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THE PHYSIOLOGICAL APPROACH TO THE PROBLEM OF RECENT MEMORY

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It is a striking fact that the investigations of higher nervous activity of animals carried out both in physiological laboratories by methods of conditioned reflexes, and in psychological laboratories by use of such other methods as maze learning, discrimination box, etc., have been almost exclusively concerned with the problem of stable memory. In fact, in all these investigations the animal is routinely trained to perform a particular task or a set of tasks and then various properties of the acquired reactions, or the very process of their acquisition, are studied. But it is easy to conceive that the performance of the more or less firmly established conditioned responses, in the broadest sense of the word, and, of course, unconditioned responses, does not exhaust the whole behaviour of the animal. We know from everyday observation of animals and man that a large part of this behaviour is often based on transient memory traces which persist for some time and then are partially or even totally abolished. Recently the clear realization of a probable difference between the mechanisms of stable and transient memory traces has turned the attention of investigators to the latter category of phenomena and has given an impetus to their studies.

I intend in the present paper to present a brief review of the methods used so far in the study of phenomena of recent memory, to propose some new methods which may be applied in this field, to examine the relations between stable and recent memory and to discuss the problems of a probable physiological mechanism of recent memory, versus that of stable memory.

I. TRACE CONDITIONED REFLEXES

As a matter of fact, the phenomena of recent memory have been implicated for a long time in some conditioned reflex (CR) studies, although their significance in this respect was not clearly understood. I have in mind the so-called trace CRs which were studied by several research-workers of the Pavlov school (Pimenov, 1907; Grossman, 1909; Dobrovolskij, 1911; Feokritova, 1912; Pavlova, 1914) in the first decade

of the work in this field. These workers established that if a given 'indifferent' stimulus is reinforced not during its action but some time — of a range of seconds or minutes — after its cessation it is possible to establish in a dog the CR not to the stimulus itself but to a short period of time just preceding the moment of reinforcement. Thus, if for example a dog repeatedly receives food 3 minutes after the cessation of the conditioned stimulus (CS), he learns to salivate not earlier than about half a minute before the moment of feeding. In a variation of such experiments the animal receives food simply at constant intervals and learns to expect it at the proper moment — 'the CR to time'. The end of the act of eating plays in this experiment a role of a trace CS.

Facts of this kind mean that (1) the CS produces some changes in the CNS which persist some time after its cessation, and (2) that the animal is able to 'measure' somehow the time elapsed after it.

The process of elaboration of a trace CR is such that first both the CS itself and the whole period between the stimulus and the reinforcement evokes salivation and then gradually the conditioned reaction is more and more postponed. This shows that first there is a generalization of the CR to all moments following the CS and then differentiation of these moments occurs.

A peculiar property of trace CRs is that they are very widely generalized: even the application of new stimuli, much different from the original CS, produces salivation in the appropriate moment after their cessation; for example, when the original trace CR was elaborated to a tactile stimulus applied to one spot of the skin, it is produced by tactile stimuli applied to quite different spots and also in response to auditory stimuli. This property of trace CRs seems to suggest that they are formed not to the traces of the given exteroceptive stimulus itself, but rather to some of its consequences which are common for various sorts of stimuli. As any external stimulus elicits an orientation reaction it may be that the proprioceptive stimuli generated by this reaction form the true basis for elaboration and occurrence of trace CRs. We shall return to this question in a later section.

2. DELAYED RESPONSES

Nearly at the same time Hunter (1913), according to the suggestion of Carr, introduced into behaviouristic psychology another method of investigation of recent memory based upon the so-called delayed responses. The general principles of this method are roughly these: the animal is taught to receive food in two or more different places (or run to the food

through several different ways). When the animal is restrained in the cage or attached on the starting platform, a signal heralding that the food is presented in a particular place is given; in many experiments such a signal is provided simply by baiting one of the bowls in front of the animal. Then after a number of seconds or minutes the animal is released and if he remembers which signal was given, he will go to the corresponding place and be reinforced there.

After the first paper by Hunter appeared, a number of authors studied the delayed responses in various species, attempting to find the maximal delay periods which can be achieved, the cues which are used by the

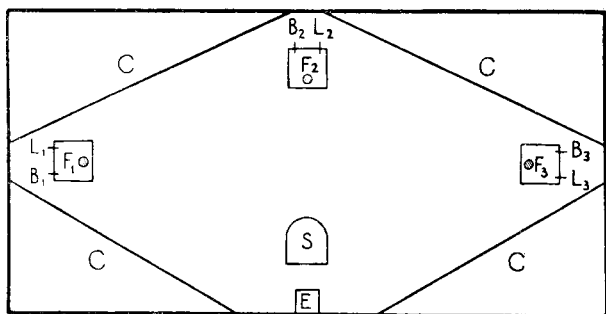


FIG. 1

Experimental setting used in our study.

