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A REVIEW OF THE BRAIN RESEARCH CARRIED OUT IN THE DEPARTMENT OF NEUROPHYSIOLOGY OF THE NENCKI INSTITUTE OF EXPERIMENTAL BIOLOGY[1]

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I. RESEARCH IN THE INTERWAR PERIOD

Investigations which were developed in the Department of Neurophysiology of the Nencki Institute in the field of the physiology of higher nervous activity after the second world war took their origin in the studies performed during the interwar period by Konorski and Miller in the Department of Psychology of the Free Polish University in Warsaw (1928—29), in the Department of Physiology of Warsaw University (1930—31), in the Laboratory of Higher Nervous Activity of the Institute of Experimental Medicine in Leningrad (1931—33), and in the Department of Physiology of the Nencki Institute (1934—39) (Miller and Konorski 1928a, 1928b, Konorski and Miller 1933, 1936, Konorski 1939, 1948).

In the earliest papers of Konorski and Miller it was shown that the classical CR which was the subject of investigation of Pavlovian Laboratories is not the only central mechanism to which all the acquired behavior of animals can be reduced. These authors established that the motor activity of animals which in behavioristic psychology is denoted

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[1] Article prepared on the occasion of the 50th anniversary of the Nencki Institute. The investigations performed in the Department of Animal Physiology in the University of Łódź and in the Laboratory of the Nervous System of the Institute of Psychoneurology in Pruszków are included.

as habits has a different structure from Pavlovian CRs and requires quite different experimental methods. Konorski and Miller denoted classical CRs as type I and those reflexes on which motor behavior is based as type II CRs. They specified the following four varieties of type II CRs which were represented by four different experimental procedures:

1. If a compound composed of an exteroceptive stimulus S_E and a proprioceptive stimulus S_{Pr} generated by the performance of a certain movement M is reinforced by an attractive unconditioned stimulus US^+ (e. g. presentation of food), but each of these stimuli acting separately is not reinforced, the animal learns to perform the movement M to the stimulus S_E ($S_E \rightarrow M — US^+$, where the arrow denotes „elicits" and the dash denotes „is followed by").

2. If a compound of exteroceptive stimulus S_E and proprioceptive stimulus S_{Pr} generated by movement M is reinforced by an aversive unconditioned stimulus US^- (e. g. electric shock), but each of these stimuli acting separately is not reinforced, then the animal learns to perform the movement antagonistic to movement M ($\backsim M$) in response to S_E ($S_E \rightarrow \backsim M — \backsim US^-$).

3. If an exteroceptive stimulus S_E is reinforced by US^- and the compound composed of S_E and S_{Pr} generated by movement M is not reinforced, then the animal learns to perform the movement $\backsim M$ antagonistic to M in response to S_E ($S_E \rightarrow \backsim M — US^+$).

4. If an exteroceptive stimulus S_E is reinforced by US^+ and the compound composed of S_E and S_{Pr} generated by the movement M is not reinforced, the animal learns to perform that movement in response to S_E ($S_E \rightarrow M — \backsim US^-$).

These four varieties of motor responses are prototypes of habits consisting in the performance of the motor acts leading to the acquisition of an attractive stimulus or the avoidance of an aversive stimulus, or in restraining from the performance of a motor acts leading to the operation of an aversive stimulus or the deprivation of an attractive stimulus (the method of reward and punishment).

Konorski and Miller made a thorough analysis of the properties of particular varieties of type II CRs and their relations to type I CRs. Among other things these authors have established the following facts:

1. If an alimentary type II CS ceases to be reinforced by food, the type II CR (motor act) is extinguished more or less in parallel with the extinction of type I CR (salivation).

2. In the fourth variety of type II CRs ($S_E \rightarrow M — \backsim US^-$) the conditioned response is virtually unextinguishable.

3. An alimentary type II conditioned response can be elicited by an extinguished alimentary type I CS, but not elicited by a fully active

CS. On the other hand, a defensive type II conditioned response (avoidance response) can be elicited by a fully active aversive type I CS, but it is not elicited by an extinguished CS.

4. If in two different experimental situations two type II CRs are established to two CSs and thereafter the CS belonging to one situation is presented in the other situation it elicits the type II conditioned response corresponding to that situation.

On the basis of these investigations a theory of type II conditioning was proposed, according to which the type II conditioned response is elicited by an exteroceptive stimulus if the compound composed of that stimulus and the proprioceptive stimulus generated by this response is the type I CS but the elements of this compound are inhibitory. Depending on whether the reinforcing US is attractive or aversive, the animal performs the motor act complementing the exteroceptive stimulus to the compound, or on the contrary performs the antagonistic motor act preventing the appearance of this compound.

II. FURTHER DEVELOPMENT OF THE INVESTIGATIONS OF TYPE II CONDITIONING

In the postwar period the study on type II CRs, called in the American literature instrumental CRs, were carried out with great impetus in our Department and they led to the discovery of facts which compelled us to change radically the original concept of these reflexes early formulated by Konorski and Miller.

Investigations in the new direction were begun by Wyrwicka. On the basis of a number of experimental studies this author has proposed a new model of alimentary type II CRs. According to this model the connections between the CS center and the center of the motor response run both directly and indirectly, through the mediation of the alimentary center (Wyrwicka 1950, 1952a, 1952b, 1958, 1960). The joined operation of both these kinds of connections leads to the performance of the type II conditioned response. In experiments on goats Wyrwicka and her colleagues have shown that if the animal is taught to perform an instrumental response in a given situation for obtaining food, then the stimulation of the hypothalamic alimentary center carried out in that situation in satiated goats elicits the given motor act. However, the same stimulation applied outside that situation produces a general excitement of the animal without that movement (Wyrwicka et al. 1960a, 1960b, Wyrwicka and Dobrzecka 1960).

The further analysis of the reflex arc of type II conditioned reflexes was conducted by Sołtysik (1960b). This author has shown that the

„alimentary center" should be divided into the hunger center which controls the activities connected with *providing* food and the consummatory center controlling *digesting* food when it is in the mouth. According to Sołtysik the alimentary center mediating the type II CR is precisely the hunger center. On the other hand, excitation of the consummatory food center produces inhibition of the hunger center (Fig. 1). This concept is in agreement with the fact that, as found by Wyrwicka and other authors, the center situated in the lateral hypothalamus is precisely the hunger center.

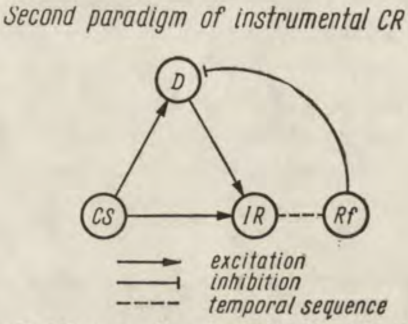

Fig. 1. A scheme of type II CR according to Sołtysik. CS, the CS center; D, hunger drive center; IR, the center of instrumental response; Rf, center of food reinforcement. Arrows denote excitatory connections; stopped line, inhibitory connection; interrupted line, temporal sequence (Konorski 1964)

Further studies performed in our Department have shown that the model proposed by Wyrwicka with Sołtysik's correction enables one to explain a great number of experimental facts in the field of type II CRs. In particular it has been established that the messages conducted along both pathways, direct and indirect, are not only mutually complementary, but also that they may partially replace each other. For instance, in the studies of Dobrzecka and Wyrwicka (1960) and Dobrzecka and Konorski (1962) it was found that in the presence of strong direct connections between the CS center and the motor center the weak messages running through the indirect pathway are sufficient for the elicitation of the trained movement. The authors used a tactile stimulus applied to the limb participating in the instrumental response and compared the responses to this stimulus with those to the auditory stimuli. It was found that the type II CR to the specific tactile stimulus is much more resistant to food satiation and to extinction than CRs to other stimuli. It was further found that by dissecting the fibers connecting the sensory area of the cortex with the motor area this peculiar property of the type II CR to the specific tactile stimulus is completely abolished (Dobrzecka et al. 1965).

It may be noticed that the model of the type II CR just described does not postulate that the proprioceptive stimulus generated by the performance of the instrumental movement must be a type I CS, as was accepted in the previous theory of type II conditioning advanced by Konorski and Miller. This problem was thoroughly examined in a number of papers of our Department and it has been shown that this postulate in fact does not hold.

First of all in a number of papers (Jankowska 1959, Górska and Jankowska 1959, 1961, Górska et al. 1961) it was established that deafferentation of the limb taking part in the type II CR is not necessary either for the elicitation of this reflex or even for its formation. The investigation was performed on dogs, cats and rats. The instrumental CR consisted either in lifting the leg or in a movement which originated from some UR such as the scratch reflex. It was found that after deafferentation of the limb the animals are able to perform the trained movement with that limb. This shows that the kinesthetic stimuli generated by this movement are not needed for its performance.

On the other hand, the experiments performed on cats and dogs (Tarnecki 1962a, Tarnecki and Konorski 1963) have shown that if an instrumental CR is established by food reinforcement of the movement of the hind leg, obtained by electrical stimulation of the cerebral cortex, then the following phenomena may be observed: if the motor act is elicited by stimulation of the sensory area of the cortex, then this motor act is very easily instrumentalized; if, however, the movement is evoked by stimulation of the motor area, this movement fails to become a type II conditioned response.

From these experiments two important conclusions may be drawn: first, the type II CR may fail to be established in spite of the fact that the kinesthetic stimulus generated by the performance of the corresponding movement is reinforced by food; secondly, it comes out that only those movements can become type II conditioned responses which have the reflex character in the broader sense of the word.

Thereafter, a more thorough analysis of the Konorski and Miller method of the formation of type II CRs by means of the passive flexion of the limb was carried out. Kozak (unpublished experiments) has found that purely passive displacement of the limb reinforced by presentation of food does not lead to the formation of an instrumental response. Konorski (1962b) put forward a hypothesis that the passive flexion of the leg induced in a dog standing on the stand elicits originally the myotatic extension reflex which subsequently is replaced by a flexor reflex (the so called clasp-knife reflex); this very reflex is the basis for the formation of the type II CR. In fact, as shown by Górska and

Jankowska (1960), if in a dog after deafferentation of the foreleg this leg is passively lifted and placed on a platform, an instrumental CR cannot be established in spite of the fact that the dog sees a change of the position of the limb. This failure is due to the fact that in the deafferentated limb the myotatic reflexes are abolished.

Finally, in experiments performed by Ellison and Konorski (1965, 1966) it was explicitly shown that the formation of an instrumental movement to a certain stimulus is not necessarily bound up with the formation of the classical conditioned response to the kinesthetic stimulus generated by that movement. In these experiments the dogs were trained to perform lever pressing movements repeatedly to a type II CS; after a given number of movements was performed a type I CS followed which preceded immediately the presentation of food. In this condition the type II CS elicited repeatedly the instrumental response which was not accompanied by salivation. On the contrary, during the operation of the type I CS the instrumental response was absent while salivation was very copious.

In other experiments (Sołtysik and Kowalska 1960, Sołtysik 1960a, 1963, Sołtysik and Zieliński 1962, 1963, Sołtysik and Jaworska 1963, Zieliński and Sołtysik 1964) a similar analysis of the defensive type II CRs was carried out. It was found that here, too, there is a two way reflex arc in which the direct pathway connects the CS center with the center of the motor response, while the indirect pathway runs through the fear drive center. The reinforcement of this type II CR is provided by the cessation of the fear drive due to the withdrawal of the CS eliciting this drive.

To summarize these considerations we can present the mechanism of type II conditioning in the following way.

1. A type II conditioned response can be formed only from the motor acts of *reflex origin*, that is those which occur by the mediation of the central nervous system. Purely passive movements, or movements elicited by stimulation of the motor area of the cortex cannot become type II conditioned responses.

2. The necessary conditions of the formation of a type II CR are that the given motor act should be performed against the background of a particular drive (hunger, fear, etc.) and that after its performance that drive should be reduced. This reduction may be produced either by the secession of a drive-provoking stimulus (as is the case in the defensive CRs) or by the operation of a drive-inhibiting stimulus (as is the case in alimentary CRs). Konorski (1967) put forward a hypothesis that this drive reduction is due to the excitation of the *antidrive center* reciprocally related to the drive center.

3. A type II conditioned response is formed owing to the connections directed both from the centers of exteroceptive stimuli accompanying the performance of a given movement and from the drive center to the kinesthetic center representing the movement. Whereas the connections between the centers of exteroceptive stimuli and the motor center *determine* which movement should occur in a given situation, connections between the drive center and the motor center *release* the movement determined by the former connections.

The problem concerning the structure of the connections linking the CS center with the center of the instrumental response was thoroughly studied recently by Ławicka (1964), Dobrzecka and Konorski (1967, 1968) and Szwejkowska (1967). The following facts have been discovered. If an animal is trained to perform two different motor responses to two different acoustic CSs under the same reinforcement, then the succes of this differentiation depends on the character of these CSs. If the CSs elicit different orienting responses (as is the case when these stimuli operate from different places), then the differentiation is easy even when there is no qualitative difference between the stimuli. If, however, the CSs differ only in their quality but not in their position, then the differentiation is very difficult or even impossible.

From these results the conclusion can be drawn that the acoustic stimuli cannot form direct associations with kinesthetic stimuli representing particular movements. Such associations are formed only through the mediation of the kinesthetic representation of corresponding orienting responses. On the other hand, if the animal is trained in go-no go differentation, then both the quality of CSs and their position can play a role, but the quality is more important than the position.

In this way an important biological principle has been established to the effect that in various tasks to be mastered by the animal different aspects of CSs play a decisive role. This principle was earlier shown with regard to inborn responses of animals (instincts) (cf. Konorski 1962a).

To end this discussion the results of Górska and Jankowska on dogs and cats should be reported concerning the efferent pathways necessary for the performance of instrumental responses (Górska et al. 1966a, 1966b, Górska 1967). According to these results the role of pyramidal tracts in performing the given instrumental response depends on the character of that response. Thus, simple type II conditioned responses such as placing the foreleg on a platform are not impaired after pyramidectomy. On the other hand, more precise movements, such as pressing a small button, become crude and awkward. Instrumental response originating from spinal reflexes (for instance the scratch reflex) virtually disappear, the fact explained by the facilitatory influence of the pyramidal tracts upon these reflexes.

III. INTERNAL INHIBITION AND TRANSFORMATION OF CONDITIONED REFLEXES

In a monograph by Konorski (1948) a hypothesis was advanced that internal inhibition, that is extinction, differentiation, or inhibition of delay, is due to the formation of inhibitory connections between the CS center and the US center. It was assumed that these connections are formed because the excitation of the CS center coincides with the *fall* of excitation in the US centre which occurs when the CS is not followed by the US. The hypothesis obviously implies that inhibitory connections develop only when the excitatory connections between the centers concerned have been previously established. In other words, the essence of internal inhibition was assumed to consist in neutralization of excitatory connections by inhibitory connections.

In a series of papers by Konorski and Szwejkowska (1950, 1952a, 1952b) it was found that this hypothesis is incorrect. The authors have shown that if among positive CSs a stimulus is presented which is never reinforced by food, then a strong inhibitory CR develops to this stimulus. This is proved by the fact that if this stimulus is occasionally paired with an excitatory CS the conditioned response to the letter is strongly reduced (Szwejkowska and Konorski 1959). Moreover, if the inhibitory CS is reinforced by food, its transformation into the excitatory CS is very difficult (Konorski and Szwejkowska 1952b, Szwejkowska 1959). In contradistinction to this, if after the extinction of the CR to a given CS this CS is again reinforced by food, the restoration of the positive CR occurs almost immediately. Since the stimulus never reinforced by food obviously does not coincide with the fall of excitation of the US center, its inhibitory character cannot be explained by the previous theory of Konorski.

A stimulus which acquires inhibitory properties by not being reinforced from the very beginning of its presentation has been called by Konorski and Szwejkowska „a primary inhibitory CS". On the other hand, a stimulus which was before a positive CS and thereafter is subjected to extinction has been called „a secondary inhibitory CS". It was assumed that the center of the primary inhibitory CS is linked with the US center by only inhibitory connections, whereas the center of the secondary inhibitory CS is linked with the US center by excitatory and inhibitory connections.

In the following study Konorski and Szwejkowska (1956) established heterogeneous CRs to different stimuli, i. e. an alimentary CR to stimulus S_1 and a defensive CR to stimulus S_2. Thereafter they reinforced stimulus S_1 by shock to the paw and stimulus S_2 by food. It was found that such transformations of the corresponding CRs occurred with great difficulty, while the restoration of the original CRs by returning to their previous reinforcement was achieved very easily.

On the basis of all these experimental data the following theory of transformations of the CRs was proposed (Konorski 1967).

The formation of a CR to a given stimulus by means of the reinforcement of that stimulus with a given US occurs owing to the development of actual connections between the corresponding centers. If we begin to reinforce the given CS with another US, then between the CS center and the center of the new US actual connections should be formed. However, if the two reinforcing stimuli produce antagonistic reflexes, the formation of new connections is hampered because the CS produces excitation of the center of the previous reinforcing US, which exerts the inhibitory influence upon the center of the new US. In consequence, the new CR is established with great difficulty and is never fullsized, because the CS centre is connected with two antagonistic US centers. This conclusion is supported by the fact that this CS can elicit either the alimentary CR or the defensive CR depending on which drive dominates in the given moment.

Since the general principles of transformation of excitatory CRs into inhibitory CRs, and vice versa, are exactly the same as the principles of transformation of heterogeneous CRs, it may be concluded that the former transformation has the same mechanism as the latter one. Accordingly it is assumed that the non-reinforcement of the given stimulus with food in the alimentary situation leads to the formation of connections between the center of this stimulus and the center representing no-food in the mouth. In the case when an originally positive CS is not reinforced with food the center of this stimulus forms connections with two reciprocally related centers, namely with the food center and the no-food center. Since these two centers are antagonistic to each other, the process of extinction of the CR occurs with difficulty, since the previously established connections between the CS center and the food center hamper the development of the connections between the CS center and the no-food center (so called resistance to extinction). On the other hand, if a given stimulus presented in the alimentary situation is never reinforced with food from the very beginning of its presentation, then the connections are formed only between the center of this stimulus and the no-food center. In consequence, if this stimulus is later transformed into the positive CS, this transformation occurs with great difficulty, the phenomenon which may be denoted as resistance to conditioning.

To summarize, it may be concluded that the so-called internal inhibition is not based on the formation of inhibitory connections between the CS center and the US center, as it was previously assumed, but on the formation of excitatory connections between the CS center and the no-US center.

IV. THE FUNCTIONAL ROLE OF THE PREFRONTAL AREA OF THE CORTEX

The studies on the brain activity which are conducted in the Department are concerned mainly with two problems. One of them, which was discussed in the previous chapters, concerns the physiological mechanisms of CRs, both classical and instrumental, both excitatory and inhibitory. A second problem concerns the functional organization of particular parts of the cerebrum. The investigations on this problem are carried out in such a way that first various forms of CRs are established in the animals and thereafter the disorders of these reflexes are examined after removal of particular parts of the brain. By analysing experimental results following lesions we try to conclude what is the functional significance of the removed part of the brain.

Most of the experimental studies carried out in our Department were concerned with the function of the so-called prefrontal area, situated in the most rostral part of the cerebral cortex (Fig. 2).

The first series of investigations concerning the functional significance of this area was performed on alimentary CRs. In dogs the excitatory and inhibitory instrumental CRs were established and thereafter the prefrontal area was removed. It was found that after surgery the positive CRs are not impaired but inhibitory CRs (differentation, conditioned inhibition) are disinhibited. When these inhibitory CRs are retrained they are gradually restored, they do not attain, however, their preoperative level (Brutkowski et al. 1956, Ławicka 1957b). Similar results were obtained on monkeys (Brutkowski et al. 1963) and on rabbits (Balińska et al. 1966, Balińska 1966).

