound difference between the 'Pavlovian type of response' consisting in stimulus substitution and the 'Thorndikian type of response' based on the 'law of effect' (Thorndike, 1932, chapter XVI; Grindley, 1932; Skinner, 1935, 1937; Schlosberg, 1937; Kellog, 1938; Youtz, 1938*a, b*, 1939; Hilgard & Marquis, 1940; Mowrer, 1947, etc.).

Owing to lack of space we cannot enter here into a detailed analysis of the views of the above authors nor discuss the concepts of other authors as, for instance, Hull (1943), who, on the contrary, attempt to base both types of conditioning on one and the same principle. We shall undertake this task elsewhere.

VI. SOME OTHER FORMS OF LEARNING

In the preceding section we put the question whether the Pavlovian conditioned reflex exhausts the whole of acquired animal behaviour, and we demonstrated that there exists another mechanism of learning which we called conditioned reflex of the second type. Now we may ask again whether these two types of conditioning cover all animal behaviour, or whether there are other elementary mechanisms of learning not reducible to these two.

We have a good deal of psychological evidence indicating that there is a special kind of behaviour based on 'reasoning' or 'insight' and called 'intelligent behaviour' which is claimed to be distinct from habit behaviour and is often contrasted with it. In this section we shall attempt to examine this kind of behaviour and inquire into its specific character.

On the basis of the experimental evidence provided by the authors who have been particularly concerned with the subject, especially by Köhler, Maier and Tolman, we can present the following definition of intelligent behaviour:

If, owing to previous training or experience, the animal 'knows' (see below)

that in situation s_1 the movement r leads to situation s_2 (the latter being neither positive nor negative), and after the acquisition of this knowledge, to situation s_2 a conditioned reflex (either of the first or of the second type) is established, then when placed in situation s_1 the animal will perform the movement r if the reinforcing stimulus is positive and avoid the performing of this movement if the reinforcing stimulus is negative.

Here are some examples to illustrate this type of behaviour:

(a) Köhler's experiment (1925):

(1) An ape 'knows' how to carry objects from one place to another; i.e. he 'knows' that if an object is in place s_1 , then the movement r (taking and carrying it) transfers it to a new place s_2 .

(2) The ape 'knows' that if an attractive goal is hung high above the ground and beneath it there is an elevated object (say a box), then he can climb the object and reach the goal. In other words, the animal has established the following reflex of the second type: the sight of the goal hung high and an object beneath it elicits the movement of climbing which is followed by a positive reinforcement.

Both these things are learnt through everyday experience.

(3) In the crucial experiment the box is placed some distance from the hanging goal. If the animal displays 'insight' he seizes the box, carries it beneath the goal, climbs it and reaches the goal.

(b) Maier's experiment (1929):

(1) A rat has become acquainted with a given environment and knows that from place s_1 he can reach place s_2 by means of the movement r (say leaping through a barrier).

(2) The rat has been taught to run from place s_2 to place s_3 where it finds food, i.e. a conditioned reflex of the second type to the stimulus s_2 has been established.

(3) Put in situation s_1 , the rat runs to s_2 and thence to food.

(c) Unpublished experiments by Spence and Lippitt (Tolman, 1948):

A Y-maze contains two goal-boxes, one with food the other with water. Rats which are neither hungry nor thirsty are made to run through the maze and thus become acquainted with the location of the two goals. After several days of such training the rats are tested, when hungry or thirsty. If the hungry animals run towards food and the thirsty animals towards water, it signifies that the animals have displayed insight.

All these experiments possess one particular element which was not met with in the previous types of learning. It is that the animal acquires the 'knowledge' that (to put it in Tolman's words) 'a given spatially and

temporarily stimulus-object (sign) is going to lead, as the result of a particular type of behaviour (or lack of behaviour) on the part of the animal, to a spatially and temporally more distant stimulus-object (significate)' (Tolman, 1937). What is essential in this is that not only the antecedent stimulus (sign) but also the subsequent stimulus (significate) are neutral stimuli.

So the question is bound to arise how does the animal learn 'what leads to what', if the subsequent stimulus is neither positive nor negative, and consequently the animal's behaviour is not reinforced and therefore cannot be fixated according to the principles of conditioning? In the above-cited experiments (similarly as in the majority of experiments concerned with this problem) such a type of learning occurred as the result of the investigatory behaviour of animals. The apes of Köhler had undoubtedly been long used to carry various objects from one place to another without any particular purpose; similarly, in Maier's experiments the thorough exploration of the environment explicitly constituted the first part of his experimental series.