F_1 , F_2 , F_3 , left, middle, and right food tray. The bowls are automatically moved into position by the experimenter using an electromagnetic device. E , table and seat for experimenter. S , starting platform. B_1 , B_2 , B_3 , buzzers, L_1 , L_2 , L_3 , lamps situated on the respective food trays. (After Konorski, J. and Ławicka, W., 1959. *Acta Biologica Experimentalis*, **19**, 175-198).

animals to solve the task, and the way in which the delay period is 'bridged' by the animal (Walton, 1915; Yarborough, 1917; Cowan, 1923; Yerkes and Yerkes, 1928; Tinklepaugh, 1928; McAllister, 1932). This form of experimentation grew in importance in the 'thirties of this century when Jacobsen (1936) showed that delayed responses are dramatically impaired or abolished by prefrontal lesions in monkeys and apes. The results of these studies will be discussed in a later section.

The delayed responses have been recently studied in our laboratory by Ławicka and Konorski (Ławicka, 1957, 1959; Konorski and Ławicka, 1959; Ławicka and Konorski, 1959) in dogs and cats by using the experimental setting presented in Fig. 1. The animal was on the leash or in the cage on the starting platform and a signal, visual or auditory, which we

shall call a 'preparatory stimulus', from one of three food trays was given. When after being released the animal ran to the proper food tray, the bowl with food was automatically presented. In certain series of experiments the source of preparatory stimuli was situated not on the food trays but at the starting platform, and the animals had to learn by trial and error which signal denoted food in which food tray.

Here are some results of these experiments (Ławicka, 1959).

1. In response to the preparatory stimulus the animal as a rule displays an *orienting reaction* (of the whole body, of the head or only of the eyes) *towards the corresponding food tray*. This is true even in those experiments in which the source of the preparatory stimulus is not situated in the direction of the goal.

2. As shown earlier by other experimenters, the preservation of the bodily orientation towards the given food tray during the delay period is, as far as normal animals are concerned, not at all necessary for the correct reaction after release. In fact, during this period the animals nearly always change their position many times and take different attitudes which does not in the least affect their post-delay reaction.

3. During the delay period normal animals may be distracted in many different ways, by presentation of extra-stimuli from different places, by screening the food trays, by giving the animals food on the starting platform, or by taking them out of the experimental room, and in the majority of trials these measures will not prevent them from running to the correct food tray.

4. If in the triple-choice delayed response method two preparatory stimuli are given one after another in the same trial, the animal, after being released, is able to go to both food trays and ignore the third one.

These data seem to suggest that the 'locating' of the food tray in space during the action of the preparatory stimulus constitutes the cue the animal uses in the post-delay run. Since the bodily orientation is not maintained during the delay period — the animal may even have been removed from the room — the memory of this cue is based purely on the intracentral nervous processes going on in the brain during the delay period, which processes are precisely responsible for those forms of phenomena which are called recent memory.

3. RECENT MEMORY TESTS FOR VARIOUS SORTS OF STIMULI

From what has just been said about the delayed response test it can easily be seen that this test concerns a *particular kind* of recent memory,

namely the recent memory of directions in space. Although we do not know exactly which sorts of stimuli are involved in determining these directions (labirinthine, proprioceptive, or a compound of them) we do know that these stimuli were acting when the preparatory signal was applied and the animal remembers them during the delay period. But obviously not only these kinds of stimuli but also exteroceptive stimuli and their various modalities can leave their transient memory traces which may be easily detected in human beings, by use of introspection. However, as far as animals are concerned, the methods for examination of recent memory of these stimuli are not so obvious because we must be sure that the given test really concerns the stimuli in question and not their proprioceptive effects. We have seen for example in Section 1 that even in trace CRs we cannot be sure that the animal remembers the exteroceptive stimulus itself and we have some reason to believe that rather its proprioceptive counterpart constitutes the basis of this form of reflexes. In order to study the recent memory of various modalities of exteroceptive stimuli the following test has been devised (Konorski, 1959).

We choose a certain group of stimuli $S_1, S_2 \dots S_n$ whose recent memory we wish to examine — e.g. tones of various pitch, lights of various intensity, tactile stimuli applied to various places of the body, etc. — and apply them according to the following schedule: the compound composed of *the same* stimulus, whatever it is, repeated twice ($S_x S_x$) is reinforced, while the compound composed of two different stimuli, whichever they are ($S_x S_y$), is not reinforced, or vice versa. And so when the first component of the compound is applied, the animal does not 'know' whether he will get reinforcement or not because this depends on comparison with the second component which is presented several seconds after the first one. Consequently, the animal has no possibility of preparing himself beforehand for a particular kind of reaction, and thus to make use of proprioceptive cues, as is the case in delayed responses or in some other tests in which the first element of the compound determines by itself the character of the conditioned reaction.¹

The test described was applied by Chorażyna (1959) in dogs for the study of recent memory of tones, and by Stępień and Cordeau (personal communication) in monkeys for the study of recent memory of rhythms of acoustic and visual stimuli.

¹ For instance, in conditioned inhibition the CS alone is reinforced, while the same stimulus preceded by another stimulus (conditioned inhibitor) is not reinforced. In this case already during the action of the conditioned inhibitor the animal takes the negative attitude towards the food tray and preserves it — or remembers it — during the action of the CS.