Afterwards it was established that disinhibition affects not only instrumental but also classical CRs (Brutkowski 1957). Similarly, it was found that if the instrumental CRs are reinforced not with presentation of food but with presentation of water in the thirsty animals, the inhibitory CRs are also disinhibited (Żernicki 1961). The results were ambiguous, however, with regard to defensive CRs because in one series

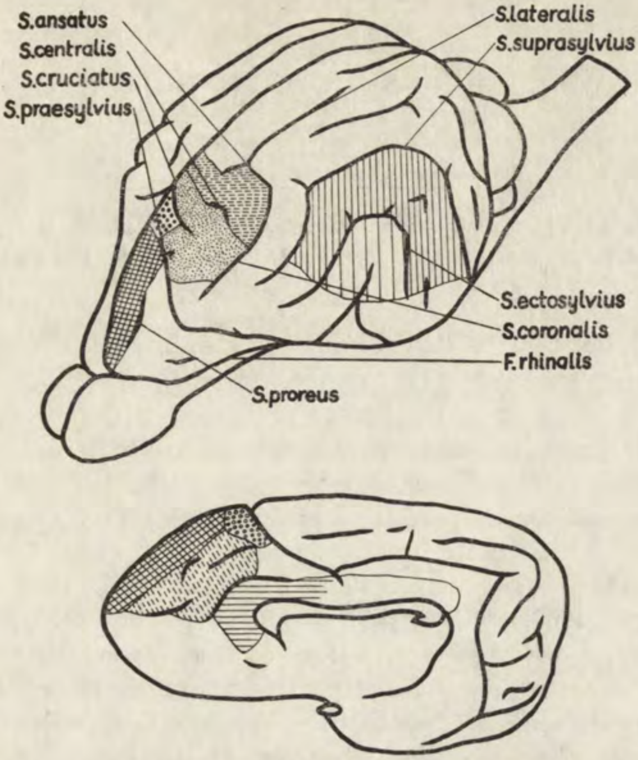

Fig. 2. Cerebral cortex of dog. Above, the dorsolateral aspect; below, the medial aspect. Double hatching denotes area whose removal produces impairment of delayed responses; oblique dashes, area whose removal produces disinhibition; circles, area whose removal produces magneto-reaction; dotted field, motor area; horizontal dashes, sensory area; vertical hatching, auditory area; horizontal hatching, anterior part of gyrus cinguli

of experiments inhibitory responses were impaired (Auleytner and Brutkowski 1960) while in another one this result was not confirmed (Sołtysik and Jaworska 1967).

Another series of investigations was devoted to the problem of the effect of lesions in the prefrontal area upon the delayed responses in dogs and cats (Ławicka 1957a, Ławicka and Konorski 1959, 1961, 1962, Konorski and Ławicka 1964). In order to make more easy the analysis of wrong responses, the triple-choice method was applied (Fig. 3). It has been shown that bilateral lesions in the prefrontal areas in both these species produce very strong disorders of the delayed responses which are particularly manifest when distractive stimuli are presented during the delay period. In cats a strong perseverative tendency is observed after prefrontal lesions. In a recent study by Divac (1968) it was found

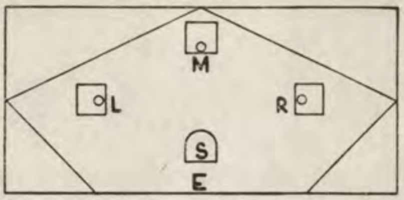

Fig. 3. Experimental situation for delayed responses. E, the place of experimenter; S, starting platform; L, M, R, left, middle and right feeder

that in cats lesions in the caudate nucleus also produced strong disorders of delayed responses.

The following investigations were concerned with more precise localizations of lesions producing either disinhibition or the delayed response disorders. It was established that whereas lesions in the medial part of the prefrontal cortex produce mainly disinhibitory symptoms, more lateral lesions (within the proreal gyrus) give rise to disorders of delayed responses (Szwejkowska et al. 1963, Ławicka et al. 1966, Brutkowski and Dąbrowska 1966, Brutkowski 1964, Szwejkowska 1965, Szwejkowska et al. 1965). The different localizations of lesions producing each of these syndromes indicates that their respective mechanisms are different. As far as the mechanism of disinhibition is concerned, we assume that it consists in the impairment of inhibition of the hunger drive. If it is postulated that the hunger antidrive is a separate physiological function possessing a definite nervous center, we may conclude that the destruction of this very center is followed by disinhibition of inhibitory CRs. Accordingly it is assumed that in that part of the prefrontal cortex which functionally belongs to the limbic system the higher order hunger antidrive center is situated.

Further studies on the disorders of alimentary inhibitory CRs have shown that these disorders are produced by lesions situated in a number of other structures belonging to the limbic system, namely the rostral part of the cingular gyrus (Brutkowski and Mempel 1961), the pyriform gyrus (Brutkowski et al. 1960), the hippocampus (Dąbrowska, in preparation) and septum (Srebro, in preparation). Accordingly there is a large integrated functional system which controls the hunger antidrive. Its organizations requires further studies.

Concerning the impairment of delayed responses after prefrontal lesions, its mechanism is completely different. Not entering into a detailed discussion of this mechanism we think that it depends on the disorder of kinesthetic gnosis. It is assumed that delayed responses are based on the recent memory of kinesthetic compound stimuli representing the approach to a definite feeder. Consequently, the impairment of the area representing these stimuli should produce a disorder of this very function (Konorski 1967).

Finally, there is another symptom connected with lesions of the prefrontal area which is obtained after removal of the medial region situated in front to the cruciate sulcus in dogs and cats (Fig. 2) (Stępień and Stępień 1965, Stępień et al. 1966). The animal is situated in a compartment enabling him to move freely around. A locomotor alimentary CR is established to an auditory CS which is not contiguous to the feeder. After the lesion the animals, instead of running straight to the feeder, consistently approach the source of the CS remaining there throughout its duration. This symptom has been called „magneto-reaction". It is characteristic that this reaction concerns only the positive CSs but not the inhibitory ones.

To summarize, we may conclude that lesions in the prefrontal area may produce, depending on their localization, three types of disorders, namely:

1) disinhibition of inhibitory alimentary CRs;
2) impairment of delayed responses;
3) magneto-reaction.

It seems that the disorders of inhibitory CRs and of delayed responses depend on different mechanisms, while the magneto-reaction may depend on a similar mechanism to that of the disinhibitory symptom.

The studies on the role of frontal lobes were also performed on rats by using somewhat different methods than those described above.

Łukaszewska (1959, 1961) has invented a method called by her „the return method" in which the animal after running to the place where food is presented must immediately return to the starting cage. This cage may be situated at the ends of two arms of the reverse T-maze (Fig. 4). In special experiments it was found that the return reaction

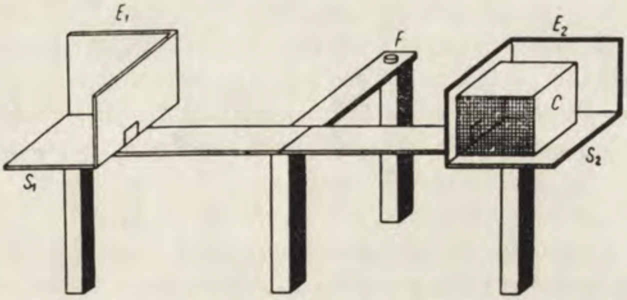

Fig. 4. The maze for studying the return responses. S_1, S_2, starting platforms; E_1, E_2, screens; F, bowl with biscuit; C, starting cage (Łukaszewska 1963)

is based not on visual but on kinesthetic cues (Łukaszewska 1963). Accordingly lesions in the frontal lobes significantly impair the return reaction (Łukaszewska 1966).

Dąbrowska (1959) carried out experiments on rats consisting in multiple reversal learning of runs in a quadruple choice four units maze (Fig. 5). It has been established that in normal rats the succesive reversal trainings occur more and more rapidly. This indicates that rats are able to integrate the run in the maze reducing it to a single „zigzag". Rats with frontal lesions do not acquire this skill. This fact shows that they are not able to perform kinesthetic integration of this habit (Dąbrowska 1964a, 1964b).

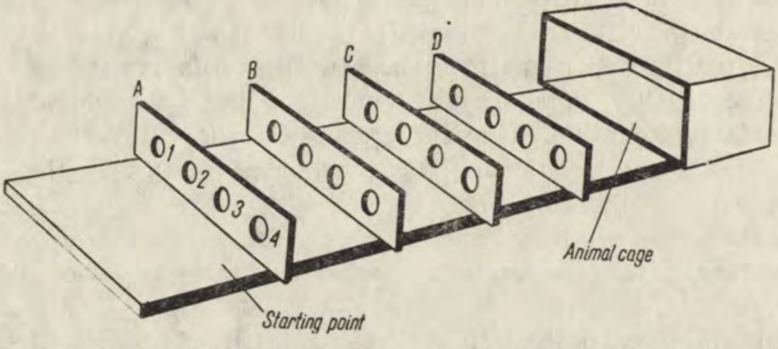

Fig. 5. Four units quadruple choice maze. A, B, C, D, walls; 1, 2, 3, 4, doors; on the left, starting platform; on the right, goal (Dąbrowska 1959)

V. THE FUNCTIONAL SIGNIFICANCE OF THE SENSORIMOTOR AREA OF THE CEREBRAL CORTEX

The original aim of the research work in this field was to explain whether or not a simple instrumental motor act consisting in placing the foreleg on the platform depends on the sensorimotor cortex (Fig. 2). To answer this question an instrumental CR in dogs consisting in placing the foreleg on the feeder was established and thereafter the effects of lesions in the sensorimotor area upon this reflex was investigated (Stępień and Stępień 1959, Stępień et al. 1960a, 1961).

These experiments have shown that if a lesion is unilateral, the instrumental response performed by the contralateral limb may be temporarily absent, but it is restored spontaneousely, although the movement is somewhat awkward. When the lesion is bilateral the motor disorders are more conspicuous. The dog turns over when he runs quickly and fails to change incorrect postures of his body. In spite of this a few weeks after operation, or even earlier, the instrumental response is restored without any training. It may be said that the trained movement is not performed immediately after operation for purely technical reasons. When the general motor disability of the animal subsides, this movement becomes possible. In other words we may conclude that in spite of the defect of motor skillfulness the *programming* of the instrumental response is normal.

Similar disorders were observed in cats in which the sensorimotor cortex was removed (Jankowska and Górska 1960) or lesions involved the thalamus or medial leminiscus (Tarnecki 1962b, 1962c).

The question arose as to whether there exists such a cortical area whose removal would lead to the abolition of the programming of movements. Unfortunately we are not able to answer this question. It was found that after lesions in the premotor cortex some peculiar disorders of the trained movement occur: although particular elements of the instrumental response are fully preserved, the animal is not able to integrate them into one fluent motor act. Whereas a normal dog after the onset of a CS turns very quickly to the source of the stimulus, then to the feeder and thereafter places the leg on the feeder, in a dog with lesion in the premotor area these elements become disintegrated. Nevertheless the ability to perform the trained movement is normal (Stępień et al. 1960b, 1963).

In some pilot experiments the head of the caudate nucleus was removed in dogs and cats (Sołtysik 1960c). After this lesion the trained instrumental movement disappeared and could not be reestablished.

All these experiments allow us to draw the following conclusions concerning the mechanisms of trained motor acts. The sensorimotor area of the cerebral cortex is indispensable for the correct performance of a motor act by making this act fluent, rapid and precise. These properties of a performed movement depend largely on the information arriving from periphery because either deafferentation of the limb, or the thalamic lesions produce a clear impairment of the skillfulness of the movement. On the other hand, neither the sensorimotor cortex nor the thalamus participate in the programming of the trained movement. This occurs probably in the basal ganglia for primitive movements and in the premotor cortex for more complex movements. Since the lower mammals, such as dogs and cats, do not possess highly refined motor acts, their chief controlling center is situated in the basal ganglia. On the other hand, in primates the chief role is played by complex manipulative responses which are programmed in the premotor area of the cortex.

VI. FUNCTIONAL ORGANIZATION OF THE LIMBIC SYSTEM AND THE HYPOTHALAMUS

The studies in the field of the brain activity conducted in the last decades led to the conclusion that this organ can be divided, both in regard to its function and its anatomy, into two systems: one of them, including specific thalamic nuclei and the neocortex can be called the *gnostic system,* while the second including nonspecific thalamic nuclei, the hypothalamus and the paleocortex (denoted now as the limbic system) may be called the *emotive system.* In recent years the activity of the latter system has been thoroughly studied in our Department. The characteristic feature of these studies is that they are not concerned too much with the unconditioned responses controlled by emotive centers, but mostly with the role of these structures in CRs.

In one of the previous chapters the investigations of Wyrwicka and her colleagues were quoted in which it was shown that stimulation of the lateral hypothalamus (the hunger center) in satiated goats provokes the earlier established alimentary instrumental response. On the contrary, stimulation of the ventro-medial hypothalamus (satiation center) elicits inhibition of the instrumental responses in hungry animals (Wyrwicka et al. 1960a, 1960b, Wyrwicka and Dobrzecka 1960).

Further investigations of the hypothalamic alimentary functions were carried out on rabbits and cats in the Department of Physiology of the University of Łódź under the guidance of Wyrwicka and later of Brutkowski (Balińska et al. 1961, Balińska and Brutkowski 1964, Lewińska 1964, Balińska et al. 1966, Lewińska and Romaniuk 1966). It was established that lesions in the hunger center produce in animals not only aphagia but also the full abolition of alimentary instrumental responses. Afterwards the animals begin to take food again, but the instrumental responses return much later and require special training. The impairment of the hypothalamic satiation center produces hyperphagia accompanied by much more intensive performance of the instrumental movements than before the operation. Thus we see that the centers of hunger and satiation exert their control not only upon the food intake itself, but also upon the animal's behavior directed towards providing food. Other experiments were devoted to the problem of the hypothalamic control of the fear drive. This was done by studying the effects of stimulation or destruction of various hypothalamic regions on defensive CRs.

Fonberg (1967) has shown that stimulation of various points in the hypothalamus produces three types of defensive responses, i. e. a rage response, fear response and mixed response of fear and rage. Whereas stimulation of the fear points may serve as reinforcement for the formation of instrumental defensive CRs, stimulation of the rage points does not produce this effect.

Romaniuk (1962, 1967) has thoroughly examined in cats and rabbits those hypothalamic regions which represent fear or rage respectively. He came to the conclusion that the ventro-medial part of the hypothalamus is the center of rage, while the dorso-medial part is the center of fear. Finally, Balińska et al. (1964) have shown that after the destructions of the lateral hypothalamus not only alimentary instrumental CRs, but also defensive instrumental CRs are abolished. This result throws a new lights on the localization of emotive centers in the hypothalamus.

The studies of the limbic system are also carried out both in the Department of Neurophysiology of the Nencki Institute (Brutkowski et al. 1960, 1962, Fonberg et al. 1962, Fonberg 1963, 1966, Fonberg and Sychowa 1968), and in the Department of Animal Physiology in the University of Łódź (Lewińska 1968a, 1968b). The experiments are conducted on dogs and cats, either by means of lesions performed in various parts of the amygdala or by means of stimulation of various points of this nucleus through implanted electrodes. The effect of both these procedures upon natural responses of animals and on alimentary and defensive CRs are investigated. The results of these studies may be summarized in the following way.

There is an area in the amygdaloid complex which controls the hunger drive. Stimulation of some part of this area elicits an increase in food intake, while its removal produces a temporary decrease of food intake. Stimulation of another part of this area gives rise to inhibition of the food intake or even aversion towards food, while its removal produces an increase of the food intake.

Another area of the amygdaloid complex controls the defensive activity of the organism. Here we can distinguish an area whose stimulation produces the fear drive and flight and another area whose stimulation produces aggression.

On the basis of these data it may be assumed that the amygdaloid complex represents a higher center controlling drive processes in animals. Particular drives are represented in different parts of the amygdala. It is possible to separate areas controlling the excitation of a given drive and those controlling its inhibition. It is probable that the amygdala is an intermediary in the formation of drive CRs.

Finally it should be noted that the prefrontal area whose removal produces disinhibition of inhibitory food CRs (cf. Section IV) should be also included in the higher level of the emotive system. This area is responsible for inhibition of the hunger drive in those situations in which the animal fails to receive food. Lesions in this area lead to the impairment or abolition of inhibitory CRs. In consequence, after these lesions the hunger drive depends only on humoral factors and not on environmental factors.

VII. PLASTIC CHANGES OF UNCONDITIONED REFLEXES[2]

In his monograph concerning the neuronal organization of conditioned reflexes Konorski (1948) formulated the notion of nervous plasticity as the neurological equivalent of the processes of learning and memory. The author postulated that the basis for this nervous plasticity is, on the one hand, the formation and multiplication of synaptic contacts between the axon collaterals of the one nerve cell and the soma (with dendrites) of the following cell, as a result of reflex training; and, on the other hand, the diminution and atrophy of nervous contacts as a result of cessation of training.

In his lecture given during the fourth Symposium of the British Society for Experimental Biology (1950) Konorski discussed, among other subjects, the plasticity of unconditioned reflexes and pointed out that repetition of a stimulus leads either to a gradual extinction of the reflex, as is the case with the orientation reaction, or to its facilitation, as is the case with the reflex salivary secretion to acid introduced into the mouth. It has been shown that certain regularities in the functioning of the effector itself, i. e. the salivary gland (Bruner and Kozak 1954, Czarnecka and Sołtysik 1962, Kozak and Westerman 1966a) should be taken into consideration when interpreting the diminution or augmentation of the salivary reflexes. That is to say, the same stimulation of the secretory nerve can produce different effects depending on the length of time elapsed from the preceding stimulation; the differences in secretion volume may be as high as 50% (Kozak 1965).

The theme of nervous plasticity was later taken up by J. C. Eccles and McIntyre and formulated so that if during the learing process the brain synapses should be created or grown as a result of the impulse bombardment, then a similar growth, though to a lesser degree, would occur also in the spinal cord under the influence of excess use of the synapses. Experimentally, this problem was attacked from the opposite side, namely, by producing disuse of the synaptic pathways in the spinal cord by severance of the dorsal roots in cats. Several weeks after the operation it was found that the disused monosynaptic reflexes were considerably reduced in size. Repetitive stimulation caused a marked reflex enhancement which could be observed during several hours after the stimulation. These results were interpreted by the authors as sup-

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[2] Section VII and part of the Section VIII was prepared by W. Kozak.

porting the postulate of the deleterious effect of disuse of nervous pathways upon the synaptic transmission within them.

In order to continue the work interesting for both scientific teams, W. Kozak together with J. C. Eccles and his collaborators started joint investigations on the effect of tenotomy of extensor muscles upon the monosynaptic reflexes elicited from those muscles. The results of these experiments were contradictory to the postulate of depression of synaptic transmission due to disuse. It was found that the reflex from tenotomized muscles became enhanced when tested several weeks after the operation (Kozak and Westerman 1961). Later on, control experiments were conducted on the effect of sparing of innervation of one of antigravity muscles while the innervation of the remaining synergists was severed. In these control experiments two additional factors were introduced with the aim of eliminating entirely any excess usage of the spared muscles and of their receptors: the operated leg was immobilized by plaster of Paris in extended position and the spinal cord was severed at the time of operation (Eccles et al. 1962). In spite of these procedures the reflexes from the spared muscles were enhanced similarly to the control ones, as was the case in the experiments of R. M. Eccles and R. Westerman on the effect of sparing of innervation of one of synergist muscles upon its monosynaptic reflex.

The conclusion appeared justifiable that the experiments involving severance of nerves or tendons give an equivocal answer as to what is the effect of use and disuse of nervous pathways, because they cause additional processes of degeneration, chromatolysis, regeneration and others, whose effects can mask the results of disuse or excess use.

On the other hand, more unequivocal results were obtained in the experiments on the effect of use and disuse upon the reflexes in chronically spinalized cats (Kozak et al. 1962, Kozak and Westerman 1966a, b). In these animals, whose hind parts from a sort of "simplified organism", several weeks after the spinalization (performed soon after birth) the excitability of the reflexes form the skin receptive fields was markedly increased. This enhancement has been shown both in the acute and chronic experiments (Kozak and Westerman 1966a).

On the other hand, when one selected spinal reflex was elicited daily during ten to twenty minutes, this procedure led to a marked diminution of reflex excitability until the response disappeared altogether. A break in training resulted in a recovery of reflex responses almost back to their original level. A secondary training three months after the primary one led to a much quicker disappearance of the reflex. One was dealing here with examples of plasticity of unconditioned spinal reflexes belonging to the category of body-cleaning reactions such as the scratch-reflex, toefanning during foot-licking, shaking-off reflexes and others. It is interesting to compare the repeated extinction of these reflexes with the well-known experiments on repeated extinction of conditioned reflexes. In both cases the speed of extinction increases with repetitions of the extinction procedure.

In the experiments involving standing and walking reactions in chronically spinalized and normal animals with one extensor muscle spared, it was shown that these reflexes behave differently than the body-cleaning reactions. Namely, they increase with use and are depressed by disuse (Kozak and Westerman 1966a). Parallel with these investigations conducted in Australia, in our Department Z. Afelt undertook experiments on chronic spinal frogs (Afelt 1963, 1965, 1966). She found that daily eliciting of wash-reflexes with a given frequency leads to their abolition, whereas the locomotor reflexes, when daily elicited, became increased; she qualified this phenomenon as "learning without reinforcement". She investigated also the effect of cord severance level upon the appearance of certain reflexes and the effect of a general increase of excitability of the chronic preparation upon the release of the previously masked reflexes. Later she started investigations of the chronic preparations of the isolated spinal cord segment in cats, both behaviorally and electrophysiologically.