We can also arrange the experiments in such a way that the learning process of 'what leads to what' is even more regular and observable. Let us imagine a dog in a stand (situation s_1), which is compelled from time to time to raise his leg (the movement r) by various means, each of these movements being followed by the sounding of a tone (stimulus s_2). This is the first part of the experiments. In the second part we apply the tone separately and reinforce it by food. If the animal did 'associate' the raising of the leg in situation s_1 with the tone he would now raise the leg 'spontaneously' to secure himself the conditioned stimulus that signals the food.

As is seen from these examples, in this type of learning the animal acquires 'knowledge' of the external world, which knowledge does not manifest itself until it is necessary, i.e. until stimulus s_2 becomes a signal of some positive or negative agent. For this reason psychologists often call this type of learning 'latent learning'. Clearly it can be detected in animals only by introducing a special final test which should, so to say, 'develop' the plate impressed in the animal's brain, i.e. make manifest the hidden associations established between stimuli.

The wider the scope of the stimuli which the animal is able to associate in this way, in other words, the greater his capacity for acquiring such a 'knowledge' of the external world, the greater is the possibility that he will display 'insight'. Scarce as is the experimental evidence concerning this subject, it seems very probable that the above-described capacity to form associations between neutral stimuli does not extend equally to all their kinds, but is, within a given species, highly selective. Thus, according

to the vast experimental evidence, the rat possesses a highly developed spatial orientation (which is undoubtedly connected with its mode of life), i.e. it learns very easily 'what leads to what' in spatial situations, and hence in this field it is capable of displaying a great deal of 'intelligence'. However, in a somewhat modified experimental arrangement when stimulus s_2 is not a spatial situation but an 'object' (such as food for a satiated animal), the 'intelligence' of the rat fails more often (cf. the experiments of Spence & Lippitt (1946), Kendler & Mencher (1948), Grice (1948), in which the test of latent learning gave negative results). Probably, if stimulus s_2 were an auditory stimulus, no latent learning could be detected in the rat at all.

The ape has a highly developed (in comparison with other animals) 'practical intelligence', i.e. the knowledge of 'what leads to what' in the field of manipulation with objects. But the highest level of capacity to form associations between neutral stimuli is, of course, achieved in man, where this kind of association constitutes a greater part of his higher nervous activity far surpassing the two discussed mechanisms of conditioning.

The problem of the selective capacity to form associations between various categories of stimuli still awaits its thorough and detailed investigation.

However, when speaking of intelligent behaviour we must keep in mind that the knowledge of 'what leads to what' is only its prerequisite. Another no less important moment concerns the way in which the individual makes use of this knowledge.

To explain this point let us suppose that an animal finds itself in situation s , and that it 'knows' (owing to previous training) that particular motor reactions r_1, r_2, \dots, r_n may lead to particular new situations s_1, s_2, \dots, s_n respectively. Suppose that one of these situations s_k is a conditioned stimulus and signals a positive reinforcement. To reach the goal the animal must, among various possible reactions, *choose* that one which will lead to s_k . It is clear that the possibility of making an appropriate choice may not be an easy matter for the animal and may depend on very many factors, such as: the total number of reactions among which the animal has to choose, the relative degree of 'knowledge' which reactions lead to which particular situations $s_1 \dots s_n$, the character of and the differences between these situations, the existence of some facilitating or misleading cues which may make the choice more easy or more difficult, etc.

So the problem of how and when the latent knowledge is *utilized* in particular situations is quite distinct from that of how such knowledge is acquired, and its analysis raises many interesting difficulties. This problem, however, does not belong to the topic of the present paper.

VII. ANALYSIS OF THE MECHANISMS OF PLASTIC CHANGES

So far, when discussing various types of plasticity, we have been trying to keep closely to the experimental facts, and any generalizations made were of a purely empirical character. In this section we shall attempt to formulate some hypotheses which would enable us to explain the above facts from the point of view of their central mechanisms.

As this subject has been extensively discussed in my recent monograph, and it is needless to repeat here previous arguments, I shall confine myself only to a brief account of main statements and shall deal a little more fully only with those questions which were not discussed in that monograph.