4. ON THE PHYSIOLOGICAL MECHANISM OF RECENT MEMORY

It is now almost generally accepted that recent memory is based on the activity of reverberating circuits of neurones which are connected with a group of neurones excited by the actual operation of a given stimulus. Such activity causes this group to continue to be excited for some period after the cessation of the stimulus itself (Hebb, 1949), and either dies out spontaneously within a lapse of time or is knocked out by some inhibitory influence arising from other foci of antagonistic excitation (the so-called external inhibition).

In order to develop this hypothesis a little further and make it more precise, the following well-known facts from the field of CR studies should be taken into account.

1. If a CS is suddenly discontinued before the moment of its usual reinforcement, the conditioned response proceeds uninterruptedly almost with the same intensity as if the CS were still acting (Kupalov and Lukov, 1932). On the contrary, if the reinforcement is usually presented several seconds *after* the CS is discontinued, the conditioned response appears already *during* its operation. This shows that a high degree of generalization exists between the actual action of a stimulus and its traces.

2. If an actual stimulus is not reinforced, but the 'trace stimulus' is, then differentiation of the two stimuli is gradually established. As a result the animal always displays the conditioned response only after the cessation of the stimulus.

3. The animal is also able to differentiate early traces from late traces of the stimulus (cf. section 1). This differentiation is, however, much more difficult than that between the stimulus itself and its traces.

If we hold the view developed in detail elsewhere (Konorski, 1948) that generalization, or similarity, of stimuli is due to the overlapping of their central representations, while differentiation of them is possible when in at least one of these representations there are elements which do not belong to the other one, then the above facts can be understood as follows:

According to the vast evidence of facts concerning the responses of various nerve-cells to the incoming impulses on all levels of the nervous axis, we may admit that the central representation of a given stimulus consists of the following types of neurones: Neurones which are activated only at the beginning of the operation of the stimulus (pure on-elements, group 1a); neurones which are activated during the whole action of the stimulus but not after its cessation (group 1b); neurones which are

activated not only during the operation of the stimulus but also, by virtue of reverberating circuits connected with them, some period after their cessation (group 2); neurones which are activated only after the cessation of the stimulus (pure off-elements (group 3)). This is illustrated in Fig. 2.

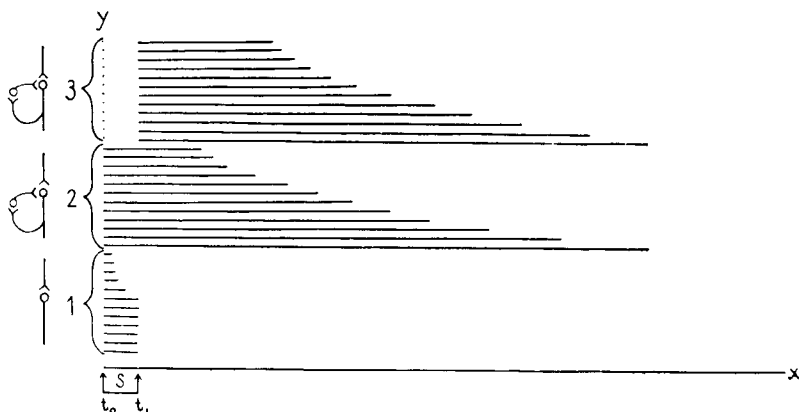


FIG. 2

Diagrammatic representation of the physiological structure of a trace stimulus.

The x axis represents time, t_0 is the beginning of the operation of the particular stimulus, t_1 , its termination.

Along the y axis are represented three groups of neurones: (1) a group of neurones activated during, and only during the operation of the stimulus; (2) a group of neurones activated both during the operation of the stimulus and, owing to the reverberating circuits of neurones, for some time after its termination; (3) a group of neurones activated *after* the cessation of the stimulus (off-neurones). All off-neurones are represented as acting for some time after the cessation of the stimulus by way of reverberating circuits. On the left the respective type of neurones of each group is indicated. The horizontal lines represent the periods of excitation of each particular neurone. The whole group 1 is activated only during the operation of the stimulus, some quickly adapting on-elements being also shown. Group 2 is activated during the operation of the stimulus and after its cessation, gradually becoming less active in the course of time. The whole group 3 is activated by the cessation of stimulus and then becomes gradually less active as in the case of group 2. Further explanations in text. (After Konorski and Ławicka, 1959. *Acta Biologica Experimentalis*, **19**, 175-198.)

As we see the neurones of group 1, being activated only *during* the operation of the stimulus, but not after its cessation, are responsible only for its actual effects; group 1a — i.e. the pure on-neurones group — causes the beginning of the stimulus to have a greater reflexogenic strength than its continuation — a well-known fact from CR experiments. On the other hand neurones of group 2 continue to be activated after the cessation of the stimulus and thus form a basis of the recent memory traces of that stimulus. As far as neurones of group 3 are concerned — pure off-elements — they account for the *active role* played by the cessation of a

stimulus (again well known from the CR experiments) and also for the recent memory traces of this cessation. And so while neurones of group 2 account for *common* features of a stimulus and its traces and provide a basis for their mutual generalization, neurones of group 3 account for diversity of the stimulus and its trace and form a basis for their possible differentiation. Various moments of the trace of the stimulus differ among themselves in that with a lapse of time fewer and fewer elements of groups 2 and 3 are activated. And so the more remote the trace of the stimulus, the less its reflexogenic strength, a fact which is again supported by much experimental evidence.