Moreover, B. Żernicki with his collaborators (Affanni et al. 1962a, b, Żernicki and Dreher 1965, Żernicki et al. 1967, Żernicki 1968) studied another "simplified organism", the pretrigeminal preparation of the cat. These authors showed that the ocular fixation reflex became gradually attenuated with repetitive presentation of visual stimuli until it completely disappeared. A break in training resulted in spontaneous recovery of the reflex, a subsequent training led to a faster disappearance than was initially observed. It is thus possible to obtain a chronic habituation of either fixation or following reflexes. Ablations of the cortical frontal eyefields reduced the speed of habituation (Dreher and Żernicki 1969).

On the basis of the investigations mentioned above concerning reflex plasticity in chronic spinal animals and in pre-trigeminal preparations, and also on the basis of experiments demonstrating the ease of transformation of unconditioned cleaning reflexes into instrumental alimentary reflexes in normal animals (Jankowska and Sołtysik 1960; Górska et al. 1961), Kozak and Westerman (1966a) put forward a new concept of plastic changes in the nervous system. According to this concept the unconditioned reflexes having positive feedback (i. e. those in which the motor act increases the afferent input) are the plastic reflexes; they habituate during repetition and instrumentalize when reinforced by reflexes having negative feedback. The latter ones (i. e. those in which motor act reduces the afferentation) do not habituate; on the contrary, they increase with repetition under certain circumstances. They are good as reinforcers. The authors pointed out that the properties of both types of reflex match the properties of presynaptic inhibition and facilitation of the afferent pathways.

VIII. FURTHER PERSPECTIVES OF THE RESEARCH WORK IN THE DEPARTMENT OF NEUROPHYSIOLOGY

In this chapter we shall delineate further perspectives of investigations which were conducted in preceding years as well as those investigations which were begun recently and which promise further development.

In Sections I, II and III the achievements of the Department in the field of physiological mechanisms of the CR activity of animals were described. In particular, the mechanisms of internal inhibition (Section III) as well as the mechanisms of instrumental CRs (Sections I and II) were discussed. The research work in this field will be further developed on the basis of new concepts concerning these phenomena, which were formulated in a recently published book by Konorski entitled "Integrative activity of the brain" (1967). Besides the experimental studies on animals, the modelling of the corresponding nervous processes by an artificial nerve-net was undertaken in collaboration with Gawroński from the Institute of Automatics of the Polish Academy of Sciences.

The study of the physiology of CRs has been so far concerned only with the plastic phenomena, i. e. with stable memorization of corresponding associations. It is known, however, that besides the stable memory traces there exist transient memory traces which serve for the temporary preservation of the given stimuli or associations. Here belong, among other things, the delayed responses described in Section IV which are based on transient memory traces of kinesthetic stimuli generated by orienting responses (Konorski and Ławicka 1959). However, it is possible to study not only transient memory of kinesthetic stimuli but also of stimuli of other modalities, auditory, visual, etc. Such investigation may be carried out by the method of comparing stimuli (Konorski 1959). Briefly, the method consists in presenting two compound CSs one of which is reinforced by food and another not. If the compound is composed of two successive stimuli of the given modality which differ from one another, this compound is reinforced by food; if the compound consists of the same stimulus repeated twice, it is not reinforced. In order to master this differentiation the animal must remember the first element of the compound when the second element is given, i. e. he must possess the transient memory traces of a given modality of stimuli. Such experiments were undertaken a few years ago in dogs by Chorążyna (1959, 1967) with acoustic stimuli. Chorążyna and Stępień (1961) have shown that lesions in the ventral part of the temporal lobe including claustrum abolish transient memory of this modality.

Another line of investigations was undertaken a few years ago in collaboration with the Institute of G. Moruzzi in Piza. This author and his associates have shown that if the cerebrum of the cat is separated from the rest of the nervous system on the level of the pons (so called pretrigeminal preparation), it is in a state of permanent wakefulness in spite of the fact that it receives from the outside world only visual and olfactory stimulation. The supposition was put forward that in such isolated cerebrum the CRs can be established by using visual stimuli as CSs and hypothalamic stimulation producing dilation of pupils as the US. In the work performed by Żernicki and associates in Moruzzi's laboratory it was shown that such conditioning in the pretrigeminal preparation is indeed possible (Affanni et al. 1962b). Żernicki and his co-workers continue to study the functional properties of this preparation by keeping it alive for a number of weeks. It has been shown that it is possible to establish in the isolated cerebrum a differentiation of two visual stimuli (Żernicki and Osetowska 1963). Furthermore, by utilizing the fact that in the pretrigeminal preparation there exist fixation reflexes and following reflexes, the study of their mechanisms and habituation was undertaken (see Section VII). It was established that the arc of the fixation reflex runs both through the cerebral cortex and through the lower centres (Dreher et al. 1965). It was also found that after lesions in the frontal cortex the process of habituation is strongly impaired (Dreher and Żernicki 1969).

Another important area of study recently developed in our Department is the field of physiological mechanisms of perceptive phenomena and, in particular, of vision.

The laboratory concerned with this problem has been organized by W. Kozak, who earlier studied animal vision in Australia together with P. O. Bishop.

Problems investigated in the laboratory of afferent systems include:

1. Study of the role of various subcortical visual centres in the process of vision.
2. The problem of encoding of information about light and darkness in the spike trains of single retinal neurons.
3. Transformation of information at the synapses in the visual centres.
4. Investigations of visual evoked responses in cat and man.

Ad 1. It was found that the neurons of the accessory optic tract nuclei in the midbrain react differently than the nerve cells of the lateral geniculate nucleus, because the former ones respond only to new stimuli and have receptive fields of immense size. The accessory optic tract serves therefore probably as a detector of novel stimuli and excitor of visual attention. Chronic experiments with implanted electrodes are planned in order to study the behaviour of the cats when these tracts are stimulated or destroyed.

Experiments are being conducted on the responses of neurons in the pretectal area and superior colliculus. A great percentage of pretectal nerve cells respond to figures moving in a selected direction. A small minority of superior collicular neurons respond in a similar way. In both these areas many neurons show clear habituation to repetitive stimuli.

Ad 2. It was found that the ganglion cells of the retina react differently to light and darkness, with two types of impulse coding: in some cells, the mean frequency of impulses is changed by light and in others, there appear different statistical distributions of interspike intervals, in light and in darkness while the mean frequency of spikes remains the same (Kozak et al. 1968).

Ad 3. The relationship between incoming and outgoing signals was investigated in single neurons of the lateral geniculate nucleus. It was found that the progression of outgoing impulses differs from the incoming by the number of signals and, among others, by the phenomena of adaptation and augmentation. This transformation of information leads to an enhancement of contrasts, contours and movement of figures seen against a contrasting plain background; it forms then the basis for object vision.

Ad 4. The results indicate that in light both the electroretinogram and the evoked responses in the lateral geniculate nucleus of the cat contain an oscillatory component having frequency identical with the modal frequency found in the impulse activity of the retinal neurons in light (cf. paragraph 2).

During the investigations on humans it appeared that the evoked potentials recorded from the occipital scalp and analysed using an electronic computer can serve as an objective index of the subjective detection of threshold visual stimuli (Kulikowski and Kozak 1968).

Acute and chronic experiments on rats are planned in order to test for the effect of a visually impoverished environment upon the functional properties of the visual cortical neurons, particularly upon their selective responsiveness to visual patterns.

SUMMARY

In the pre-war period Miller and Konorski began and carried out their work on instrumental (type II) conditioned reflexes (CRs) and their interrelations with the classical (type I) CRs. These authors distinguished four varieties of type II CRs according to whether the reinforcing stimulus is attractive or aversive, and whether the trained movement signals the appearance of the reinforcing stimulus or its absence.

In the post-war period the studies on type II conditioned reflexes were continued in our Department and the following basic principles concerning this conditioning were discovered:

1. The type II CR may be formed only from the reflex motor acts, that is from those acts which occur by the intermediary of the CNS. The purely passive movements and the movements evoked by stimulation of the motor area of the cortex cannot become type II conditioned responses.

2. The indispensable condition for the formation of the type II CR is that the motor act be performed against the background of a definite drive and that after its performance the drive be reduced; this reduction is accomplished by inhibition of hunger drive, when the food is placed in the mouth, or by cessation of the fear producing stimulus.

3. The type II CR is formed and produced by the joint action of connections running directly from the CS center to the kinesthetic center of the movement and from the drive center to the kinesthetic center. Connections running from the CS center to the kinesthetic center determine the movement to be performed, whereas connections running from the drive center to the kinesthetic center release the movement determined by the former connections.

4. The proprioceptive feedback of a motor act is in principle not indispensable either for the formation of an instrumental response from this act, or for its execution, since the type II CR may be formed or preserved after deafferentation of the limb involved.

Another line of research has been concerned with the problem of the so called internal inhibition and transformations of CRs. It was found that a stimulus presented without a reinforcing agent among positive CSs acquires strong inhibitory properties with regard to that agent. It is hypothesized that this stimulus becomes a CS signalling no-US, and as such it is antagonistic to a CS signalling the presentation of the US. In this way the extinction of a CR by non-reinforcement of the appropriate CS may be considered as a transformation of the positive CR into the negative one, and it obeys the same rules as those obeyed in transformations of heterogenous CRs.

A great part of the research work performed in the Department is concerned with the problems of functional organization of particular regions in the brain. Much work was done on the function of the prefrontal area. It has been established that lesions in this area may produce the following behavioral disorders: a) disinhibition of inhibitory alimentary CRs, b) impairment of delayed responses, and c) „magneto-reaction" consisting in strong directional response to the source of a CS. It seems that these symptoms are independent from one another and are produced by a different placement of lesions.

Studies on the functional role of the sensori-motor cortex led to a conclusion that this region is important for a technical aspect of the execution of the learned motor act, but not for its programing. It seems that this programming is accomplished by the caudate nucleus with regard to simple movements and by the premotor cortex with regard to skillful movements.

A great deal of work was performed on the functional role of the emotive brain and in particular of the hypothalamus and amygdala. Experimental data show that these two structures are concerned with various drives, and in particular with hunger, fear and anger. There is some evidence to show that the centres controlling particular drives consist of two sub-centers, one being concerned with excitation of the drive, and the other being concerned with its inhibition or satisfaction. Since, as stated before, instrumental CRs are produced by reduction of appropriate drives, there is a close relation between stimulation or removal of particular parts of the emotive brain and instrumental responding.

The study devoted to the problem of plasticity of URs led to the conclusion that the intensity of these reflexes changes considerably with their mere repetition: some of them tend to increase by repeated elicitation, others on the contrary tend to decrease and even disappear.

In recent years two important lines of investigation have been started in the Department, namely the study of the function of the isolated waking cerebrum obtained by pretrigeminal transection, and the study of functional properties of the visual system.

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REFLEX AS THE UNIT OF NEURO-BEHAVIORAL ACTIVITY: A THEORETICAL MULTIDISCIPLINARY APPROACH TO THE REFLEX ACTIVITY IN HIGHER ANIMALS

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I. INTRODUCTION

As is well known, for several decades particular fields of research connected with CNS activity (spinal cord physiology, brain physiology, behavioral sciences, human psychopathology) developed in striking isolation from each other. In addition, introspective psychology was almost completely abandoned. Since about the forties the interdisciplinary approach to CNS research has been initiated. Many authors have been trying to build some bridges between particular fields, especially between brain physiology and behavioral sciences. However, multidisciplinary approaches to the CNS activity have been much less frequent. The aim of the present paper is a comprehensive discussion (based on different sorts of available information) of the concept of reflex activity of higher animals. It should be noted that this task is considerably easier due to the recent discussion of reflex processes by Konorski (1967).

Definition of reflex. As a reflex we shall understand all neural processes (or neural responses) and following effector responses evoked by any currently acting stimulus.

A number of terms used in this definition need a further explanation. First of all, it should be noted that by a *stimulus* we understand a physical event (or a change in physical energy), which elicits the activity of receptors or higher levels of the afferent part of the nervous system (e.g. receptive neurons in the respiratory and alimentary centers). Besides, in this definition the stimulus is a collective term comprising both the *evoking* stimulus and those corresponding *cue* stimuli, which are produced by the effector response (see below).

The term *currently* means that the appropriate neural and effector responses are evoked by the stimulus without involving any „holding" mechanism (see Hebb 1958). In other words, it may be assumed that the effector response may be delayed (with regard to the moment of the end of stimulus presentation) for seconds but not for minutes. In the delayed-response situation, for example, the „preparatory stimuli" may evoke the long-lasting (non-reflexive) central processes (see below).

As is well known, neural processes involve central and peripheral processes. The latter obviously play only a secondary role: they are mainly the conducting links between the receptors and the CNS on the one hand, and between the CNS and effectors, on the other. Therefore, for the sake of simplicity our discussion of neural processes will be limited only to *central* processes. It may be assumed that the central part of a reflex is composed of a number of *unitary* central processes. As a unitary central process we will understand the action of any neural center, in the anatomo-functional meaning of the latter term.

In some reflexes (in consummatory and preparatory reflexes, see Chapter III, Section 3) the effector responses form a complex entity, which will be called a *behavioral* response. The behavioral response of chain reflexes needs some comment. It may be considered as composed of a number of *unitary* behavioral responses. In the reflex evoked by the sight of food, for example, two behavioral units may be clearly distinguished: running to the food and taking it into the mouth.

To end our consideration on reflex definition, it should be noted that we are aware that the term *reflex* has several more limited meanings (see English and English 1958). However, for the purpose of our discussion it seemed to be more reasonable to use this term in its broad reference than to create a new term. In addition, in the light of many essential similarities between the activity of the cerebrum and lower parts of the CNS (see Konorski 1948), we believe that such a broad application of the term reflex is correct.

Non-reflexive central processes. It is important to make a distinction between reflexive and non-reflexive central processes. The latter are not the subject of this paper but for the sake of clarity they will be briefly commented on. The non-reflexive central processes may be subdivided into *autogenic* (or spontaneous) processes (those observed in the isolated central structures, for example), and *acquired* processes. The latter exist due to stimuli which acted in the past.

Two features of the acquired non-reflexive processes should be noted.

First, these processes may influence the reflexive ones. In the mentioned delayed-response situation, for example, the non-reflexive central processes evoked by the „preparatory stimulus" (presented some time ago) influence the reflexive central processes evoked by the „releasing stimulus".

Second, the acquired non-reflexive processes may evoke directly some effector responses. As an example, the following situation may be given: a man is „resting" with closed eyes in an armchair; after a good while spent on thinking about a number of things, he suddenly realizes that he has forgotten to close the door; then he gets up and does this. This behavioral response obviously is not evoked by the reflexive central process (to any currently acting stimulus), but by the acquired non-reflexive process which appeared due to the appropriate stimulus which acted some time ago.

Basic stimuli and cue stimuli. According to their biological role the stimuli may be divided in two categories. The stimuli of the first category are directly biologically important (e.g. nociceptive stimuli) and will be called *basic* stimuli. The stimuli of the second category play a subsidiary role with regard to the basic stimuli and will be called *cue* stimuli. Their main role is to signal the basic stimuli (the sight and smell of the predatory animal signal the appropriate nociceptive stimuli, the sight and smell of food signal the taste stimulus, etc.), and to inform about the effector response performance (see below).

It should be noted, however, that some stimuli have obviously double meaning: basic meaning with regard to one reflex and cue meaning with regard to other. For example, a nociceptive stimulus (i.e. the basic stimulus with regard to the appropriate defensive reflex) may simultaneously signal the food. For the sake of simplicity, the double meaning of the particular stimuli will be usually neglected in our discussion.

Feedback control in reflexes. In some simple reflexes feedback control plays a relatively small role (Jankowska 1959, Górska and Jankowska 1961, Górska et al. 1961, Knapp et al. 1963). On the other hand, in complex reflexes, particularly in chain reflexes, this control is obviously essential.

Feedback control may be executed in three ways. First, the effector response modulates directly the intensity of the evoking stimulus (Fig. 1, loop I). In the flexor reflex to the nociceptive stimulus, for example, the effector response decreases the intensity of the evoking stimulus.

Second, the effector response provides a number of proprioceptive and exteroceptive cue stimuli (loop II). In the approach alimentary reflex evoked by an auditory stimulus, for example, the sight of food and its odor (which appear in the course of reflex) are such cue stimuli.

Third, the effector response modulates the intensity of the cue stimuli (loop III). In the afore-mentioned alimentary reflex, for example, the effector response (running towards food) will increase the intensity of the appropriate visual and olfactory stimuli.

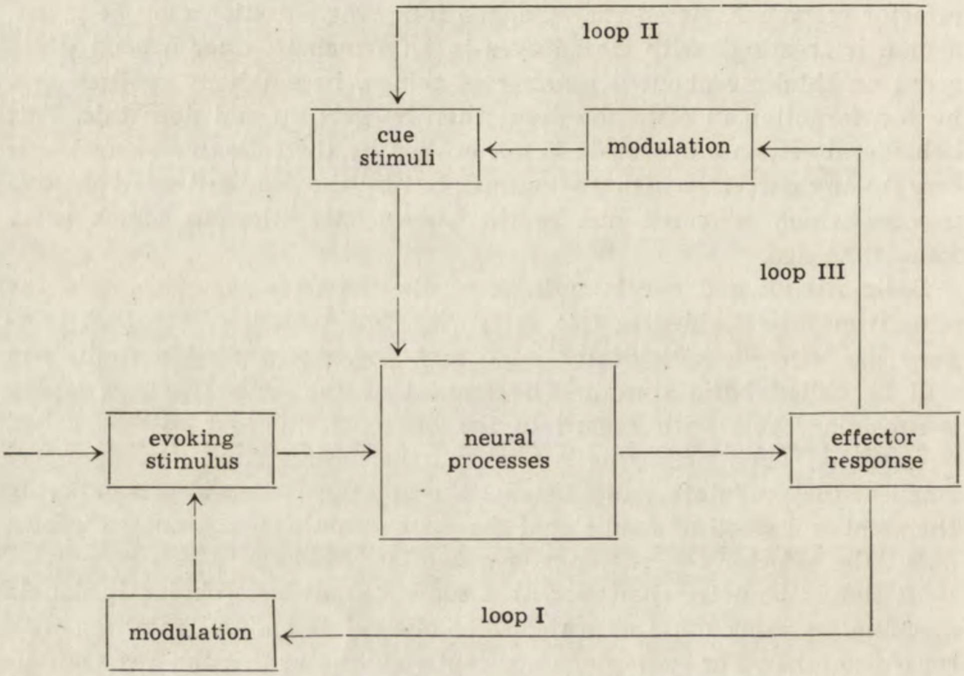

Fig. 1. Feedback control in a reflex

II. ESSENTIAL COMPONENTS OF REFLEXES

1. Central part of reflex

As has been already mentioned, there is a number of unitary central processes in each reflex. Unfortunately our knowledge of these processes, especially of those present in an intact animal, is unsatisfactory. In this Section an attempt will be made to characterize briefly some important kinds of central processes.

Neuropsychic processes. As is well known introspectively, in man some stimuli produce *psychic* responses. It is reasonable to assume that the latter are also present in higher animals (Beritov 1965, Thorpe 1966, Doty 1967, Konorski 1967). Moreover, it will be assumed that psychic responses are manifestations of definite unitary central processes. The latter will be called *neuropsychic* processes.

There are several kinds of psychic responses. Some are affectively indifferent and will be called *gnostic* responses. On the other hand, some are unpleasant or pleasant and will be called negative and positive *emotional* responses (or negative and positive *emotions*), respectively. For example, a painful stimulus applied to the skin or a tasty food in the mouth produce in addition to the somesthetic gnostic responses, the negative or positive emotions, respectively. Accordingly, *gnostic* and *emotional* neuropsychic processes will be distinguished, and the latter subdivided into *negative* and *positive* processes.

In addition, the psychic responses may be divided into perceptions and images. The corresponding neuropsychic processes will be called *perceptual* and *imaginal* processes, respectively. In consequence, four main types of neuropsychic processes may be distinguished:

Perceptual-gnostic process
Imaginal-gnostic process
Perceptual-emotional process
Imaginal-emotional process

We have good reasons to believe that neuropsychic processes are located in the cerebrum. The gnostic processes seem to be located mainly in the associative cortex, and the negative and positive emotional processes are situated in different places of the limbic system and hypothalamus (for localization of the emotional processes see Olds 1956).

On the other hand, there is no clear evidence to answer the question of whether the perceptual and imaginal neuropsychic processes have the same or different localization. Konorski (1967) put forward a hypothesis that both perception and image are manifestations of excitation of the same neurons. According to this author, the different psychic responses (perception versus image) are due to different ways of excitation of these neurons, from the periphery and by association, respectively. In the first case, the orienting response (see Section 2) is present, which gives to the experience the mark of externalization and reality of which the image is devoid.