So far as the conditioned reflex of the first type is concerned the elaboration of its physiological theory does not involve great difficulties. Taking into account that this reflex, when established, has many properties in common with innate reflexes (the laws of summation, facilitation, occlusion, antagonism, etc.), we can reasonably assume that the conditioned reflex, similarly to the unconditioned, has its 'reflex arc' (with all the reservations connected with this term), the only difference being that it is formed during the animal's life through its individual experience, while the unconditioned reflex arc is formed according to the developmental pattern where the individual experience plays a lesser role. In other words, we assume that if two stimuli are applied in overlapping sequence the excitatory-inhibitory pattern elicited in the central nervous system by the antecedent stimulus changes in such a way that it partially reproduces the excitatory-inhibitory pattern specific to the subsequent stimulus. How such a transformation of excitatory patterns occurs is still unknown, although we believe that the problem is not very far from being solved. In the quoted monograph (chapter v, §4) certain simple hypotheses concerning this subject have been put forward, and though I make no claim to their being strictly adequate, I have shown their usefulness in explaining experimental facts. It has been assumed that: (1) a prerequisite for the establishment of a conditioned reflex is that the 'centre' of the stimulus to be conditioned (the 'emitting centre') and the 'centre' of the unconditioned stimulus (the 'receiving centre') must be joined by potential nervous connexions directed from the first centre to the second; (2) when excitation of the first centre coincides in time with the rise of excitation in the second centre, potential connexions between these centres are transformed into actual excitatory connexions; (3) the substratum of conditioning is a morphological process consisting in the growing and multiplication of contacts (synapses) between the axon-endings of neurons of the emitting centre and neurons of the receiving centre.

So far as the inhibitory conditioned reflex is concerned we must recall (§IV) that its original form arises when the two stimuli in question are applied in reverse overlapping sequence, the reinforcing stimulus coming first. This leads us to our fourth assumption, according to which, when the excitation of an emitting centre coincides in time with the fall of excitation in a receiving centre (the excitability of this centre remaining constant), inhibitory connexions are formed between these centres. As we have pointed out, the same relation between the centres is present in ordinary cases of inhibitory conditioning, e.g. in extinction and differentiation.

More complicated is the mechanism of the second-type conditioning, and we are not in a position to deal here with this problem in detail. To put it briefly we have shown in our experiments that a conditioned reflex of the second type arises against the background of more or less manifested general motor agitation of the animal, which we have denoted as 'a state of exaltation of the motor cortex'. This state comes into being (1) during the action of a conditioned stimulus which signals a negative reinforcement (i.e. when the animal is awaiting for some nociceptive agent), and (2) when a conditioned stimulus which usually signals a positive reinforcement *is not* reinforced (i.e. when the expected positive agent was not presented). In other words, the state of motor exaltation arises when there is a rise of excitation in the centre of a negative stimulus, or a fall of excitation in the centre of a positive stimulus. If in such a state the animal performs a movement which leads to avoiding a negative reinforcement or to getting a positive reinforcement, i.e. to a removal of exaltation of the motor cortex, then excitatory connexions are formed between the centre of the conditioned stimulus and the centre of the movement. If, however, a movement does not lead to the achievement of these 'goals', i.e. if it does not abolish the exaltation of the motor cortex but instead causes its increase, then inhibitory connexions arise between the two centres, and this leads to the performance of the antagonistic movement.

Although this interpretation of the second-type conditioning cannot be regarded as exhaustive and faultless, it satisfactorily accounts for the elaboration of the four varieties of conditioned reflexes, second type, as well as for their inhibition and other properties.

We pass now to an attempt at the interpretation of the next type of learning, which forms the basis of intelligent behaviour. As we said in the previous section, it consists in the capacity to form associations between 'neutral' stimuli. These stimuli can be associated by a mechanism analogous either to that of the first-type conditioning (the animal acquires the knowledge that stimulus s_1 is followed by stimulus s_2) or to that of the second-type conditioning (the animal acquires the knowledge that in the

presence of stimulus s_1 the movement r will lead to stimulus s_2). Now, the cardinal question arises: what is the difference between this type of learning—in which the subsequent stimulus is 'neutral'—and the simple conditioning of the first or second type—in which stimulus s_2 is an unconditioned stimulus, positive or negative?

The problem which we are considering now is completely obscure and unexplored, and therefore we can only propose certain alternative hypotheses which would facilitate its further examination.

The first hypothesis would be that the mechanism of association of neutral stimuli is exactly the same as that of simple conditioning of the first or of the second type. While discussing the mechanism of conditioning we pointed out that when two centres are concurrently excited they can form actual connexions only if there exist innate potential connexions directed from one of these centres to the other. Now, we may assume that the higher the developmental level of the animal's brain, the more far-reaching and many-sided is its system of innate potential connexions. Therefore the so-called higher animals have the capacity to form associations between categories of stimuli which cannot be associated by the lower animals, because they lack the appropriate morphological connexions. In other words, the whole stock of potential connexions between nervous centres of any given animal would delimit its learning capacity.

On the other hand, however, we are in possession of some experimental evidence which would suggest a more profound difference between the process of conditioning and the associating of neutral stimuli.

Let us adduce some of our experiments performed in 1939 just before the war, which we were unable to publish because relevant materials were destroyed.