We have a strong inclination to believe that the 'sense of time' of men and other animals, i.e. the sense of the varying durations of time which have elapsed since a definite event, is based on nothing else than the strength of traces left by this event at various moments after its cessation. The weaker these traces the more remote in time the given event seems to be.

5. THE PROBLEM OF LOCALIZATION OF REVERBERATING CIRCUITS

If the above hypothesis is correct then the problem arises as to where the reverberating circuits responsible for recent memory are situated. The simplest assumption is that they are localized in the associative areas of the cerebral cortex — as decorticated animals possess hardly any recent memory — in close vicinity to the respective sensory projection areas. In consequence we may expect that the destruction of these associative areas should lead to the abolition of recent memory for stimuli in the given sensory modality.

Let us analyse from this point of view the functions of the prefrontal area, i.e. that associative area which was first recognized as having to do with recent memory in the classical experiments by Jacobsen (1936). As is well known this author demonstrated that after bilateral ablations of the prefrontal area in monkeys delayed responses are abolished and he attributed this defect to the loss of 'immediate memory', as contrasted with the full preservation of 'stable memory'. The results of Jacobsen were afterwards confirmed by many authors, but his interpretation was subjected to much criticism. It was argued that the impairment of delayed responses is due not to the lack of 'immediate memory' but to the enhanced distractibility of prefrontal animals (Malmo, 1942; Wade, 1947; Harlow *et al.*, 1952), to their hypermotility (Wade, 1947) or to the impairment of associative functions (Nissen *et al.*, 1938; Finan, 1942).

In our experiments on delayed responses with dogs (Ławicka and Konorski, 1959) we used an experimental setting (Fig. 1) which allowed us to observe and analyse the changes in animal's behaviour after operation more clearly than was possible in the Wisconsin apparatus. We have found that after ablations of the frontal poles rostral to the presylvian sulcus (Fig. 3) the animals, completely or almost completely, lose their

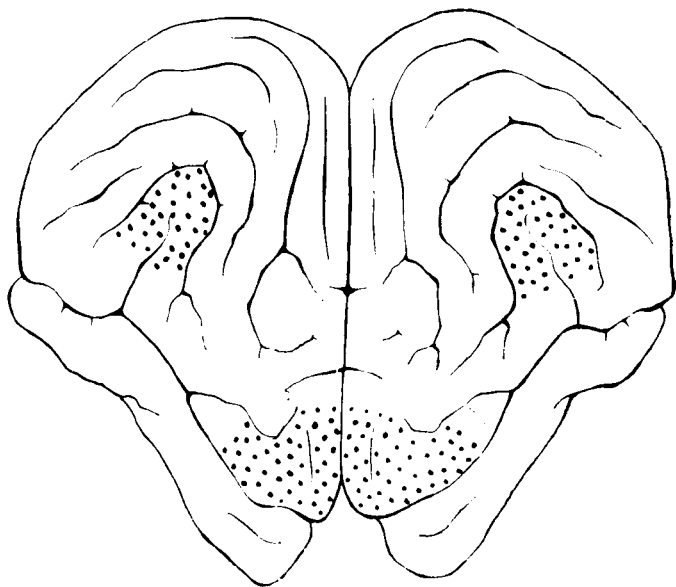


FIG. 3

The cerebral cortex of dog represented in two dimensions (if the sheet of paper is bent along the longitudinal axis, the three-dimensional picture of the cortex is obtained). The prefrontal associative areas and temporal associative areas removed in corresponding experiments are stippled.

capacity to remember in which direction they have to go in the delayed response test. Being released after the delay period they 'follow their nose', i.e. go to that food tray to which they are just turned. If the delay period is short and no distracting stimulus has intervened, the dogs are able to preserve their bodily orientation towards that food tray which was signalled and then they are able to react correctly; we have called this type of reaction a 'pseudo-delayed response' since it is due not to the recent memory of the cue but to the actual direction of the body and head. But if the animals' attention is diverted for a moment, so that they change their

bodily orientation, then they will go either in the other direction or will not go anywhere. Of course they are also not able to go to the proper food tray after receiving food on the starting platform, or after being taken out of the room. When two signals are given, one after the other, the dog after release, if not distracted, goes correctly to the last signalled food tray and does not go to the other one. In other respects the general behaviour of our prefrontal dogs does not differ from that before operation, in particular they do not display any hyperactivity or exaggerated reactions to new stimuli.