Extra-acting processes. Some unitary central processes of a given reflex may affect central processes of other reflexes and, therefore, they will be called *extra-acting* central processes. Their effect may be clearly antagonistic or synergic to the central processes of other reflexes, and in this way detected when the latter are in operation. For example, some defensive reflexes may inhibite some alimentary reflexes as shown by the diminution of the behavioral and psychic alimentary responses.

All neuropsychic processes seem to be extra-acting. The effect of the emotional extra-acting processes is usually strong. On the other hand, the gnostic processes are usually easily inhibited by extra-acting processes.

Modifying processes. Some central processes produce durable central changes, which have been called *plastic* changes by Konorski (1948) and are manifested by such phenomena as habituation, perceptual learning, conditioning and extintion. In other words, these central processes modify the reflexes. Consequently they will be called *modifying* central processes.

Before further analysis of the modifying central processes, the phenomena of habituation and conditioning must be commented upon. Several facts indicate that there are two kinds of habituation, namely, a *slow* habituation and a *rapid* habituation. In slow habituation, reflexes become considerably diminished only after hundreds of trials (e. g. habituation of spinal reflexes, Kozak and Westerman 1966, Thompson and Spencer 1966). On the contrary, during rapid habituation reflexes become considerably attenuated already after a few trials (e. g. habituation of orienting reflexes).

Similarly, a *slow* conditioning and a *rapid* conditioning should be distinguished. In the slow conditioning an unstable conditioned response appears only after many trials (conditioning of spinal reflexes, see Morgan 1965 for review; conditioning of patellar reflex; conditioning of light reflex, see for review Żernicki 1964; conditioning in the isolated midbrain, Żernicki et al. 1969; etc.). On the contrary, in rapid conditioning the conditioned response appears after a few trials or even after one trial (one trial learning).

With regard to the neuropsychic criterion (see above) three types of modifying processes may be distinguished:

Non-neuropsychic modifying process
Gnostic modifying process
Emotional modifying process

It may be assumed that the effects of the non-neuropsychic modifying processes consist in slow habituation and slow conditioning; the effects of the gnostic modifying processes, in rapid habituation, perceptual learning and slow conditioning; and the effects of the emotional modifying processes, in rapid conditioning.

The plastic changes may appear either in this reflex in which there are the corresponding modifying processes, or in other reflexes, or in both. Accordingly, we will distinguish between *intra-reflex* and *extra-reflex* plastic changes. The latter are obviously evoked by the extra-acting modifying processes. The intra-reflex plastic changes are manifested by habituation, perceptual learning, conditioning and extinction; the extra-reflex plastic changes only by conditioning.

The elaboration of the intra-reflex conditioned processes needs a comment. It occurs due to the *interaction* between the central processes to the evoking stimulus and those to the cue stimuli (see Chapter I). For example, in the flexor reflex evoked by a nociceptive stimulus the animal can learn to make the flexion in the most efficient way due to the interaction of effects of the nociceptive stimulus and proprioceptive stimuli.

2. Effector part of reflex

To begin with, it should be noted that in some reflexes there are practically no overt effector responses. The inhibitory reflex to a fully differentiated stimulus and passive avoidance reflex are good examples of such reflexes. In man the reflexes without overt effector responses are obviously numerous. For example, central processes evoked by the visual and auditory stimuli emitted by a television set may be almost not followed by any overt behavioral responses.

In a given reflex three different kinds of effector responses may be usually distinguished: the specific response, the targeting (or orienting) response (see Konorski 1967), and the arousal response. These responses are obviously closely interrelated but for the sake of clarity they will be described separately.

The specific response. In particular reflexes there are strong differences in degree of complexity of the specific response. Particularly in chain reflexes the specific response may be very complex (see Chapter I). Nevertheless, the basic properties of all specific responses may be analysed jointly.

It may be assumed that the essential role of the specific response is to change the intensity of a definite basic stimulus (see Chapter I). In the reflexes evoked by the basic stimuli, the role of the specific response is to change the intensity of the evoking stimulus. This is executed by the feedback effect of the specific response on the stimulus. Consequently such specific response will be called *feedback* response (Fig. 2A). Putting on a pullover in a cold room may be an example of a feedback specific response; the evoking stimulus (cold) is the basic stimulus, and the role of the specific response (putting on a pullover) is to decrease its intensity.

In the reflexes evoked by the signalling cue stimuli, the role of the specific response is to change the intensity of the expected (signalled)

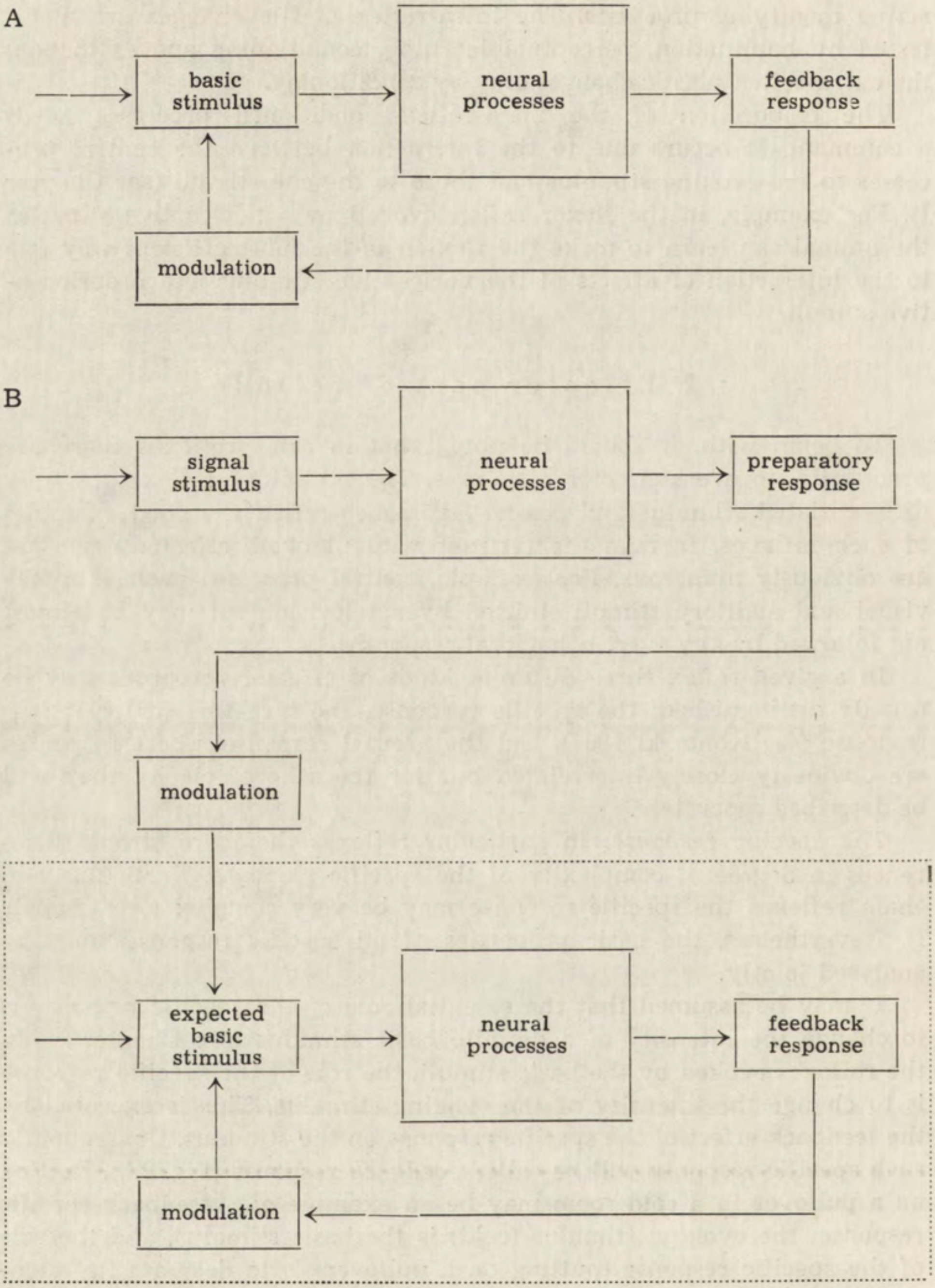

Fig. 2. The comparison of the effects of feedback response (A) and preparatory response (B). The reflex to be expected is surrounded by dotted line

stimulus. In other words, the specific response has a preparatory character with regard to the expected basic stimulus. Consequently it will be called *preparatory* response (see Sherrington 1906) (Fig. 2B). Putting on a pullover in response to the information "central heating is off" may be an example of the preparatory response (putting on a pullover will attenuate the expected cold stimulus) [1].

The feedback responses may be furthermore subdivided in two types. The responses of the first type are never preceded by the appropriate preparatory responses and will be called *simple* feedback responses. The responses of the second type can "have" the appropriate preparatory responses and accordingly will be called *consummatory* responses (see Sherrington 1906, Craig 1918, Tinbergen 1955). For example, the mentioned feedback response (putting on a pullover in a cold room) is the consummatory response because it may be preceded by the appropriate preparatory dressing response.

The specific response of a given reflex may either decrease the stimulus (either the evoking stimulus or the expected one) or increase it (see Kozak and Westerman 1966). Accordingly, both feedback and preparatory responses will be divided into *negative* and *positive* responses. Six types of specific responses obtained in this way and their examples are presented below:

Negative simple feedback response	Constriction of pupils to light stimulus
Positive simple feedback response	Grasping response
Negative consummatory response	Putting on a pullower in a cold room
Positive consummatory response	Eating food being in mouth
Negative preparatory response	Putting on a pullower before going out
Positive preparatory response	Putting food into the mouth

Concerning the preparatory responses, it must be noted that due to the negative preparatory response the effect of the expected stimulus is usually decreased to nil, i. e. this stimulus is avoided. For example, due to flight painful contact with an enemy may be avoided. On the other hand, without the positive preparatory response the effect of the expected stimulus would be usually nil, i. e. this stimulus would not be available. For example, without putting the food into the mouth the taste of the food stimulus would not be available.

It is useful to introduce special terms for the negative and positive consummatory and preparatory responses. The negative and positive

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[1] Recent experiments of Stępień and her associates (Stępień and Stępień 1965, Stępień et al. 1966, Stępień and Stamm, in preparation) showed that in cats and monkeys with frontal lesions the cue stimulus may produce the targeting response instead of the preparatory one. Such operated animals run to the source of the signalling stimulus instead of to the food.

consummatory responses will be called *escape* and *consumptive* responses, and the negative and positive preparatory responses, *avoidance* and *approach* responses, respectively:

Consummatory responses	Preparatory responses
Escape response	Avoidance response
Consumptive response	Approach response

Besides, the common term for both escape and avoidance responses will be *defensive* responses; and for both consumptive and approach responses, the *acquisitive* responses:

Defensive responses	Acquisitive responses
Escape response	Consumptive response
Avoidance response	Approach response

The relation of specific responses to neuropsychic responses. Introspectively, we know that some effector responses are preceded by the psychic response, or responses. For example, the behavioral response of putting tasty food into the mouth is preceded by seeing this food (gnostic response) and feeling of a definite appetite (emotional response). It will be assumed that such effector responses are mediated by the appropriate neuropsychic processes (neuropsychic links).

With regard to the neuropsychic links there is an essential difference between the simple feedback responses on the one hand, and the consummatory and peparatory responses, on the other. The simple feedback responses do not seem to be mediated by the neuropsychic links, while the consummatory and preparatory responses seem to be mediated.

The *emotional* neuropsychic links corresponding to the latter responses need special consideration. As is well known, particular types of consummatory and preparatory responses are accompanied by different emotional perceptions:

Consummatory responses; consummatory emotions

Escape response; pain, displeasure
Consumptive response; pleasure

Preparatory responses; preparatory emotions

Avoidance response; fear
Approach response; appetite

It may be assumed, therefore, that the appropriate emotional neuropsychic processes corresponding to the particular responses (pain neuropsychic process, pleasure neuropsychic process, etc.) have different anatomical localization, i. e. are situated differently in the limbic system and hypothalamus.

Furthermore, it may be assumed that emotions, which accompany defensive responses (pain, displeasure, fear) are *negative;* while those, which accompany acquisitive responses (pleasure, appetite) are *positive* (see Section 1). However, it should be noted that the sign of the preparatory emotions is less clearly determined than that of the consummatory ones. Particularly, the positive meaning of the appetite may be introspectively questionable. However, we know that stimuli evoking appetite may be the reinforcers in instrumental learning. The reinforcing value of strip-tease seems to be a good example.

The targeting (orienting) response. This response improves the perception of a stimulus. It may be assumed that the targeting response is at least partially mediated by a defective perceptual-gnostic process (Fig. 3B). The role of the targeting response is obviously important for perception of the cue stimuli (particularly those acting on distance-receptors). In response to the basic stimuli, however, the targeting response (if compatible with the specific response) is also usually present. In the reflex elicited by a painful stimulus applied to the leg, for example, the targeting response usually consists in turning the head and eyes towards the source of stimulation, and in eye accomodation.

Our information concerning the reflex arc of the targeting responses are incomplete. After the lesions of the sensory cortex targeting responses disappear in man and are seriously affected in animals. After the ablation of the visual cortex, for example, the fixation response disappears in man (see Holmes 1938) and is affected in the cat (Dreher et al. 1965). Besides, we have good reasons to believe that the frontal cortex has an inhibitory significance for the targeting response (Butter 1964, Alvarado-P. 1967, Dreher and Żernicki 1969).

For the sake of clarity it will be already noted that the reflex evoked by the so called „neutral" stimuli has no specific response and is composed exclusively of the targeting and arousal responses. This reflex will be called *targeting* (or orienting) reflex.

The arousal response. The role of the arousal response is unsatisfactorily understood. Among others it increases the general responsiveness of an animal. This effect is largely produced by excitation of a number of effectors related to the analysers. In the visual analyser, for example, the arousal response to a stimulus of any sensory modality consists in exophtalmus, retraction of the nictitating membrane and pupillary dilatation.

As is well known, the arousal response is mediated by the reticular formation and the reticulo-cortico-reticular loop (see for review Rossi and Zanchetti 1957, Magoun 1963). It may be assumed, that arousal responses to some stimuli are mediated by the emotional neuropsychic links (see Lindsley 1951). Consequently in some reflexes the loop between the reticular formation and the limbic cortex may be important for the arousal response.

III. CLASSIFICATION OF REFLEXES

1. Introductory remarks

The first attempt at a coherent reflex classification (in the broad meaning of this term) was made by Sechenov as early as 1863. This author distinguished three types of reflexes: pure, passionate and psychic (Sechenov 1935, Beritov 1967). Later on, however synthetic approaches to the neurophysiological and psychological problems have been infrequent (see Chapter I). In consequence, at present there is no full and generally accepted reflex classification.

However, there is a number of general reflex divisions, which are in common use. First of all, the reflexes are divided into unconditioned and conditioned (Pavlov 1928). The latter are further subdivied into classical and instrumental reflexes (see Hilgard and Marquis 1940) or first type and second type reflexes (Miller and Konorski 1928). Besides, defensive and appetitive (see Craig 1918) reflexes, and excitatory and inhibitory reflexes are distinguished.

Recently, some authors put forward important ideas concerning reflex classification:

Beritov (1965). This author distinguishes three types of behavior: innate (or instinctive) behavior, conditioned behavior, and image-driven (or psychoneural) behavior. In respect to the last type of behavior, Beritov reports numerous experimental data suggesting that images are present in higher vertebrates. Beritov assumes that image-driven behavior, if repeated many times in the same environment and automatized, is transformed into chain conditioned behavior (chain conditioned reflex).

Hebb (1958). The classification of Hebb resembles that of Beritov. Hebb distinguishes essentially three types of behavior: reflex, conditioned reflex, and behavior controlled partially by mediating processes (ideas, thinking). In addition, Hebb distinguishes the phenomenon of set, which may be either humoral or neural.

Konorski (1967). Konorski divides reflexes in three ways: unconditioned (or basic) versus conditioned reflexes, preservative versus protective reflexes, and preparatory (or drive) versus consummatory reflexes (see footnote in Section 3). The last division is essential in Konorski's theory concerning the organization of brain activity.

Our reflex classification is related to the attempts of aforementioned authors. In particular, due to the unsatisfactory amount of neurophysiological data, it is also mainly based on the psychic and behavioral criteria. However, our classification is more elaborated, taking into account several aspects of reflexes discussed in Chapter II.

2. Neuropsychic criteria

Depending on the presence of the neuropsychic processes, the *non-neuropsychic* and *neuropsychic* reflexes will be distinguished.

Anatomically, there is an important difference between these two kinds of reflexes, namely, the non-neuropsychic reflexes are essentially not mediated by the cerebrum (as shown by numerous observations on decerebrate animals) while the neuropsychic reflexes are so mediated (see Chapter II, Section 1). Accordingly, the non-neuropsychic and neuropsychic reflexes may be also called *spinal cord-brain stem* reflexes and *cerebral* reflexes, respectively.

In the majority of the neuropsychic reflexes both gnostic and emotional neuropsychic processes are involved. These reflexes will be called *gnostic-emotional* reflexes. In some instances, however, we have to do with *pure-gnostic* reflexes or *pure-emotional* reflexes. As an example of a pure-gnostic reflex, the targeting reflex may be given, whereas the hunger and satiation reflexes (see Chapter IV) are examples of the pure-emotional reflexes.

Introspectively, it is difficult to say whether in gnostic-emotional reflexes a gnostic response and the corresponding emotion appear at the same time or successively. For example, it is difficult to say whether we realize at the same time that a cooky is sweet (gnostic response) and good (emotion), or first we know that it is sweet and then that it is good. In consequence, we do not know whether the arc of o gnostic--emotional reflex has two cerebral branches (which seems to be more likely), one running through the associative cortex and the second through the limbic system; or whether simply the arc of a neuropsychic reflex runs successively through both these structures.

In some neuropsychic reflexes there are only perceptual processes, while in others there are in addition the imaginal ones. For example, leg flexion to a nociceptive stimulus may be simply mediated by the corresponding perceptual link; while in avoidance reflex to an acoustic, stimulus the auditory perceptual process is followed by the visual imaginal process (manifested by the image of the nociceptive stimulus). The reflexes of the first kind will be called *perceptual* reflexes and those of the second kind, *perceptual-imaginal* reflexes, or briefly *imaginal reflexes.*

Summing up, according to the neuropsychic criterion, first of all two big groups of reflexes may be distinguished:

Non-neuropsychic reflexes
Neuropsychic reflexes

Furthermore, the neuropsychic reflexes may be divided independently according to the gnostic-emotional and perceptual-imaginal criteria:

Pure-gnostic reflex	Perceptual reflex
Pure-emotional reflex	Imaginal reflex
Gnostic-emotional reflex	

It should be noted that if Konorski's concept, that both perceptions and images are manifestations of functions of the same neurons (see Chapter II, Section 1), were true; the perceptual reflexes and imaginal reflexes would essentially differ only in the number of neuropsychic centers involved: the perceptual reflexes would involve only one center, while the imaginal reflexes at least two.

3. Behavioral criteria

As was already indicated in Chapter II, Section 2, the *specific* effector response is an essential component of a reflex, while the targeting and arousal responses play only a subsidiary role. For the sake of simplicity, therefore, the latter responses will be ignored in the following division of reflexes. In consequence, this division will not include the targeting reflex, in which the specific response is absent.

Feedback and preparatory reflexes. In accordance with the division of specific responses made in Chapter II, Section 2, three types of reflexes will be distinguished:

Simple feedback reflex
Consummatory feedback reflex
Preparatory reflex[2]

The stimuli evoking the consummatory and preparatory reflexes will be called the *consummatory* and *preparatory* stimuli, respectively. The latter (in contrast to the consummatory stimuli and the stimuli evoking the simple feedback reflexes) usually act on the distance-receptors.

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[2] It should be noted that recently the term *preparatory reflex* was used by Konorski and Sołtysik with a partially different meaning (Sołtysik and Konorski 1966, Konorski 1967). Accordingly to these authors, in the preparatory reflex (or drive reflex) the essential role is played by the "hunger stimuli". On the other hand, we think that these stimuli evoke separate "hunger reflexes", which control the corresponding preparatory and consummatory reflexes (see Chapter IV).

There are mutual relations between the consummatory reflexes and the corresponding preparatory reflexes. On the one hand, as defined, the preparatory reflexes "work" for the corresponding consummatory reflexes. On the other hand, the consummatory reflexes facilitate the corresponding preparatory reflexes. For example, eating a small portion of tasty food (consummatory reflex) facilitates the corresponding preparatory reflex (see Wyrwicka 1952, Żernicki and Ekel 1959).