We established conditioned defensive reflexes of the second type (third variety) in two dogs. This was done in such a way that the sounding of a tone was reinforced by an air-puff into the ear, while the tone accompanied with passive flexion of the leg was not reinforced. Very soon in both dogs the tone began to evoke a vigorous flexion of the leg, a movement by which the animals avoided the air-puff. When this reflex had been firmly established we began to apply the air-puff (without any signalling stimulus) in overlapping sequence with the presentation of food. Thus we transformed the air-puff into a pure alimentary conditioned stimulus. The movement of shaking off, a characteristic response to the air-puff, disappeared, and the dog instead contorted its head slightly and pricked up its ear, while salivating copiously. This done, we returned to the application of the tone. It appeared that in both dogs this stimulus continued to provoke a vigorous defensive response in the form of a flexion of the leg without any trace of

the alimentary reaction. It was very easy in one and the same experiment to show alternately both reflexes: the air-puff itself produced a pure alimentary reflex, but the tone, which was the signal of the air-puff, gave only a defensive reaction. In spite of many days of such procedure the dogs displayed no tendency to change their behaviour.

How is this fact to be interpreted? If the dog was no longer 'afraid' of the air-puff (which could be judged from his behaviour), the defensive reaction to the tone should have automatically disappeared, just as for instance, an alimentary conditioned reflex disappears when the dog is satiated.

It seems that this fact may be explained, if we assume that 'the centre of the air-puff into the ear' in the combination *tone : air-puff*, and 'the centre of the air-puff' in the combination *air-puff : food* are two different centres. We may suppose that in the first case, when the air-puff is a reinforcement, we have to do with the centre of 'protopathic' sensations (to extend Head's terminology) or the 'affective' centre, while in the second case, when the air-puff is a conditioned stimulus, the 'gnostic' or 'epicritic' centre of the stimulus is involved. Thus, in these two cases the air-puff represents two different experiences for the dog, and so it is not surprising that he fails to identify them and consequently reacts in a manner inadequate to the situation.

So we dare to formulate a hypothesis asserting, first, that the stimuli evoking unconditioned responses possess two different aspects, which might be called the protopathic or affective aspect, and the epicritic or gnostic aspect, and secondly, that the 'true' conditioning consists exclusively in the formation of connexions between the gnostic centre of the stimulus to be conditioned and the affective centre of the reinforcing stimulus. Since the so-called unconditioned stimuli (such as pain, food, other sex, etc.) have their gnostic aspect poorly developed while their affective aspect is very strong (which is manifested by their strong autonomic effects), whereas the so-called neutral stimuli have, on the contrary, a strong gnostic side and a very poor affective side (hence the name 'neutral'), it is not surprising that in the laboratory practice (as well as in everyday experience) the first are always applied as reinforcing agents and the second serve as conditioned stimuli.

Now, intelligent behaviour is based on a new mechanism according to which mutual connexions can be formed between the gnostic centres. This property is very poorly developed in such animals as the dog or cat, is more strongly expressed in apes, and represents a chief feature of the higher nervous activity of man.

These considerations may throw some light on certain types of neurotic

behaviour in which a patient reacts with anxiety (or other feeling) to particular neutral stimuli, not realizing whence this feeling comes and why it appears. If in childhood a neutral stimulus had been conditioned to some defensive reaction, the gnostic aspect of the reinforcing stimulus, being rather weak, could become forgotten, while the affective side has remained intact. Now in presence of the conditioned stimulus the subject experiences fear without knowing of what, perhaps in the same way as in the discussed experiments our dogs displayed fear to the sounding of the tone. The essence of psycho-analytical method may consist in the fact that owing to the strenuous efforts of the patient to recall the original conditioning situation, the unconditioned stimulus is gnostically reproduced, and can be submitted to the control of the mechanism of intelligent behaviour. Similarly, if we were able to render our dogs conscious of the fact that the stimulus which is signalled by the tone of which they are so afraid is the same stimulus which heralds food and which is not to be feared at all, they undoubtedly would stop displaying a defensive reaction to the tone, and the flexion of the leg to this stimulus would disappear.

VIII. SUMMARY

In this paper an attempt has been made to separate and to define certain simple types of learning, and to some degree to analyse their physiological mechanism. The following types have been discussed: (1) the modifiability of unconditioned reflexes, and especially the extinction of the orientation reflex; (2) classic (first-type) conditioning, both excitatory and inhibitory; (3) motor (second-type) conditioning; (4) latent learning, i.e. association of 'neutral' stimuli. Some applications of this analysis to the phenomena of everyday practice and animal experimentation are discussed.

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