Our experimental data seem to support the original idea of Jacobsen that the impairment of delayed responses in prefrontal animals is due to the loss of recent memory. However, this statement requires one substantial qualification, namely, that not *all* kinds of recent memory are impaired after prefrontal lesions but only recent memory of *directional cues*. In fact we have so far no evidence to show that other sorts of recent memory are also affected by these lesions and we have already some evidence that it is not so. One bit of it is provided by Mishkin and Pribram (1956) who have found that delayed responses in simple go-no-go tests were not impaired in prefrontal monkeys. Another one will be presented later.

The important problem arises as to why it is that only the recent memory of directional cues is destroyed after prefrontal lesions. We think that a tentative answer to this question can be given.

The extensive study made recently by Soltysik in our laboratory (in preparation) concerning the effects of caudate lesions on delayed responses revealed that these lesions produce striking disorders of orienting reactions. The animals either do not visibly pay any attention to the auditory stimuli, or are not able to locate correctly the source of the stimulus even during its operation. When after some time this deficit is compensated the delayed responses are as much destroyed as in prefrontal animals. These animals are also severely impaired in all locomotor CRs, not being able to find their way to the familiar places they ran to hundreds of times before operation.

Although premotor cortex was not specially studied from this point of view, nevertheless as observed by I. Stępień *et al.* (in preparation) premotor lesions, and even more so premotor-prefrontal lesions, also produce striking defects in the animal's orientation in space and orienting reactions. The connections between caudate nucleus and pericruciate region were emphasized by several authors (cf. Purpura *et al.*).

All these data show that both premotor area and the rostral part of caudate nucleus play an important part in general orientation of animals in

space, i.e. in reacting correctly to directional cues and in formation and retention of locomotor CRs. Therefore, it is quite reasonable to believe that the prefrontal area, or rather some yet undefined part of it, is closely functionally connected with these regions supplying the reverberating circuits responsible for recent memory of those cues which subserve this orientation.

But it seems that much more precise analysis of the relations between projection areas and adjacent associative areas can be carried out with respect to the recent memory of exteroceptive stimuli on the basis of the test described in section 3. The corresponding experiments were performed by Chorążyna and L. Stępień in our laboratory (unpublished). After the dogs were trained to differentiate between pairs of identical tones ($S_x S_x$) and different tones ($S_x S_y$), the areas situated ventral to the auditory projective area, namely gyrus sylviacus anterior and posterior (Fig. 3), were bilaterally removed. After this operation the dogs lost completely and irreversibly the ability to differentiate such pairs, although not only *simple* differentiations, but even conditioned inhibition (see footnote on page 6) was fully preserved (Fig. 4). In other words, the animal was able to differentiate between the auditory stimulus S — positive CS — and the auditory compound $S_0 S$ — inhibitory CS — because stimulus S_0 elicited a negative *attitudinal* reaction which was retained or remembered during the action of S .

On the other hand ablation of the prefrontal area did not impair the performance of our test.¹ This shows that the prefrontal area has probably nothing to do with recent memory of auditory stimuli. It is of interest to note that partial bilateral ablations of the auditory projection area also did not affect this test.

Similar results were obtained by Goldberg *et al.* (1957) in cats. After bilateral removal of ventral parts of the temporal region discrimination between groups of tones which differed only in temporal patterning was lost, although simple tonal discriminations were preserved.

Even more convincing experiments were recently performed by Stępień *et al.* (personal communication). These authors, as mentioned before, used our test for investigating visual and auditory recent memory in monkeys. After the animals were trained to differentiate between pairs of identical and different rhythmical stimuli, both acoustic (clicks) and visual (flashes), different parts of the temporal lobes were bilaterally

¹ After prefrontal ablation the animal was disinhibited for several weeks (Brutkowski *et al.*, 1956) and therefore displayed a positive reaction to both excitatory and inhibiting stimuli, but this defect was soon totally compensated.