Negative and positive reflexes. Again in accordance with the division of specific responses (Chapter II, Section 2) the following types of reflexes will be distinguished:

Negative simple feedback reflex
Positive simple feedback reflex
Negative consummatory reflex
Positive consummatory reflex
Negative preparatory reflex
Positive preparatory reflex[3]

Furthermore, the short names applied for the negative and positive consummatory and preparatory specific responses will be extended to the corresponding reflexes:

Consummatory reflexes	Preparatory reflexes
Escape reflex	Avoidance reflex
Consumptive reflex	Approach reflex

Finally, again in accordance with the terminology of the specific responses, the *defensive* and *acquisitive* reflexes will be distinguished:

Defensive reflexes	Acquisitive reflexes
Escape reflex	Consumptive reflex
Avoidance reflex	Approach reflex

The stimuli evoking the defensive and acquisitive reflexes will be called *aversive* and *attractive*, respectively.

4. Neuropsychic and behavioral criteria combined

To begin with, it should be stated that feedback reflexes are either non-neuropsychic or neuropsychic (see Chapter II, Section 2). On the other hand, the preparatory reflexes are usually (or possibly always) neuropsychic.

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[3] The terms negative reflex and positive reflex are used by some authors in different meaning, namely, for denoting the inhibitory and excitatory conditioned reflexes, respectively.

The neuropsychic feedback reflexes may be pure-gnostic (see below), pure-emotional (hunger and satiation feedback reflexes) or gnostic-emotional. The pure-gnostic feedback reflexes and the non-neuropsychic reflexes form the group of simple feedback reflexes. On the other hand, the pure-emotional feedback reflexes and gnostic-emotional feedback reflexes are just the consummatory reflexes.

The preparatory reflexes may be either pure-emotional (hunger and satiation preparatory reflexes) or gnostic-emotional (majority of reflexes).

Taking into account all above considerations, according to both neuropsychic and behavioral criteria five main types of reflexes may be distinguished (Fig. 3):

Non-neuropsychic simple feedback reflex
(or shortly, non-neuropsychic reflex)

Targeting (or orienting) reflex

Neuropsychic simple feedback reflex
(or pure-gnostic neuropsychic feedback reflex)

Consummatory reflex

Preparatory reflex

Except for targeting reflexes, all of these may be subdivided into negative and positive.

The neuropsychic simple feedback reflex needs a comment. It this reflex the specific response is not mediated by the neuropsychic link but the targeting response is present and the stimulus is perceived (Fig. 3C). The reflex evoked by a beam of weak light may be given as an example. There are good reasons to believe that in this reflex the specific response (constriction of pupils) is not mediated by a neuropsychic link, but the targeting response (fixation of eyes) is mediated (Żernicki et al. 1969).

The neuropsychic feedback reflexes may be considered as the non-neuropsychic reflexes (spinal cord-brain stem reflexes) enriched by the cerebral arc. In the pure-gnostic feedback reflex the specific response is mediated by the spinal cord and/or brain stem, and the targeting response by the cerebrum (Fig. 3C). In the consummatory reflex the specific response is mediated by two separate branches of the reflex arc: one runs exclusively through the spinal cord and/or brain stem, and the second in addition through the cerebrum (Fig. 3D). As an example, the reflex evoked by a painful stimulus applied to the leg may be considered. In the decerebrate animal, this stimulus produces flexion of the leg (the spinal cord branch of the reflex arc is in action). In the intact animal, however, due to the cerebral branch the stimulus usually evokes a complex behavior, which in man may even include taking a pain relief pill.

It may be noted that some stimuli, which usually produce non-neuropsychic reflexes (spinal cord-brain stem reflexes), evoke the consummatory reflexes (cerebral reflexes) when the intensity of the stimulus is increased. The humoral stimulus evoking the respiratory reflex (increase of CO_2 content in blood) is a good example. This humoral stimulus normally evokes the brain stem reflex involving only the respiratory muscles, but when its intensity is increased, more or less complex consummatory reflex will appear (opening the window, for example).

Finally, the problem of the imaginal link in the neuropsychic reflexes should be considered. It may be assumed that the pure-gnostic reflexes and some consummatory reflexes are perceptual. On the other hand, the majority of complex consummatory and preparatory reflexes are imaginal (see next Section). It may be assumed that in the preparatory reflexes the image of the expected stimulus is usually present. In both consummatory and preparatory reflexes the images of the expected cue stimuli may be present. For example, in a defensive reflex (in escape reflex or avoidance reflex) the image of the appropiate tool, necessary to escape or avoid the nociceptive stimulus, may be present.

5. Learning criteria

Unmodifying and modifying reflexes. Depending on the presence of modifying central processes (see Chapter II, Section 1), the *unmodifying* reflexes and *modifying* reflexes will be distinguished.

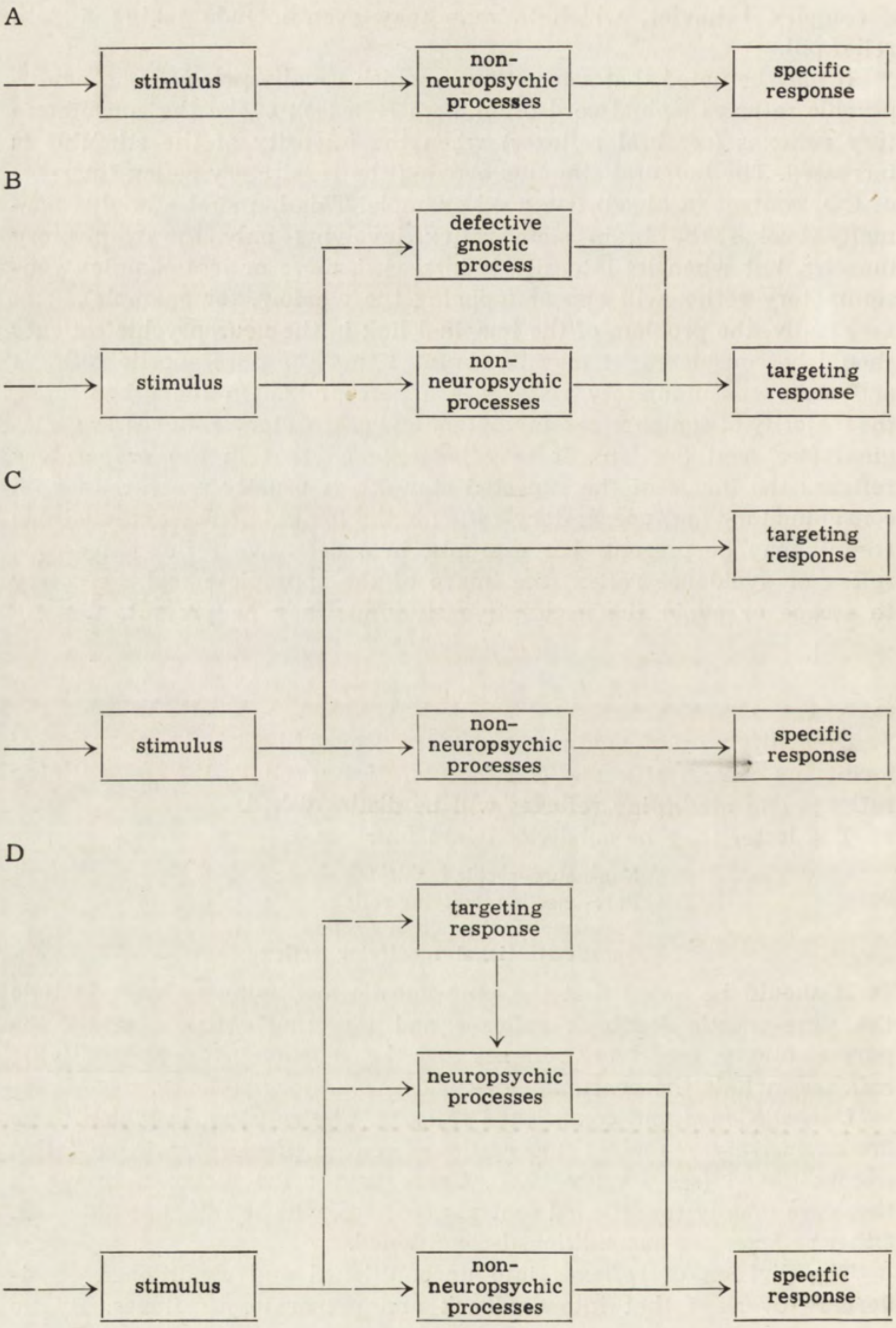
The latter may be subdivided into four types:

Non-neuropsychic modifying reflex
Pure-gnostic modifying reflex
Pure-emotional modifying reflex
Gnostic-emotional modifying reflex

It should be noted that the pure-gnostic modifying reflexes include the pure-gnostic feedback reflexes and targeting reflexes, while the pure-emotional modifying reflexes and the gnostic-emotional modifying reflexes include the consummatory and preparatory reflexes.

Unconditioned and conditioned reflexes. The reflexes, in which there are exclusively or mainly unconditioned central processes, will be called *unconditioned* (see Pavlov 1928). Consequently the reflexes, in which there are mainly conditioned central processes, will be called *conditioned*. Other reflexes are *unconditioned-conditioned.*

The division of reflexes into unconditioned and conditioned considerably overlaps that into feedback and preparatory reflexes. By no


A
stimulus
non-neuropsychic processes
specific response
B
defective gnostic process
stimulus
non-neuropsychic processes
targeting response
C
targeting response
stimulus
non-neuropsychic processes
specific response
D
targeting response
neuropsychic processes
stimulus
non-neuropsychic processes
specific response

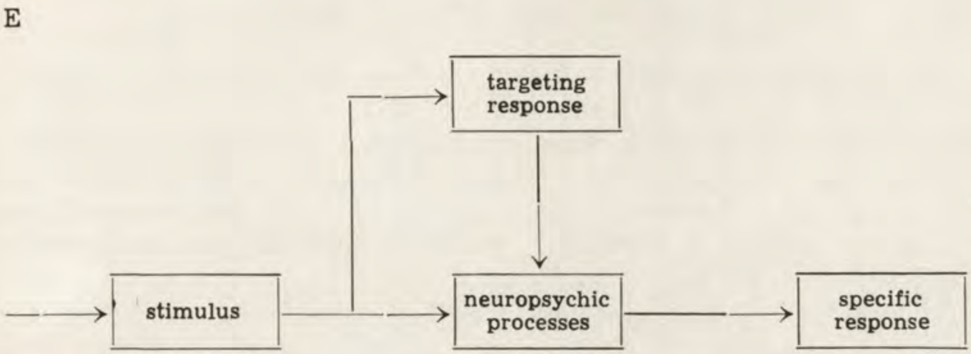


Fig. 3. Hypothetical diagrams of basic types of reflexes distinguished according to the neuropsychic-behavioral criterion (simplified). A, non-neuropsychic reflex; B, targeting reflex; C, neuropsychic simple feedback reflex; D, consummatory reflex; E, preparatory reflex. For simplicity, except of B, the central processes mediating the targeting response are omitted

means, however, is this overlapping complete. First, as already mentioned many reflexes have mixed, unconditioned-conditioned character. The feedback reflexes evoked by different kinds of food placed in the mouth are a good example. Essentially the masticatory movements are obviously innate. However, depending on the kind of food, the subject learns to modify them. For example, tasteless food will be almost immediately swallowed, while tasty food (e.g. sweets) will be carefully masticated. Another example may be the flexor reflex which in adult individuals has obviously unconditioned-conditioned character. Secondly, there is a number of purely unconditioned preparatory reflexes. For example, the sight of as nake evokes the unconditioned avoidance reflex in a chimpanzee. Similarly, the odor of meat evokes the unconditioned approach reflex in a dog (Tsitovich 1911).

The pure unconditioned reflexes seem to be either non-neuropsychic reflexes or perceptual ones. On the other hand, the conditioned and unconditioned-conditioned reflexes always seem to be neuropsychic. The conditioned reflexes in the developing stage or intrequently evoked are imaginal reflexes, while the automatized ones (e.g. car driving by an experienced driver) seem to be perceptual reflexes (see Beritov 1965).

This may explain why the newly acquired conditioned reflexes are very fragile and may be easily affected by a number of factors (among others by the extra-acting processes of other reflexes). On the other hand, the overtrained conditioned reflexes are in this respect similar to the unconditioned ones. For example, the overtrained conditioned reflexes are very resistant to fatigue (Żernicki and Konorski 1959).

IV. HUNGER AND SATIATION REFLEXES

As defined in Chapter III, Section 3, in the course of the positive feedback reflexes the intensity of the stimulus is increased. The strength of the stimulus is usually increased first to a maximal value and then maintained at this level. For example, in the grasping reflex the contact of the grasping object with the skin of the hand is first increased and then maintained. It is obvious, therefore, that the positive feedback reflexes (and the corresponding preparatory reflexes) must be appropriately controlled to avoid their endless operation. It is beyond the scope of this paper to discuss such control in detail. However, some important points will be emphasized.

In the simple feedback reflexes the control in question seems to be mainly due to the antagonistic effect of other reflexes. For example, in a hen perching on a stick the grasping reflex may be interrupted by the antagonistic food approach reflex.

However, to control consumptive reflexes and the corresponding approach reflexes, there exist two special kinds of defensive reflexes, namely, *hunger* reflexes (alimentary hunger reflex, thirst reflex, sexual hunger reflex, etc.) and *satiation* reflexes (alimentary satiation reflex, water satiation reflex, sexual satiation reflex, etc.) (Fig. 4). It may be noted that both hunger and satiation reflexes are defective because they have no specific behavioral responses. They are evoked, respectively by the hunger and satiation stimuli, which seem to be mainly humoral.

Depending on the role of the control by the hunger and satiation reflexes, three kinds of acquisitive reflexes may be distinguished:

i) Some acquisitive reflexes may be evoked only when the corresponding *hunger* reflexes are in operation. For example, the water acquisitive reflexes (approaching and drinking water) are present only when the thirst reflex (clearly manifested by the thirst emotional response) is present. It must be noted that there is a very intimate relation between the acquisitive reflexes of this kind and the corresponding hunger reflexes; namely, the specific behavioral responses of a given pair of approach and consumptive reflexes are *simultaneously* the specific response of the corresponding escape hunger reflex or avoidance hunger reflex. For example, water approach and consumptive reflexes may be simultaneously either the thirst escape reflex or thirst avoidance reflex: the first case takes place when we approach water and drink it because we are thirsty, the second case, when we do this because we expect that during some time we will be deprived of water.

In the control of the acquisitive reflexes of this group the satiation reflexes seem to be also in operation. The appropriate satiation stimuli

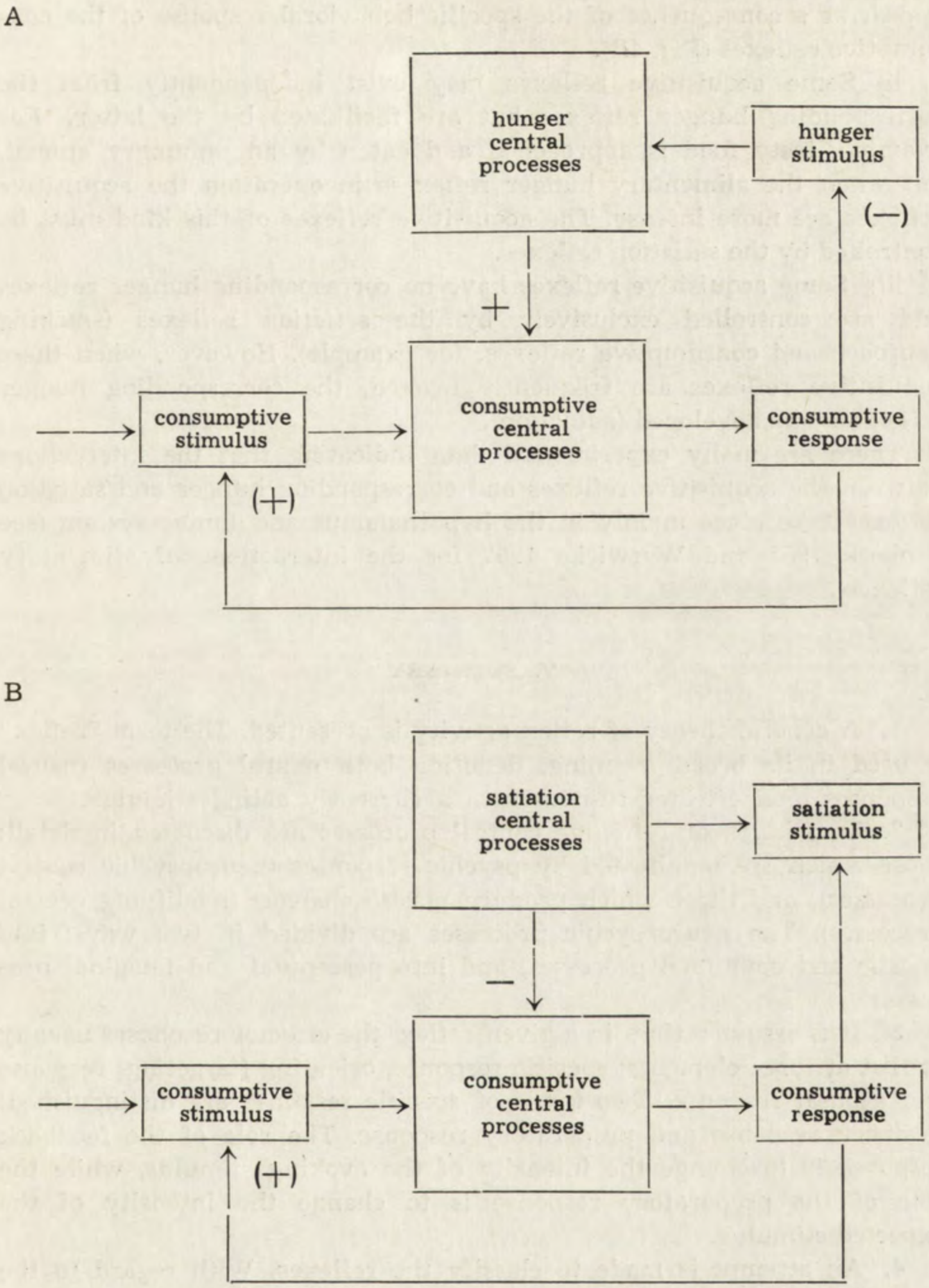


Fig. 4. The control of the consumptive reflex by the hunger escape reflex (A) and the satiation escape reflex (B). The preparatory reflexes are neglected for the sake of simplicity. (—), supressing effect; —, inhibitory effect; (+), augmentative effect; +, excitatory effect.

appear as a consequence of the specific behavioral response of the consumptive reflexes (Fig. 4B).

ii) Some acquisitive reflexes may exist independently from the corresponding hunger reflexes but are facilitated by the latter. For example, tasty food is approached and eaten by an unhungry animal, but when the alimentary hunger reflex is in operation the acquisitive reflexes are more intense. The acquisitive reflexes of this kind must be controlled by the satiation reflexes.

iii) Some acquisitive reflexes have no corresponding hunger reflexes and are controlled exclusively by the *satiation* reflexes (smoking approach and consumptive reflexes, for example). However, when these acquisitive reflexes are frequently evoked, the corresponding hunger reflex may be developed (addiction).

There are many experimental data indicating that the interactions between the acquisitive reflexes and corresponding hunger and satiation reflexes take place mainly in the hypothalamus and limbic system (see Brobeck 1955 and Wyrwicka 1967 for the interactions of alimentary reflexes).

V. SUMMARY

1. A general theory of reflex activity is presented. The term "reflex" is used in its broad meaning, denoting both neural processes (neural responses) and effector responses to a currently acting stimulus.

2. Two kinds of reflexive central processes are discussed in detail: those which are manifested by psychic responses (neuropsychic central processes), and those which produce plastic changes (modifying central processes). The neuropsychic processes are divided in two ways: into gnostic and emotional processes, and into perceptual and imaginal processes.

3. It is assumed that in a given reflex the effector responses usually consist of three elements: specific response, orienting (targeting) response and arousal response. Two kinds of specific response are distinguished: feedback response and preparatory response. The role of the feedback response is to change the intensity of the evoking stimulus, while the role of the preparatory response is to change the intensity of the expected stimulus.

4. An attempt is made to classify the reflexes. With regard to the neuropsychic and behavioral criteria the reflexes are divided into five groups: non-neuropsychic reflexes, targeting reflexes neuropsychic simple feedback reflexes, consumatory reflexes and preparatory reflexes. Besides, the reflexes are divided into negative and positive. The negative

consummatory and preparatory reflexes are called defensive, and the positive consummatory and preparatory reflexes are called acquisitive.

With regard to the learning criterion the reflexes are divided into unmodifying and modifying reflexes and into unconditioned and conditioned reflexes.

5. The control of the acquisitive reflexes by hunger and satiation defensive reflexes is discussed.

The author expresses his sincere gratitude to Professor J. Konorski for his valuable criticisms of the early drafts of this paper. Many thanks are also due to Drs. W. Kozak, R. Gawroński, T. Rentoul and S. Sołtysik for their comments.