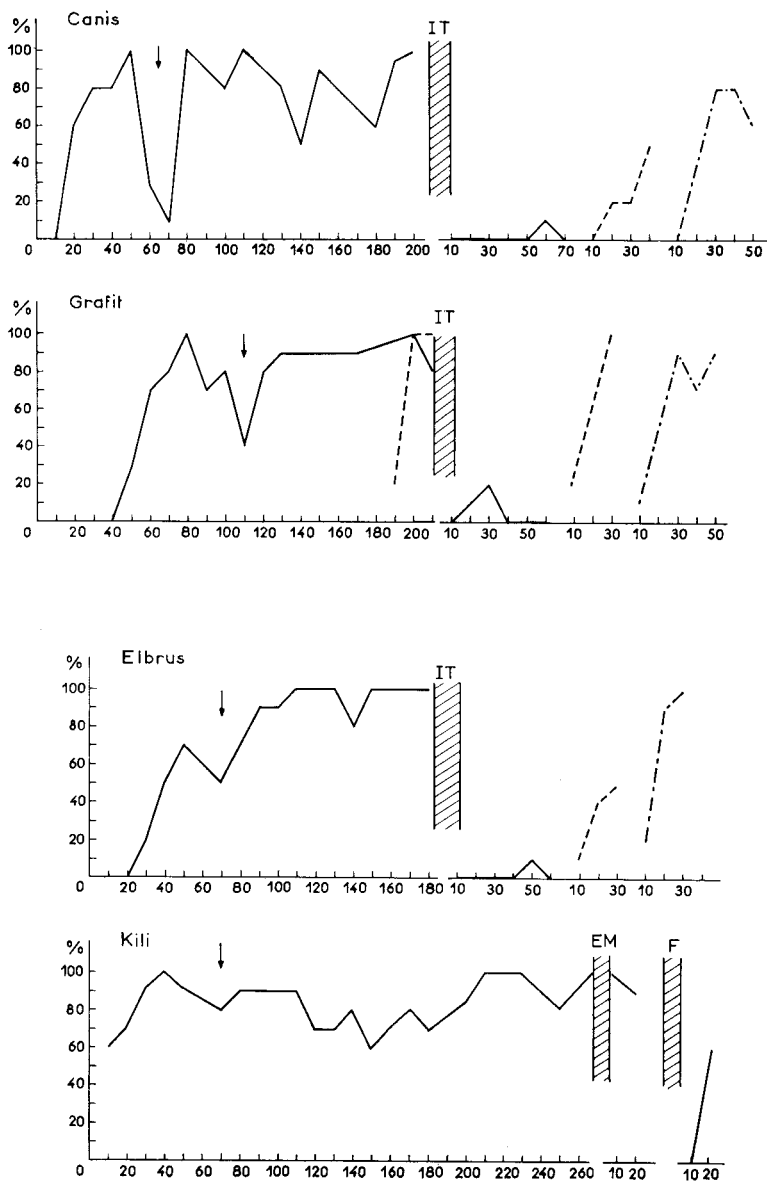


FIG. 4 (see caption on opposite page)

removed. After ablation of the anterior parts of the first and second temporal gyri the differentiation of the pairs of auditory stimuli was lost, while the performance of the same test with visual stimuli was preserved. The opposite was found after the ablation of the posterior parts of the second and third temporal gyri and gyrus fusiformis.

6. RELATIONS BETWEEN RECENT AND STABLE MEMORY

It is now generally accepted that recent memory is based on the activity of reverberating chains of neurones, whereas stable, or permanent memory is due to some structural changes produced in the brain. The kind of changes with which we have to do here has been a matter of much speculation. One of the possible hypotheses is that put forward long ago by Tanzi (1893), Ramón y Cajal (1911), Ariens Kappers (1917), Child (1921), Coghill (1929) and others, and recently adjusted to the CR experimental evidence by Konorski (1948). According to this hypothesis when an indifferent stimulus is reinforced by an unconditioned stimulus, the 'potential connections' established in ontogenesis between the corresponding groups of neurones are transformed into 'actual connections'. This is accomplished by growing and multiplication of synaptic contacts between the axons of the neurones representing the CS and bodies and/or dendrites of neurones representing the UCS.

Without going more deeply into that problem one must notice that all structural theories of conditioning have so far encountered one major difficulty: it is well known that quite often a CR is formed and proves to be stable even after a single reinforcement, the so-called 'one trial learning'. This means that a few seconds' simultaneous operation of the two stimuli would be sufficient for the formation of stable connections between the respective groups of neurones.

FIG. 4

The effects of cortical lesions on acoustic recent memory in dogs.

Each graph represents the percentages of negative (correct) responses, i.e. lack of movement for each dog to the inhibitory CS-i in successive blocks of ten inhibitory trials.

IT, infratemporal ablation, EM, ablation of gyrus ectosylvius medius, F, prefrontal ablation. Continuous lines, responses to inhibitory compound stimuli, $S_x S_y$ (acoustic recent memory test). Dashed lines, responses to inhibitory stimulus in simple acoustic differentiation. Dashed-dotted lines, reactions to inhibitory compound of conditioned inhibition, $S_0 S$.

Arrows in the course of tone-relation differentiation ($S_x S_x$ vs. $S_x S_y$) denote the end of preliminary training in which only particular pairs of tones were applied.

In the first three dogs tone-relation differentiation was totally abolished after infratemporal lesion. Both differentiation and conditioned inhibition were easily established after operation. In the fourth dog bilateral removal of middle ectosylvian gyrus did not affect the tone-relation differentiation; the removal of prefrontal areas caused the general syndrome of disinhibition which was soon compensated.

This difficulty can now be overcome if we take into account the fact that each of the stimuli taking part in conditioning leaves transient traces in the nervous system such that the respective central representations of the stimuli are excited for a much longer time than the duration of the stimuli themselves.

If the proposed mechanism of the transformation of recent memory traces into stable memory traces is correct, then one should predict that cutting the first ones short in some way or other, for instance by electroconvulsive shock, would lead to slowing down or even preventing the process of conditioning.

Such experiments were in fact performed by a number of authors and gave clear positive results. Duncan (1949) was the first to apply ECS after each conditioning trial in rats and he showed that the closer the application of the shock is to the trial, the stronger is its disrupting effect upon learning. Later the co-workers of Gerard (1955) and Thompson and Dean (1955) applied ECS at various times after a single session of discrimination learning and again proved that the shorter the interval between the learning session and the shock, the poorer is the animal's retention after 24 hours.