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RESPONSES OF SINGLE CELLS IN THE SUPERIOR COLLICULUS OF THE CAT TO DIFFUSE LIGHT AND MOVING STIMULI

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Sprague and Meikle (1965) consider the superior colliculus as a nervous centre capable of complex sensori-motor integration, particularly for visually guided behavior. Sprague (1966) has shown that ablation of the contralateral superior colliculus can restore vision in the hemianopic field resulting from ablation of visual cortex, and arrived at the conclusion that the ipsilateral superior colliculus was normally inhibited by the contralateral one and that after the ablation of the latter acquires the ability to function normally. It appears from these experiments that the superior colliculus itself, without participation of the cortex, is able to analyse visual information. In the superior colliculus of the rabbit, cells were found which reacted to specific visual stimuli, the cell responding vigorously to the movement of the stimulus object in one direction, but not in the opposite direction (Horn and Hill 1966). Straschill and Taghavy (1967) reported in cats that collicular neurons have the ability to sense or react to direction of stimulus movement. In this respect the role of colliculus superior seems to be more specifical in comparison with retina and the lateral geniculate nucleus (LGN).

The superior colliculus of the cat is composed of seven layers. From the dorsal surface these are: (i) stratum zonale, (ii) stratum griseum superficiale, (iii) stratum opticum, (iv) stratum griseum intermediale, (v) album intermediale, (vi) griseum profundum and (vii) album profundum. The optic nerve fibres enter the superior colliculus in the brachium colliculi and they end in the third layer of cells (optic stratum). The fibres of the latter cells end in the stratum griseum superficiale, contacting there large cells whose axons, in turn, constitute the tecto-bulbar and tecto-spinal tracts. These tracts innervate the motor nuclei of cranial nerves (directly or indirectly) and the ventral gray columns of the cervical spinal cord. The fibres entering the stratum griseum superficiale presumably end in its ventral parts. Very rare degeneration was observed in the stratum griseum intermedium, below the stratum opticum (Garey and Powell 1968). Thus, the main parts of the colliculus superior which receive optic fibres are the stratum opticum and the stratum griseum superficiale.

The superior colliculus has well developed connections with the retina, spinal cord, occipital cortex, reticular formation and other centres.

In the present paper we decided to investigate direction-sensitive units in the superior colliculus and simultaneously to study the general characteristics of unit activity in that nucleus.

METHODS

The preparation. 35 cats were used in acute experiments. The animals were tracheotomized under ether anaesthesia and then pretrigeminal transection performed using the method of Żernicki (1964). A trepan hole was made in the skull directly above the superior colliculus and filled with soft wax after removal of the dura (Bishop et al. 1962). Flaxedil (Gallamine triethiodide) was used for immobilization, the initial dose being 20 mg/kg of body weight, and every two hours 10 mg/kg were injected intravenously. The eyes were instilled with atropine (1% solution) in order to dilate the pupils.

The electrodes. Tungsten-wire electrodes (Hubel 1957) were sharpened electrolytically in $NaNO_2$ solution, and covered with a fine layer of vinyl varnish. The bare end of the electrode was 3—5 μ long.

Stimulating and recording apparatus. Action potentials were recorded using a cathode follower and Grass P6 and P5 preamplifiers. The waveforms were photographed using a Grass camera and Tektronix 502 oscilloscope, and also were fed into a loudspeaker after power amplification. The same waveforms were fed to Schmitt triggers. The standard pulses generated by the Schmitt triggers were fed into an interval-recorder (Kozak and Katrycz, unpublished; Huxley and Pascoe 1963) and photographed from a Tektronix oscilloscope. The CRO beam was brightened after each nervous impulse. Thus every neuronal impulse was recorded as a small dot on the steady film frame of the Grass kymograph camera. The abscissa of the resulting record was proportional to time after the onset of the stimulus and the ordinate-inversely proportional to the logarithm of the interspike interval. The stimuli were repeated many times (usually 20—100 times) and the responses were superimposed on the one frame. After taking a photograph the picture was analysed and the distribution of dots (corresponding to impulses) appreciated visually. Any condensation of dots could be easily discovered when several thousand dots were on one frame.

The receptive fields of the visual cells in the superior colliculus were defined in the following way.

The white screen of a perimeter (Kozak and Folga, unpublished) was placed at a distance of 0.75 m in front of the cat's eyes. Black cardboard disks were moved by hand starting from the periphery towards the centre. The boundary of the field was defined where the cell spike response could be heard in the loudspeaker when the black disk was waved to and fro. The dimensions of the field were measured by adjusting the position of the screen in the horizontal and vertical directions and by reading the degrees of azimuth and elevation on the scales attached to the perimeter frame and arm (see Bishop et al. 1962). Light flashes of variable duration were delivered from a photostimulator (Katrycz and Kozak, unpublished). Light disks moving with variable velocity and in preselected direction were projected onto the perimeter screen using a slide projector and remotely controlled motor-compensator (Typ eK, Messgerätewerk E. Weinert, Magdeburg).

After each experiment the cat's brain was perfused with 10% formaldehyde solution and the position of the electrode was determined histologically.

RESULTS

According to anatomical studies, the superior colliculus is supplied by the fibres from the optic tract, 85% of which are crossed and 15% uncrossed (Sprague 1966). To our surprise, the percentage of binocular neurons was found to be much higher than could have been expected from those data. 45% of all units investigated by us were binocular (70 units were investigated); this indicates that a great number of converging fibres come from the ipsilateral side. 52% of units responded only to stimulation of the contralateral eye and only 3% were purely ipsilateral.

The receptive fields of the visual cells in the superior colliculus are circular, ellipsoidal, or irregular in shape. The boundaries of the receptive fields are more difficult to define than for lateral geniculate neurons because of the irregulator shapes of the former ones. One finds giant fields of the order of 60° across (Fig. 1A, D, F), and small ones, 5° to 10° (Fig. 1G, H). The location of the fields can be in the centre of the screen (Fig. 1A, E), or extremely lateral (Fig. 1C, G). In Fig. 1 receptive fields for the contralateral eye are shown. Binocular neurons have usually monocular fields located closely to each other, in the same region on the screen.

In our investigations of the processes of transformation of information in the retina, optic tract and lateral geniculate nucleus it was found that information about the visual stimulus is transmitted in these centers more or less regularly (Kozak et al. 1968). For example, the response to light is manifested in such a way that the randomly dispersed interspike intervals, occurring spontaneously in darkness, become organized in the form of strictly selected preferred and prohibited intervals. Fig. 2 demonstrates the response of a fibre of the optic tract to blinking light

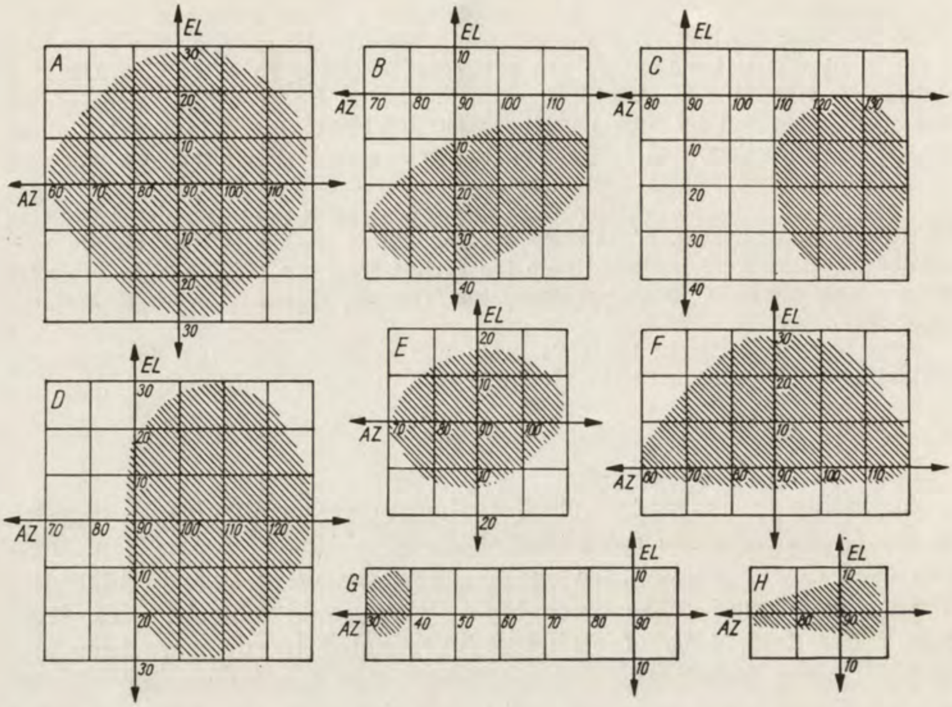

Fig. 1. Receptive fields of some neurons in the superior colliculus. The co-ordinate lines correspond to the intersections of the sagittal and horizontal planes of the skull with the spherical screen

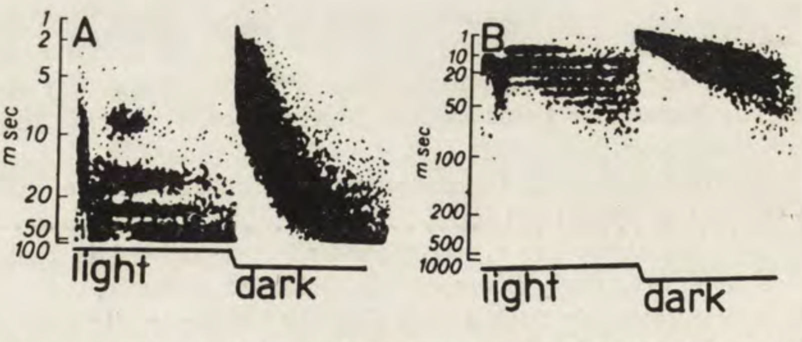

Fig. 2. Responses of a single fibre of the optic tract to blinking light. A, frequency of flashes 1/sec; duration of flash 0.5 sec; B, frequency 1/11 sec; duration of flash 5 sec (from Kozak et al. 1968)

(Kozak et al. 1968). Very regularly spaced preferred and prohibited intervals are clearly seen during light periods, whereas they turn into general random activity during darkness. Kozak and his co-workers explain this phenomenon by the mechanism of lateral inhibition. In the superior colliculus such a manner of information transfer was not found to exist. The cells sensitive to changes of the intensity of the diffuse illumination or to movements of objects, responded by an increase or decrease of their spike frequency without such reorganization of distribution of interspike intervals. In Fig. 3 the cell responds with dispersed interspike intervals in light and in darkness as well. To blinking light the cell displays off-responses without any specific organization of intervals. Only in two cases prohibited intervals, although not clear-cut, were observed, or, to put it more precisely only one prohibited interval of 20 msec length. Fig. 4 and 5 show these cases. In both of them long-lasting light-adaptation preceded the recordings. In Fig. 4, D, E, the cell response to blinking light (0.2/sec) after long light adaptation is shown. A weakly expressed prohibited interval of about 20 msec length and one preferred interval at about 15 msec can be seen in E. In Fig. 4A, B and C the responses of the same cell after long-lasting dark adaptation are displayed. The intervals are entirely random here. In Fig. 5 we can see responses of a cell which also displays a prohibited interval after a long-lasting light adaptation. In B, C interspike intervals during the

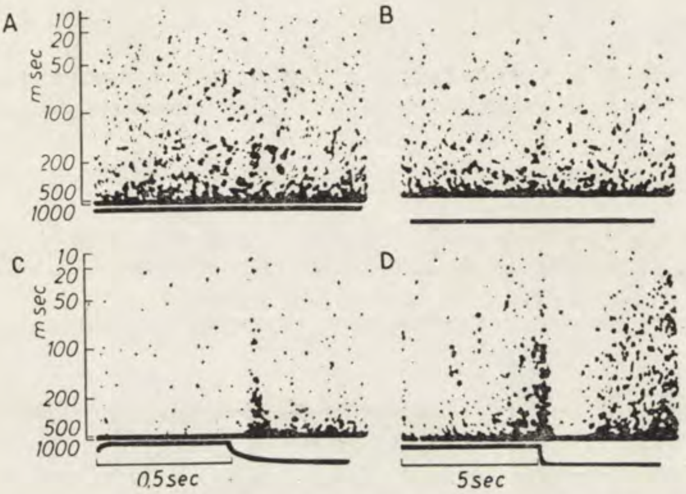

Fig. 3. Responses of a cell in the superior colliculus to diffuse illumination. A, steady light; B, steady darkness; C, light flashes 1/sec, D, light flashes 1/11 sec

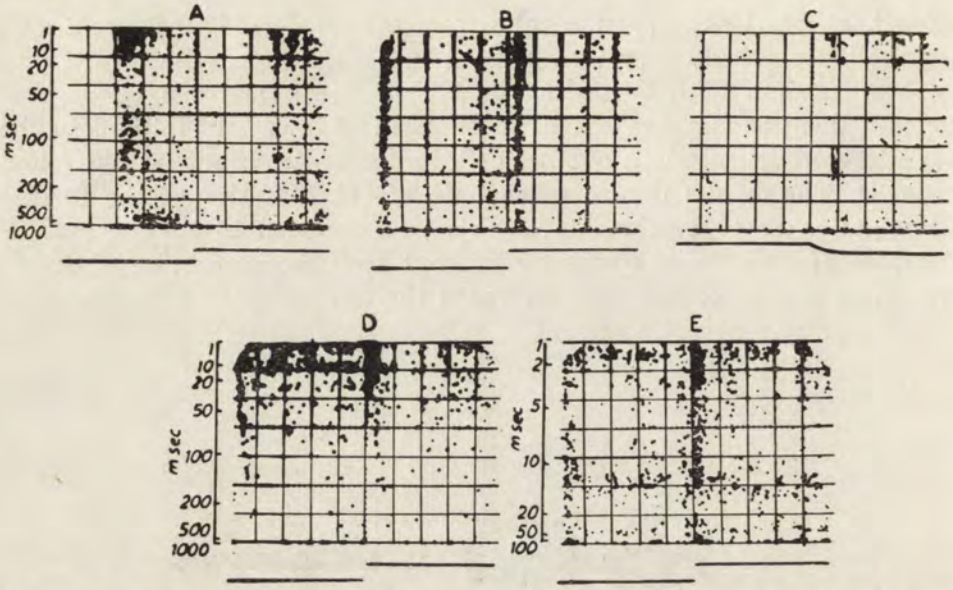

Fig. 4. Responses of a single cell in the superior colliculus to blinking light before and after light adaptation. A, B, C, responses to blinking light before light adaptation; D, E, after light adaptation

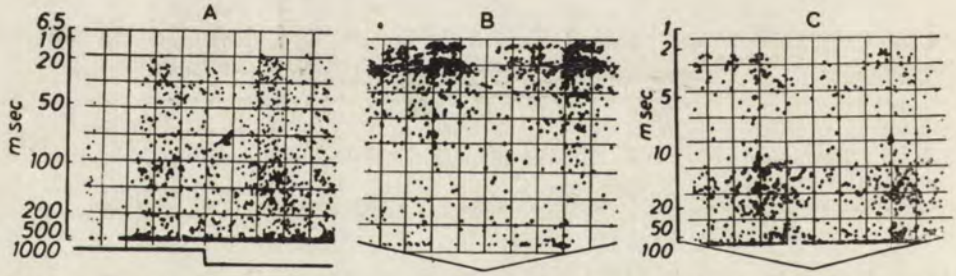

Fig. 5. Responses of a visual neuron to blinking light and to an object moving in its receptive field. A, light flashes 1/sec; B and C, a 10° diameter disk moving in the field. First half of the graph: left-to-right; second half: right-to-left movement

movement of a light disk in the unit's receptive field from left to right and back are shown. In all other cases, the superior collicular cells responding either to diffuse illumination or to the movement of the disk in the receptive field did not display such an encoding of information.

Further investigations have shown that this is not the only feature by which the superior colliculus differs from the lateral geniculate and other visual centers. Many collicular neurons proved to be able to respond only to moving objects without any reaction to changing ambient illumination. During movement of black or light disks on the screen brisk increase or decrease of spike frequency occurred, whereas a blinking light did not change the spontaneous spike activity of the cell. For example, the unit illustrated on the Fig. 6 did not respond to changing diffuse illumination but only to the moving object. On the other hand there are neurons, which react only to ambient illumination change, as for example, the cell illustrated in Fig. 3, which appears to be an off-neuron.

About 24% of superior collicular units investigated could differentiate the directions of movement (Fig. 6, 7, 8). Such neurons change the character of their activity depending on the direction of the object's movement. On Fig. 6 the general form of the response of a directionally sensitive unit is shown; the first half of the curve corresponds to the disk movement from left to right, and the second half to the reverse direction. As seen from Fig. 6A in the former direction the number of spikes is greater and equals about 33, whereas in the reverse only about 16. One can see the burst of spikes, which occurred in preferred direction, and its weakening in the null direction. Fig. 6B shows the third repetition of movement, which demonstrates response habituation in both directions. In Fig. 7 the mean-rate spike records of a directionally sensitive neuron are shown. A, B, C, D and E are the consecutive stimulus applications, each of them consisting of two movements, left-to-right (first half of the curve) and reversely (second half). From the figure the directional sensitivity of the cell (C, D, E) as well as the process of habituation after a series of stimulus presentations, are clearly seen. Fig. 8, shows an ave-

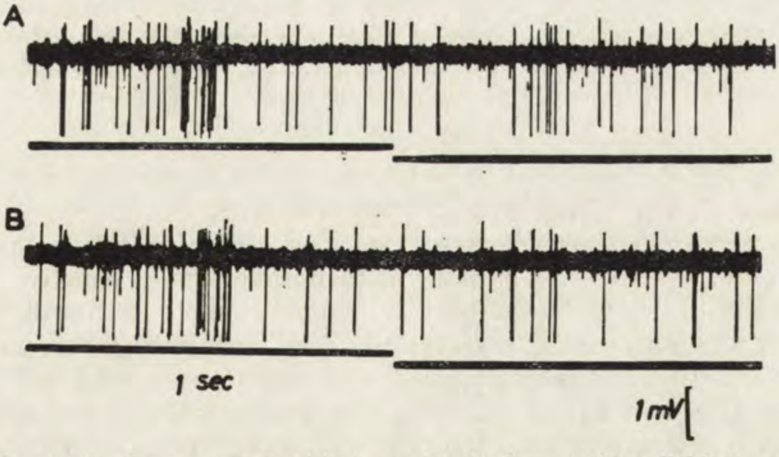

Fig. 6. Response of a neuron to object moving in its receptive field. A, response to the first stimulus; B, response to the third stimulus. In A and B the first half of the curve corresponds to a movement from left to right, the second half represents the opposite direction

raged record of responses of a directionally sensitive unit during the movement of an object in the receptive field. In Fig. 8A, B, D and F are responses to object movements in two opposite directions. There are clear difference in the number of spikes between two directions. As seen from the graph (8A, B) there were more spikes during the right-to-left movement. In Fig. 8 reactions of the same cell during steady illumination (8C), and during steady darkness (8E) were presented.

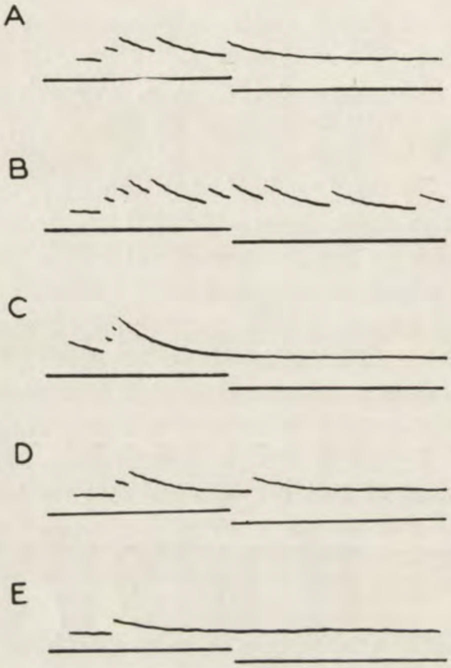

Fig. 7. Mean-rate record responses of a visual cell to repetitive stimulation with an object moving within the receptive field. A, to the first stimulus; B, to the second; C, to the third; D, to the fifth; E, to the eighth stimulus

As seen from above demonstrated examples, the information about direction of movement is encoded in such directionally sensitive neurons principally in two ways. One way is relatively simple in that the neurons respond with an increase of spike frequency during the whole movement in one direction and with a decrease, or sometimes a total inhibition in the other. A unit having this property is illustrated in Fig. 8A. There were very few spikes when the light spot moved from right to left and, on the contrary, there was intense activity when it was moving reversely. Thus the information about direction of movement is transmitted by an increase in the number of spikes during the entire time of movement.

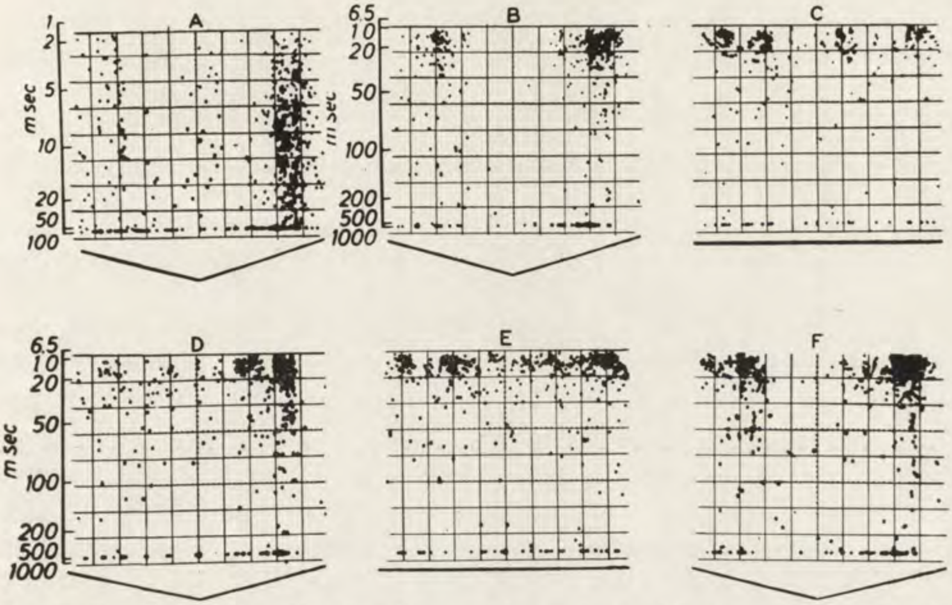

Fig. 8. Responses of a directionally sensitive unit to objects moving within its receptive field. A, B, responses to moving object; C, activity of the neuron during steady light; D, responses to moving object after light adaptation (30 min); E, activity in darkness; F, response to moving object after dark adaptation (20 min)

Another way of encoding directional information consists in a prominent increase of the number of spikes in one given moment during the passage of the object through the cell's receptive field. When the object moves in the reverse direction there is no such response or only a very weak one (Fig. 6). The second type of directional information is thus dependent on a rapid increase in the number of very short interspike intervals in a given moment during the passage of the moving object across the receptive field. In Fig. 6 such a response consists of a burst of impulses. By listening to a loud-speaker it is also easy to identify a burst occuring in one direction and its absence in the other. These directionally-sensitive neurons are similar to the complex field cells described by Hubel and Wiesel (1959) in the secondary visual cortex. Remaining collicular neurons correspond for the most part to the simple field cells in the lateral geniculate nucleus and in the primary visual cortex.

The majority of directionally sensitive neurons are binocular. Their monocular receptive fields lie close and frequently overlap in the same part of the perimeter screen. A binocular neuron responds weakly when only one eye is stimulated and its response becomes stronger when both eyes are stimulated simultaneously. The facilitation is expressed by an increase of the impulse frequency. Such a binocular facilitation was also observed by Hubel and Wiesel (1965) in the neurons of the visual cortex.

As was shown above, visual neurons in the superior colliculus have the property of fast habituation. Horn and Hill (1966) also observed a fast habituation of responses of the collicular and pretectal neurons of the rabbit to visual stimuli. In Fig. 7 such habituation of neuronal responses to a moving object is clearly visible. After a short interval the responses are restored. Habituation is also observed when stimulating with blinking light.

On the basis of well-known data (Barlow et al. 1957) indicating that both light and dark adaptation can change the retinal responses to light stimuli and consecutively, the afferent input into the colliculus, it has been interesting to study the effects of dark and light adaptation upon the characteristics of activity of the superior collicular cells. Fig. 8 shows the activity of a cell which responded specifically to moving objects. Fig. 8C demonstrates spontaneous activity in steady light; 8D, the same cell after a long lasting light adaptation. The specificity of the response is enhanced, i.e. the difference between the responses to one and the other movement direction has increased (cf. Fig. 8B). In Fig. 8F the activity of the same cell after long-lasting dark adaptation is shown. The direction from right to left which originally caused an inhibition of the cell, gives now a quite well-marked response, and a specificity of the reaction is almost abolished. As a result, ratio $\frac{\text{response in preferred direction}}{\text{response in null direction}}$ is reduced. The greater this ratio, the greater the specificity of the neuron and vice versa. Light adaptation increases and dark adaptation decreases this ratio. Sometimes dark adaptation has no influence at all upon the cell activity, and in other cases such an influence takes place, for example dark adaptation did not have great influence upon the cell activity depicted in Fig. 9. This neuron did not respond at all to changing ambient illumination, but it reacted to moving objects. In Fig. 9A, B, we can see the responses of a cell before light adaptation; in C, spontaneous activity in light; in D, E, responses to moving object in opposite directions after a long-lasting light adaptation (30 min). As a result the number of spikes increased a little and the dispersion of interspike intervals diminished. Possibly this means a certain degree of stabilization of the response. In Fig. 10A the spontaneous activity of a cell in light is shown. In 10B, movement of a disk in the receptive field; in 10C, spontaneous activity in darkness; in 10D, E, responses to moving stimulus after dark adaptation. A wide dispersion of the intervals after the dark adaptation can be seen.

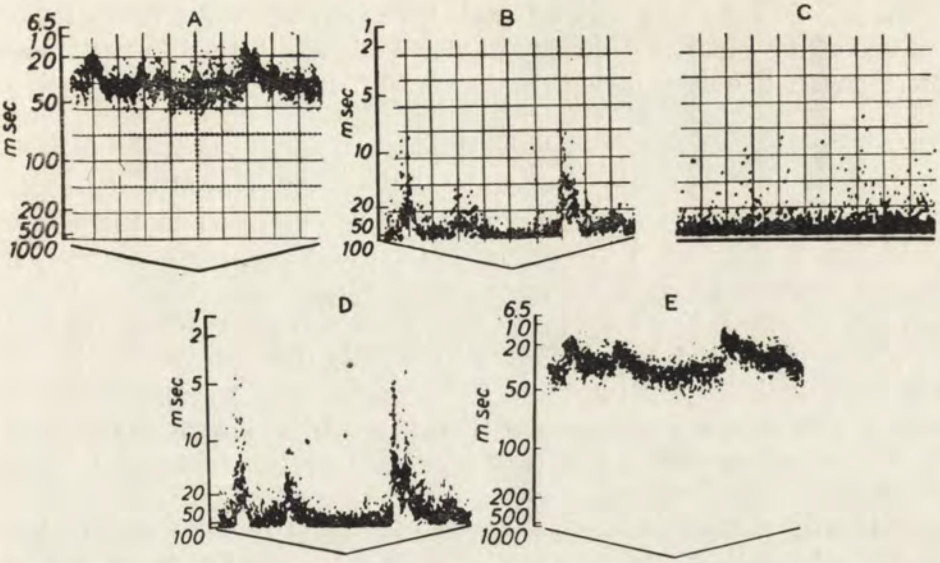

Fig. 9. Responses of a cell to moving object before and after adaptation to light. A, B, responses of a cell to moving object before light adaptation; C, spontaneous activity in light; D, E, responses to moving object after light adaptation (30 min)

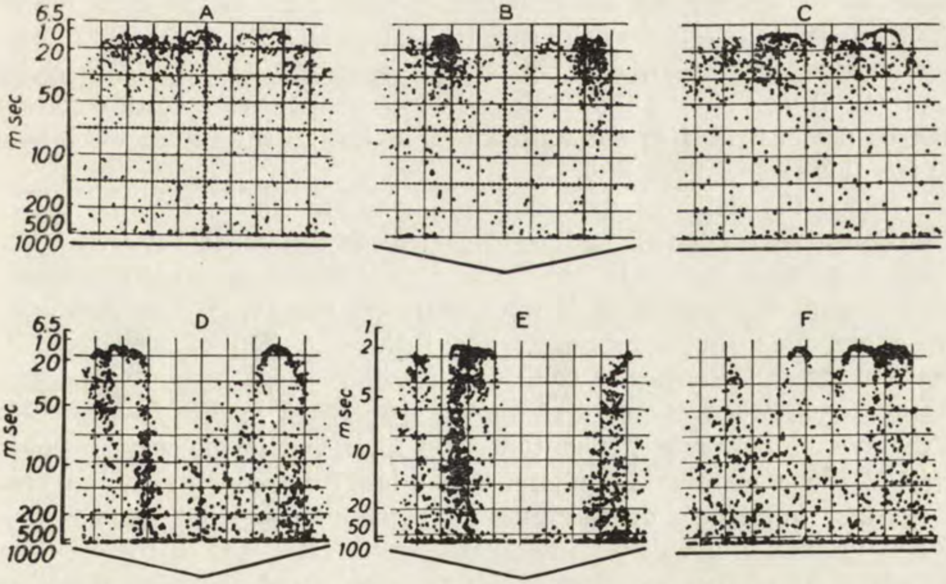

Fig. 10. Responses of a cell to moving object before and after dark adaptation. A, spontaneous activity in light; B, response to moving object before dark adaptation; C, spontaneous activity in darkness; D, E, responses to moving object after dark adaptation; F, spontaneous activity in darkness after long-lasting stimulation with a moving object

Thus both light and dark adaptation can influence the responses of neurons of the superior colliculus to visual stimulation and in particular, the responses to objects moving in the visual field.

DISCUSSION

Neurons in the superior colliculus of the cat displayed certain characteristics which are absent or very poorly expressed in the lateral geniculate nucleus or in the retina. Retinal and geniculate neurons, in general respond, to changing intensity of illumination, whereas in the superior colliculus there are many cells do which not react to intensity changes, but respond to movements of objects (frequently only in one direction), within their receptive fields. Such cells were reported by many investigators: Maturana and Frenk (1963) in the pigeon's retina, by Barlow et al. (1964), Arden et al. (1967) in the retina and visual cortex of the rabbit etc.

Evidently the superior colliculus of the cat is supplied particularly by fibres from those retinal ganglion cells which appear to be moving contrast detectors. Such a postulate requires that there should be retinal cells which respond exclusively and specifically to the movement of figures contrasting against the background. Unfortunately, so far there were no indications for an existence of such cells in the cat's retina. Another possibility is that the specific response is organized in the cortex and is transmitted therefrom to superior colliculus. Jassik-Gerschenfeld (1965) has shown that a long-latency response of cortical origin can be demonstrated in the superior colliculus. In the future we intend to test this second possibility.

Among the collicular neurons reacting to movement, 24% are direction sensitive. So far all authors consider the difference between numbers of impulses elicited by the one and the other direction of movement as the main characteristics of the directional sensitivity. One can infer from our data that information about the direction of movement is transmitted to the superior colliculus not in one, but in two ways. The difference between numbers of impulses produced by the two opposite directions of movement, constitutes one form and is the way accepted by the above mentioned authors. The other form consists in the presence of a burst or a dense cluster of short interspike intervals during the movement in one direction and absence or small size in the opposite direction. Thus the encoding of information about stimulus direction is different in either case. So far we cannot say under which conditions the one or the other type of encoding takes place. They appear without any clear regularity. It is interesting to observe that the majority of directional cells are binocular. The experiments show that light adaptation increases the directional response or specificity of the neuron whereas dark adaptation equalises the responses. It is possible that light adaptation increases periodic inhibitory processes as is the case, for example, with lateral inhibition (Barlow et al. 1957). A postulate has been put forward (Straschill and Taghavy 1967) that the depression of cell activity in the "pessimal" direction of movement is connected with a periodically occurring inhibition and it is logical to expect an increase of such processes during light adaptation.

The superior collicular neurons differ from the retinal and lateral geniculate cells by one more feature, namely, that in the LGN and in retina information about light is encoded generally in the form of prohibited and preferred intervals. In the superior colliculus no such regularities connected with intervals were demonstrated. Only in one case after the light adaptation there appeared one prohibited interval (20 msec) during blinking light and on another occasion, after light adaptation, in the response to moving object. It is well-known that receptive fields of LGN and retinal units are, in general, concentric, with a centre and surround having opposite signs, this being an instance of lateral inhibition. Kozak (1963) and Kozak et al. (1968) suggest that the presence of prohibited interspike intervals in the retina and LGN are related to lateral inhibition. During investigation of the receptive fields of superior collicular cells it appeared that they are circular, ellipsoidal or irregular in shape. We did not observe any concentric fields. Thus, one cannot speak of lateral inhibition in the superior colliculus. It is possible that this is the cause of the absence of prohibited and preferred intervals in the spike firing of these neurons.

SUMMARY

1. Responses of superior collicular cells to objects moving before the eyes and to changing illumination were studied.

2. In the superior colliculus the following types of cell were found: (i) cells reacting to changes of light intensity but not to moving objects; (ii) cells responding to moving objects but not to changes in diffuse light; (iii) cells excited by a certain direction of movement and inhibited by opposite movement direction; (iv) cells responding both to changing light intensity and to moving objects.

3. The encoding of information in the directionally sensitive cells takes place in two ways: (i) an increase of spike number during the optimal direction of movement and a decrease of that number during the null direction; (ii) an occurrence of a brief burst of spikes during the optimal direction and an absence of such a burst during the null movement.

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SINGLE UNIT ACTIVITY IN THE PRETECTAL REGION OF THE CAT

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Magoun and Ranson (1935) in their early papers described the role of the pretectal region in the cat as the brain structure responsible for the occurrence of the pupillary light reflex. More recently authors investigating the function and structure of the pretectum (Siminoff et al. 1967, Garey and Powell 1968) did not deny this role.

Unfortunately we do not have any data concerning the detailed functioning of the pretectum. There are few published data about this structure in the cat, and the supposition that it participates in this important function of the visual system, makes the pretectum an interesting subject for investigation.

Anatomy. The pretectum (pretectal region) in the cat is defined as the area of the midbrain anterior to the superior colliculus. The boundary between the pretectum and the superior colliculus is barely visible. A large portion of the pretectum situated medially forms the area pretectalis. More laterally lies three nuclear groups. The nucleus of the optic tract (NOT), consists of two parts; a lateral part, magnocellular, and a medial part, parvocellular. The third group is formed by cells of the pretectal nucleus situated ventrally to the above mentioned nuclei. Many large cells of the pretectal nuclei are interspersed between the afferent fibres of the optic tract and the basis of the superior colliculus; they form the most lateral and dorsal boundary of the pretectum (Laties and Sprague 1966).

The nucleus of the optic tract extends caudally down to the lateral part of the colliculus superior. According to Kuhlenbeck and Miller (1942) both parts of the NOT are of tectal origin.

The fibres from the retina project both to the contralateral and to the ipsilateral side of the pretectum (Garey and Powell 1968, Bishop and Clare 1955, Laties and Sprague 1966). The number of fibres crossing to the contralateral pretectum is greater (65%) (Sprague 1966) than the number of uncrossed fibres. According to data of Bishop and Clare (1955), fibres of larger diameter cross to the contralateral side and fine fibres remain uncrossed. The fibres supplying the pretectum originate from the brachium of the superior colliculus and also directly from the optic tract where it passes ventrally and medially towards the caudal part of the LGN (Garey and Powell 1968). According to the same authors NOT receives a great number of fibres of large diameter.

Laties and Sprague (1966) indicate that the medial pretectal area does not receive optic fibres from the retina. Garey and Powell (1968), on the contrary, have found degenerating fibres of retinal origin also in the area pretectalis (medial pretectum), but degenerating terminals in the nucleus of the optic tract and in the pretectal nucleus were numerically prevalent. Our electrophysiological data mostly support the observations of Garey and Powell.

Thus the retina has very potent synaptic connections with the pretectum and an investigation of the patterns of cellular activity of that region of the brain is of interest for visual physiologists.

In the text we will refer to "pretectum" as the whole assembly: area pretectalis, pretectal nucleus and nuclei of optic tract.

METHODS

The experiments were conducted on mongrel adult cats. 60 pretectal units were investigated in this study. Methods have been described in the preceding paper (Harutiunian-Kozak et al., 1968).

RESULTS

Receptive fields. The pretectal neurons reacting to visual stimulation have receptive fields generally similar to the fields in the superior colliculus i.e. circular or irregular in shape. The size of the fields ranges from large ones, up to 40—60° in diameter, down to small ones, below 10° of arc. Structurally these receptive fields are similar to the fields in the superior colliculus and differ from the retinal and lateral geniculate fields. That is to say, we did not find any concentricity in their structure, i.e. there was no difference between the responses of a cell to stimulation of various parts of the field, particularly between its centre and periphery. As is well-known, such a difference is characteristic for cells in the retina and lateral geniculate nucleus (Kuffler 1953, Barlow et al. 1957, Hubel and Wiesel 1961). The pretectal receptive fields are situated mostly near the central region of the visual field (Fig. 1), and probably related to the centre of highest visual acuity as opposed to the superior collicular fields, many of which were situated at the extreme periphery of the visual field. Such a central situation of fields indicates that area centralis of the retina projects a great deal to the pretectum.

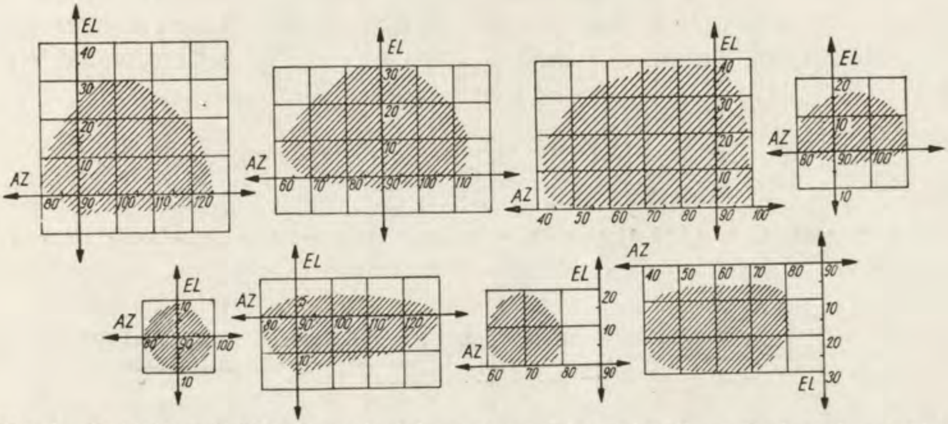

Fig. 1. Receptive fields of pretectal neurons. The azimuth and elevation scales correspond to intersections of the sagittal and horizontal planes of the skull with the perimeter screen. 1 cm corresponds to 10°

A small number of cells were found to be sensitive to the size of the visual stimulus. Some of them, for example, responded intensely to movement of a small disk and others — to a large one. However, we did not find any regularity in the relationship between the size of the stimulus and that of the field.

Among 60 cells investigated in the pretectum 17.6% were non-visual. These neurons had very pronounced spontaneous activity, sometimes with a high frequency of spike discharges. In some of them spike frequency could be slightly modulated by visual stimulation but this effect was weak and could not be analysed properly. Probably those were units with multimodal input convergence as reported by Horn and Hill (1966) in the rabbit's pretectum; or they were visual units with secondary synaptic connections. Nevertheless, we did not consider them pure visual units.

Of the visual neurons investigated, 5.3% responded only to light and did not react to objects moving in front of the eyes. One of these units is illustrated in Fig. 2A. A response to light-on is seen in the form of increased frequency and number of spikes during light and decreased frequency during darkness. The same unit was completely indifferent to objects moving in its receptive field. Such units are very infrequently found in the pretectum.

A great number of neurons (28.6%) respond to object moving in front of the eyes and frequently only to movement, without any reaction to diffuse illumination. For example, the unit in Fig. 2B responded very intensely to the movements of a black object in the visual field and, as can be seen from the graph, did not react to blinking light. Thus, Fig. 2 shows responses to blinking light of two pretectal neurons having opposite characteristics. One of them transmits information about diffuse illumination of the field and the other-about what is moving in the field. It is interesting to note that such a phenomenon of greater sensitivity to moving objects was reported by Arden (1963) in the rabbit LGN.