All these data show that after the termination of the learning trial, or a massed series of trials, the consolidation of the CR continues and that this phenomenon depends on some on-going process in the nervous system. It is quite reasonable to believe that this is exactly the same process which is involved in the recent memory phenomena described in earlier sections.

The important role played in the formation of CRs by recent memory may explain some other facts connected with learning which would otherwise be difficult to understand. It has been shown by Chow (1951), Mishkin and Pribram (1954) and others that the ablation of posterior ventral parts of the temporal lobes in monkeys abolishes or greatly impairs visual discriminations established before operation. However, Orbach and Fantz (1958) found recently that if before operation the animals were given prolonged, post-criterional overtraining, then the discrimination habit suffered little or no decrement after inferotemporal lesions. If we assume that the 'learning to criterion' of a visual discrimination is largely based on recent memory, i.e. that the animal remembers from trial to trial and from day to day which figure is positive and which negative, then this would explain why after a partial destruction of the visual association area the habit is greatly impaired. On the other hand if with long training the habit becomes based on stable memory, then no post-operative deficit would ensue. It is worth while to stress that the

ablation of the same area in monkeys produced a total abolition of recent memory of visual stimuli tested by our method in recent experiments by Stepień *et al.*

To sum up, we believe that the inferotemporal area in monkeys contains reverberating chains of neurones connected with the visual projection area and therefore lesions in this area produce the deficit of recent memory observed either directly by using our test, or indirectly by using not very firmly established visual discrimination habits.

To end this section it is necessary to draw attention to the striking deficits of recent memory found in recent years in humans after hippocampal lesions (Milner and Penfield, 1955; Scoville and Milner, 1957; and others). Similar results were recently obtained after hippocampal lesions in monkeys by Stepień *et al.* with respect to both visual and auditory stimuli. The physiological mechanism of these deficits seems to us so far not clear and they require more detailed investigation.

SUMMARY

In this paper the general review of the existing experimental material concerning recent memory in animals is presented and possible mechanisms of this phenomenon are discussed.

It has been shown that recent memory is involved in trace CRs (section 1), in delayed responses (section 2) and in those forms of CRs in which, in order to display a correct response the animal has to compare two successive stimuli (section 3). It has been assumed that the mechanism of recent memory depends on throwing into activity reverberating circuits of neurones, connected with neurones engaged in perception of a given stimulus, and probably situated in the so-called association areas surrounding the given projection area (section 4). As delayed responses appear to be based on the recent memory of directional cues, it is understandable that they are destroyed after lesions in prefrontal cortex situated in the vicinity of premotor area and caudate nucleus, structures directly concerned with the animal's orientation in space. Similarly acoustic recent memory is destroyed by lesion in gyri sylvii in dogs and cats and anterior parts of temporal gyri in monkeys; visual recent memory is destroyed after inferotemporal lesions in monkeys (section 5).

Recent memory plays a prominent role in the consolidation processes of conditioning, since it causes a much more prolonged activation of groups of neurones concerned in a given conditioning than is provided by the actual operation of the corresponding stimuli (section 6). Therefore, the

more powerful is the reverberating system of neurones within a given analyser in a given species, the more perfect and long lasting is the recent memory of the corresponding stimuli and the more rapid is the process of consolidation of the respective CRs.

GROUP DISCUSSION

ROSVOLD. I would like to ask Dr Konorski, from the point of view of the position put forth in his paper, how he would account for the fact that in the literature there are many papers that deal with the impairment of sensory discrimination following frontal lobe lesions.

KONORSKI. As we have established in our laboratory, prefrontal ablations produce two different sorts of impairment: one is that discussed in this paper, namely the loss of recent memory of directions involved in delayed response tests; the second is the impairment of inhibitory conditioned reflexes. While the first one is, according to our data, irreversible, the second one is, on the contrary, compensated with further training. It is clear that the symptom described in Rosvold and Mishkin's paper belongs to the second category. We suppose that both these symptoms are of different origin and mechanism, and we try now to check this supposition by experiments.

ROSVOLD. With reference to the permanence of these deficits, I would say that contrary to Jacobsen's earlier statements, in the chimpanzee the deficit is not permanent. Instead with training the animals gradually recover their ability to perform very well on tests of recent memory. The chimpanzee tells us another thing: a subjective thing to be sure, but we can see in watching the animals no evidence that orientation is a critical factor for those tests. In fact it is not unusual for the animal to be standing on his head when looking at the stimulus, and then turn completely over and respond correctly. Thus, even though this notion of proprioceptive recent memory being the unique function of the frontal lobes is intriguing, I am not entirely convinced that it is the answer to delayed response deficit. As Dr Konorski stated, we simply do not know what the stimulus factors in the delayed response problem really are. We have assiduously tried to determine what it is in this problem that the animal is responding to or by what means he is responding. We have not been able to demonstrate definitely what it is in the test situation that the animal uses as the basis for his solution of the problem. This is why there is so much speculation about the probable function of the frontal lobes. Probably the only resolution is the development of a test method in which the stimulus and response variables will be clearly delineated.

HEBB. I would like to add to this that bilateral total removal in another species produces no sign of defect: even better than in the chimpanzee.

KONORSKI. In man, yes.

ESTABLE. I am very much interested in Professor Konorski's communication that gives rise to so many problems. Obviously the only objection, if it can be called that, is that we have on one side techniques to study the central nervous system and on the other side techniques to study psychological problems, and the bridge is always there, but it is hard to correlate and the passage from one to the other is hard to interpret.

One must be precise with terms and when one says centre, for instance, one must not think that the centre of the spoken word means that the spoken word is generated there. If a cortical area is destroyed and the spoken word is perturbed or disappears, all that one can say is that the cortical area is necessary but not sufficient for the reproduction of the spoken word.

The fact that neurones are incapable of reproducing themselves is perhaps the price we have to pay to have memories and habits and other learned capacities which persist throughout life. If neurones died and were substituted by others, it is hard to conceive how these functions could be preserved.

Reverberation circuits may be the basis of learning but perhaps they are not enough. Do you, Dr Konorski, conceive as different phenomena: habits, organic memory and memory itself?

KONORSKI. As far as I know in dogs and in monkeys the loss of recent memory of directions after prefrontal ablations is irreversible. Moreover, in some of our animals, there was only a partial deficit of recent memory, due perhaps to smaller lesions. Why in Dr Rosvold's chimpanzee the deficit of recent memory is reversible, should be explained by further experimentation. As far as patients with prefrontal lesions are concerned, they are able to solve the delayed response test very well. We believe that it is so because their memory of directions is supported, or even based, on visual cues and also on verbal recent memory which in man, is very powerful.

I agree that we are not able so far to state definitely which sorts of cues are responsible in delayed response tests, although it seems that this problem may be solved by further experimentation.

To answer Professor Estable, I would like to stress once more that, according to our view, conditioned reflexes, including habits as a particular form, are chiefly based on stable or static, or organic memory, while such forms of behaviour which are involved in delayed responses are based on transient or dynamic memory.

OLDS. I wish to address myself to the experiments where the so-called auditory association areas were removed, and where Dr Konorski says his experiment was on recent memory, for an auditory stimulus. I wish to suggest the possibility that these were not experiments on recent memory at all, but possibly on the animal's ability to compare two stimuli. It seems to me that the way this could be tested is to have the stimulus and the comparison stimulus (another S_x or S_y) presented somehow simultaneously. If the deficit is in the animal's ability to compare, he will fail this test. If it is in recent memory, he will pass. One might also ask the question of the delayed response technique again here and ask if it is really fair to reject the delayed response as a test for recent memory of a particular (e.g. auditory) stimulus. One might develop some text in which a given tone S_x would not signify a direction but an abstract contingency and find whether excision of the auditory association areas prevented an auditory memory which involved no comparison.

KONORSKI. As to the first question of Dr Olds I agree that the test proposed by us is based on comparison of two stimuli, which is rendered impossible by the loss of recent memory. Whether or not there is any special function which may be called 'comparison' — I do not know.

As to the second question I would remind that, as shown in my paper, the removal of pre-frontal areas did not impair the recent memory of particular auditory stimuli, as proved by our recent memory test.

ANOKHIN. I should like to make two comments on Dr Konorski's very interesting report. The brain, as a specific substance has two possibilities for 'remembering', each of which can be related to what Dr Konorski relates to 'recent memory'. There is first of all the ability of a nervous substance to associate any successive stimuli coming from the inner or outer world of the organism. On account of its ability to conduct stimuli rapidly and multilaterally and of its ability to retain in the synaptic systems the molecular changes which have taken place, the nervous tissue 'remembers' any succession of stimuli brought upon it. That is the most direct and universal memory which fits under the name of 'recent memory'.

This memory, however, represents a specific advance effected by the nervous system in relation to the acting agents of the outside world.

For a given association to become stable, it has to end by a strong emotional discharge, i.e. has to end by some event which is meaningful for the life of the organism.

Thus in my view, to study the physiological mechanisms of 'recent memory' consists basically in discovering those concrete processes which occur as a result of emotional discharges and spread in the direction of the cerebral cortex, retaining there fleeting temporary associations.

As is shown by the unavoidable extinction of desynchronization when training for the association 'sound-light', a final consolidation of such ephemeral associations is indispensable.

ASRATYAN. Food boxes are very important factors in recent memory. Do you think the rule of the tonic conditional reflex, as we name it, plays a role in this recent memory?

BUSER. I wish to ask Dr Konorski if he has some information on the thalamic connections of the cortical areas which were ablated in his experiments.

KONORSKI. I think that Asratyan's 'tonic conditioned reflexes' are based on the same principles as ordinary conditioned reflexes, i.e. when firmly established, they are due to stable memory traces.

Our lesion producing the loss of delayed responses comprised gyrus proreus, subproreus and the anterior part of gyrus orbitalis. The vessels in presylvian sulcus were usually spared. These lesions produce degeneration in dorso-medial nucleus of the thalamus. Other degenerations were not so far studied.