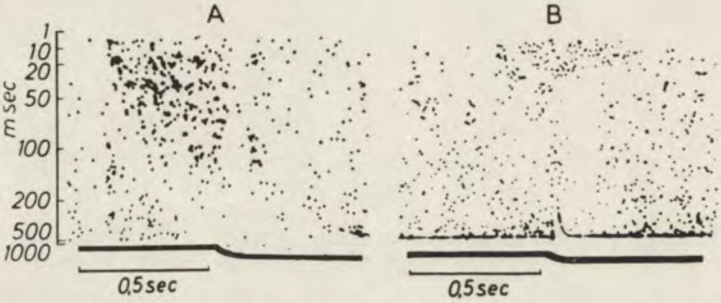

Fig. 2. Response to blinking light of two neurons. A, response to blinking light of a neuron which did respond to moving stimuli; B, absence of response to blinking light of a unit which reacted only to moving stimuli

The third group of neurons having different characteristics than the first two, consists of neurons responding both to diffuse illumination and to moving objects. Thus, this group has a more complex function. 43% of the neurons belong to this third group. Fig. 3 shows the activity of a unit responding to diffuse illumination. The same neuron reacted intensely to objects moving in its receptive field. In Fig. 4 another unit is shown which reacted to blinking light (A, B) and also to moving objects (C, D, E, F).

Apart from the characteristic features described above, the unit described in Fig. 4 has still another specific property, namely, directional sensitivity, which is manifested in a greater number of spikes in response to a stimulus moving in one direction (in this case from left to right) than in the other (Fig. 4C, E). For example, in E there are approximately

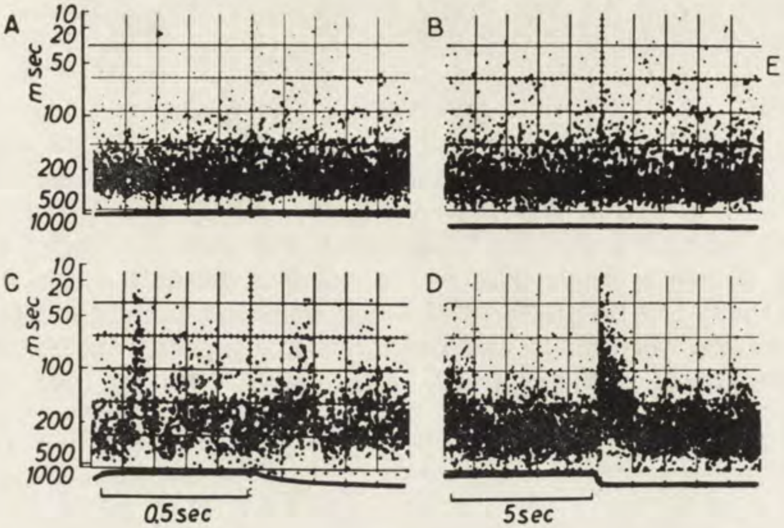

Fig. 3. Response of a cell to blinking light and steady illumination. A, spontaneous activity in steady light; B, spontaneous activity in darkness; C, light flashes 1/sec; D, light flashes 1/11 sec

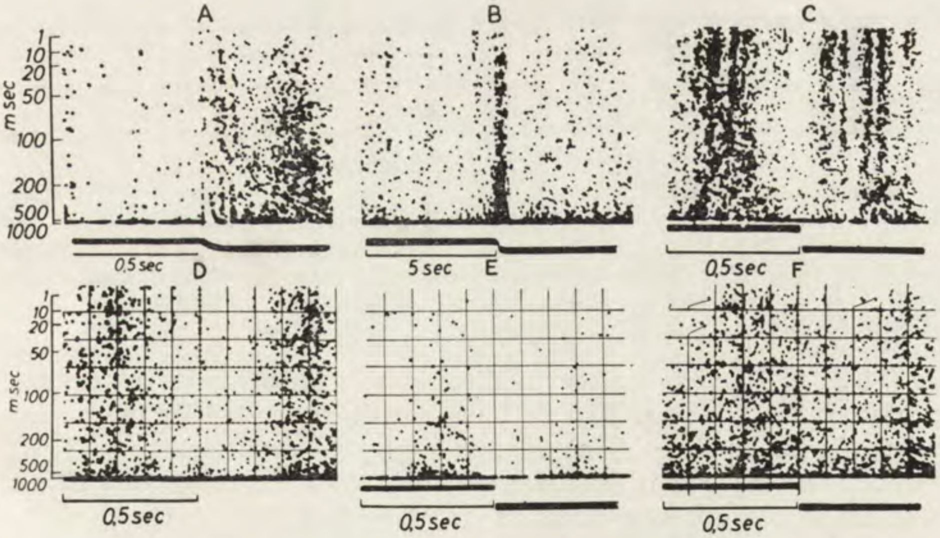

Fig. 4. Responses of a cell to blinking light and moving stimuli. A, light flashes, 1/sec; B, light flashes 1/11 sec; C, D, F, responses to moving stimuli; E, responses to three repetitions of a stimulus; first half of the curve corresponds to the left-to-right movement of a disk; second half, opposite direction

130 spikes during the left-to-right movement (preferred direction), and only about 80 spikes during the opposite movement (null direction). Such units are very characteristic for pretectum and they constitute about 36% of all its units investigated. The receptive fields of such neurones are circular or irregular in shape. We did not find any concentric structure of the fields. Directionally sensitive units were recently reported by Straschill and Taghavy (1967) and by ourselves (1968) in the cat's superior colliculus. Such specialized units can differ greatly by their response characteristics. For example the unit which was described above had its preferred direction from left to right but in other directions e.g. vertical, it was not directionally sensitive. The neuron shown in Fig. 5, on the contrary, has preferred direction from right to left (Fig. 5A, B) and is also not directionally sensitive in the vertical orientation. On the other hand, a unit sensitive directionally in the vertical is shown in Fig. 6. That neuron displays a pure directional sensitivity for the movement downwards (left half of the curve) and almost no spikes in the opposite direction (right half of the curve). Thus, the lines of the preferred and null direction have vertical orientation. It is interesting to note that this neuron does not have directional sensitivity in the horizontal orientation. Apart from these, we observed units which had no preferential orientation i.e. had directional sensitivity in both

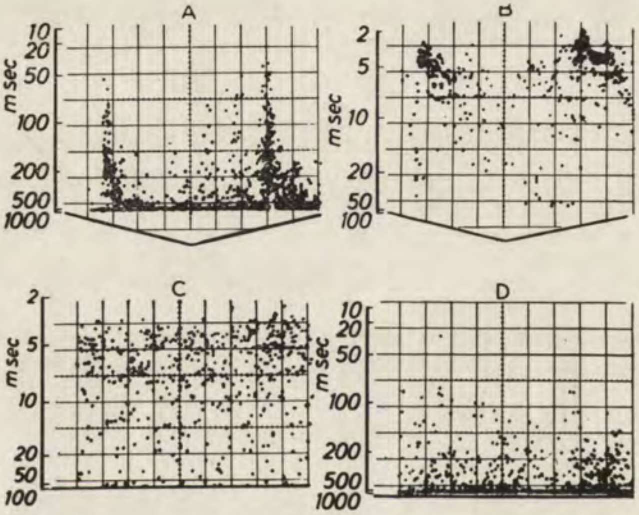

Fig. 5. Responses of a cell to moving stimuli and steady illumination. A, B, movement of stimuli in the visual field of a neuron. First half of the curve represents movements from left to right; the second half, in opposite direction; C, spontaneous activity in steady illumination; D, spontaneous activity in darkness

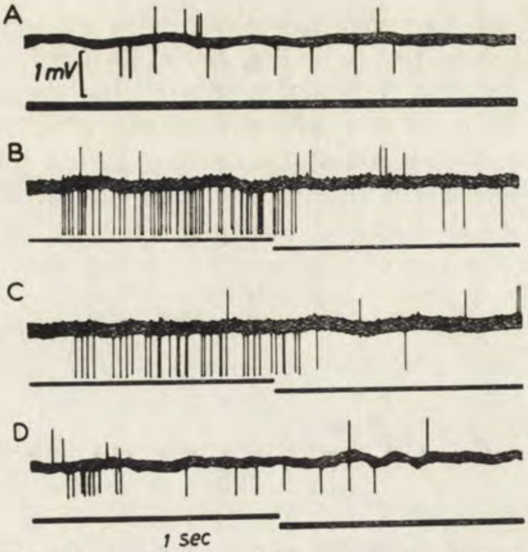

Fig. 6. Responses of a directionally sensitive neuron in pretectum. A, spontaneous activity; B, C, D, movement of a stimulus in the visual field of a neuron; first half of the curve is the movement downward and the second half upward

orientations. For example they had preferred direction from left to right and from above downwards. Summarizing, one can say that the pretectal neurones are highly specialized and more similar to the cortical visual neurons, particularly to the neurones in parastriate cortex, than to the cells in the retina and LGN. We have included all the above-described specialized units into the fourth group. Pretectal neurones belonging to this category obviously analyse the direction of movement of objects and they process the information not only about the direction of movement, but also about its velocity, because either an acceleration, or slowing of movement modulate the responses correspondingly. Apparently also an analysis of the form and size of the moving object takes place here. For example, disks of about 8° in diameter were the most effective stimuli for most neurons, objects of either smaller or larger size eliciting weak reactions. Some units responded optimally to the movements of very large objects covering nearly the whole receptive field; it seemed that they reacted to the edge of the object, or to the moving boundary between bright and dark areas. It is interesting that the majority of the directionally sensitive units were binocular, which was also the case in the colliculus superior.

Apart from the above-mentioned characteristic features, one of the most important properties of the pretectal neurons appears to be fast habituation of their responses. Habituation is manifested by a reduction of the number of spikes during repeated stimulation with the same stimulus. In Fig. 6 three consecutive responses to stimulation of 1/sec are shown. The number of spikes in Fig. 6B is 50 (first response), in C it is 30 and in D, only 14. Spikes fired during the preferential direction of movement were only counted, without the after effect. Horn and Hill (1966) observed such a fast habituation in the pretectal neurones of the rabbit. Siminoff et al. (1967) found habituation in the rat pretectum where, as they note, it is not very pronounced. We observed habituation not only in the responses of single neurones, but also in the compound (evoked) response recorded in the pretectum. In Fig. 7 one can see an averaged evoked potential in the pretectum in response to moving object. The response is larger during the right-to-left movement. There is almost no reaction in the null direction. It appears from this figure that obviously a large group of cells reacts in a manner of direction sensitivity, in unison. A rapid habituation of the whole response is striking. In A the sum of the first and second response is displayed; B is the sum of first three, and C is the sum of first four responses. In B and C the evoked potential is already nearly flat. One can conclude that habituation affects not only some sporadic units but whole groups of neurons, their majority and that this leads to a drastic reduction of the size of the compound potential.

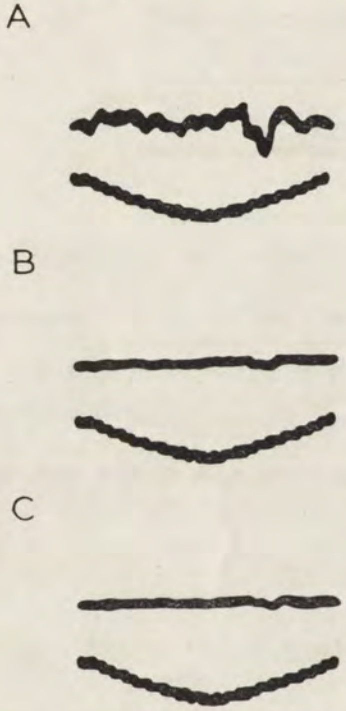

Fig. 7. Averaged evoked potentials in the pretectum in response to a moving object. A, the sum of first and second response; B, sum of the first three responses; C, sum of the first four responses

DISCUSSION

When we started this work we did not expect any habituation of the responses of the pretectal neurons. In agreement with the generally accepted view on the role of pretectum in the pupillary light, reflex, the pretectal neurons should not habituate, or at least not to a significant degree, as was found by Siminoff et al. (1967) in rats. Of course this should not apply to all neurons but to the great majority of them at least. Our experiments have shown that, in the cat, the visual pretectal neurons habituate exceedingly easily. Such a feature cannot favour the pupillary light reflex where a high degree of resistance to habituation is needed. Thus our data do not support the possibility of a pretectal localization of the centre for the pupillary reflex. Furthermore, it has been demonstrated that the majority of pretectal cells have greater sensitivity to movement and to direction of moving objects, than to diffuse illumination. This property also doesn't agree with the principles of formation of the pupillary reflex.

About 30% of the pretectal neurons display a high degree of specialization. For example, the neuron in Fig. 4 displays preferential direction from right to left and the unit show in Fig. 5 has the preferred direction of movement from left to right, opposite to the former unit. Such a narrow specialization allows one to postulate that the pretectum, as a whole, is obviously more related to the analysis of the movements of objects than to the pupillary light reflex where a steady response to diffuse light is only necessary. However, pretectal neurons, similar to that illustrated on Fig. 2A, can participate in the pupillary reflex.

Concerning the mechanism of the directional sensitivity of the visual neurons in the cat, unfortunately our experiments do not add much to the already existing suppositions in that respect (Maturana and Frenk 1963, Barlow et al. 1964). In our experiments we also found small subunits within the receptive fields of directionally sensitive neurons, described earlier by Barlow and Levick (1965). In these subunits, sometimes not exceeding 1° of size, directional sensitivity could be found. They can be roughly compared to dipoles (with inhibitory components) situated in a certain order. Barlow and Levick (1965) situated the inhibitory neuron between bipolar neurones in the retina. Straschill and Taghavy (1967), on the other hand, proposed a diagram explaining the mechanism of directional sensitivity of visual neurons, where the inhibitory neuron is situated in series between receptor cells and bipolars in retina. It may be so, and then it would be logical to expect that directionally sensitive units should be demonstrated also in the retina. According to the well-known data about cat's retina, such units were not demonstrated. Either the directional units are ganglion cells of very small diameter and they are difficult to find and record from, or the intervention of the inhibition in series doesn't take place at all in the retina but further in the brain centers.

Our data do not allow us to make far-reaching conclusions apart from suggesting that the ability to discriminate directions of movement is situated, at least partially, in the pretectum itself. This idea finds a support from the fact that the directional sensitivity was found in the cells of the lateral nucleus of the optic tract where to fibres of large diameter originating from retinal ganglion cells project; the latter have been comparatively thoroughly investigated in the cat and so far no directional sensitivity was found in them. It seems that directional sensitivity is organized beyond the retina, in the pretectum itself.

SUMMARY

1. Responses of neurons in the cat's pretectum to visual stimuli were studied.

2. The pretectal cells are more sensitive to objects moving in their receptive fields than to diffuse illumination and its changes.

3. Both the activity of single neurons and the evoked responses in the pretectum to visual stimulation habituate quickly when the stimulus is repeated.

4. Directional sensitivity is the characteristic feature of pretectal neurons.

5. The data presented here do not support the view that the pupillary light reflex has its centre in the pretectum.

6. The suggestion is put forward that the mechanism of directional selectivity of pretectal visual units is situated in the pretectum itself.

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THE RELATIONS BETWEEN SALIVARY, CARDIAC AND MOTOR RESPONSES DURING INSTRUMENTAL PERFORMANCE

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If a hungry dog is trained to press a lever in response to an external stimulus and this behavior is rewarded with food, the eventual outcome of the training is a complex conditioned reaction consisting of motor instrumental response accompanied by salivary and other autonomic responses considered as classical conditioned reflexes. Ellison and Konorski (1964, 1965) succeded, however, in separating the instrumental conditioned response (CR_{in}) from the conditioned salivation using the following training procedure. The dogs were taught to perform a series of nine lever-presses in response to the external stimulus, and just after the ninth lever-press the stimulus was discontinued and a previously established classical conditioned stimulus (CS_{cl}), followed in eight seconds by food, was presented as a reward. The authors have shown that the dogs performed the lever-presses without salivation in response to the first stimulus and salivated without performing any lever-presses during the presentation of CS_{cl}. Thus, the instrumental and classical CRs appeared to be completely separated, and the first stimulus could justly be called an instrumental conditioned stimulus (CS_{in}).

The aim of the present study was to further investigate the relations between motor and salivary responses using the Ellison-Konorski separation procedure, with the following modifications:

1. The CS_{in} and CS_{cl} in the original experiment of Ellison and

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Konorski differed in sensory modality being visual respectively and auditory, while in our study they were both auditory.

2. The number of lever-presses performed during the CS_{in} was increased from 9 to 14.

3. The number of training trials was decreased from 14 to only 4 in each daily session.

4. The cardiac response (change in the heart rate) was recorded together with the motor and salivary responses to both CSs. The main purpose of heart rate recording was to obtain some information on the emotional state of the dogs during the trials.

In order to specify more clearly the relations between the salivary, motor and cardiac responses several tests were applied.

MATERIAL AND METHODS

Subjects. The subjects were eight adult mongrel dogs, ranging in weight from 12 to 20 kg. The animals have not been used as experimental subjects before. In all the dogs a carotid loop (van Leersum 1911) and a chronic fistula of shortened Stensen's duct (Soltysik and Zbrożyna 1957) had previously been prepared for the measurement of cardiac and salivary responses.

Apparatus. The experiment was carried out in the standard soundproof Pavlovian chamber. Two auditory stimuli, a metronome (120 beats per min) and a buzzer were used as CSs. The metronome being the CS_{in} was placed behind and to the right side of the conditioning stand. The buzzer, as a CS_{cl} was set in front of the stand. The unconditioned stimulus (US) was a portion of boiled meat and bread cubes soaked in broth. Approximately 70 gramms of food was delivered as one reinforcement by the automatic feeder. The experimental manipulandum consisted of a clear plexi-glass lever, 20 cm wide, protruding 12 cm through a slot cut in a plastic box. The dog's lever-presses were recorded electrically on the kymograph together with the cardiac and salivary responses. Saliva from the Stensen's duct fistula was collected into a capsule attached to the dog's cheek and fed into the drop-recording device. Pulse rate was recorded by means of a simple piezoelectric receiver attached to the carotid loop and connected through the a.c. amplifier to the electromagnetic recorder.

Training. Six dogs were trained employing nearly the same routine as in the Ellison and Konorski study. This consisted of four stages.

1. Classical conditioning of a buzzer as a signal of food. The buzzer was presented for four seconds and the food was delivered two seconds after the onset of the buzzer. This procedure was continued for 7 days.

2. Instrumental conditioning of lever pressing. Whenever the dog pressed the lever using his right foreleg the buzzer and food were presented as in stage 1. The duration of this training varied from 3 to 13 days in different animals.

3. Differential conditioning of bar presses to metronome. The metronome was sporadically presented and only the lever presses performed in response to it were rewarded like in the stage 2. After 10 to 17 days of training the dogs learnt to wait for the presentation of this instrumental CS and the intertrial lever presses gradually disappeared.

4. The number of lever presses required in each trial for delivery of CS_{cl} and food was gradually increased to 14 while the duration of the CS_{cl} was extended to 8 seconds. It took nearly 30 days to complete this stage.

Testing. Afterwards the training was continued daily and the following tests were performed.

a. The data from the five consecutive daily sessions of training were analysed to find the degree of separation of instrumental and conditioned salivary responses to CS_{in} and CS_{cl}.

b. The effect of gradual satiation of the hunger drive upon the CRs was tested in three nonconsecutive sessions.

c. The effect of acute satiation was tested in three nonconsecutive sessions. The difference between the two satiation tests (b and c) was the following. In the gradual satiation the dog was presented the CS_{in}-CS_{cl}-US trial repeatedly until he ceased to eat. The acute satiation was produced after the first two trials by feeding the dog ad libitum and then the remaining two trials followed.

d. The effect of increased hunger was observed in four consecutive days. The level of hunger drive was increased day by day.

e. The CS_{cl} was presented without preceding CS_{in}.

f. The CS_{cl} was postponed of eight seconds; in other words an eight second pause was interposed between CS_{in} and CS_{cl}.

g. The CS_{in} was prolonged to 30 seconds and then followed, as usually, by CS_{cl} and food.

h. The same test (g) was repeated under increased hunger drive.

i. Test for the transfer of CR_{in}. A new stimulus, the flashing light, was presented for 10 seconds and followed by CS_{cl} and food. Such a trial was presented once or twice a day among normal trials. A total 42 trials with the light stimulus replacing the metronome (i.e. the CS_{in}) were applied to each animal.

j. The test "a" was repeated again to find out if the above tests "b" — "i" affected the degree of separation of CR_{in} and CR_{cl}.

k. Extinction and reconditioning was repeated three times.

Special caution was taken not to spoil the previously established CRs by applying the tests in too close succession. Therefore, the dogs were trained normally for five days before the next test was applied. In this paper the results from tests "a", "e", "f", "g", "i", "j",, and "k" are treated, whereas the remaining tests chiefly concerned with the hunger drive variable will be reported in our second paper (Miyata and Sołtysik in preparation).

RESULTS

The separation of instrumental CR from conditioned salivation

Fig. 1 was plotted by averaging the results obtained from six dogs. Left side shows the responses from the test "a". It is clearly shown that the instrumental CRs are practically restricted to the metronome and disappear in one second after the onset of the buzzer. At the end of CS_{in} the dogs pressed the lever at the rate of two per second. In this respect our data perfectly replicate the results of Ellison and Konorski, who used light as a CS_{in}.

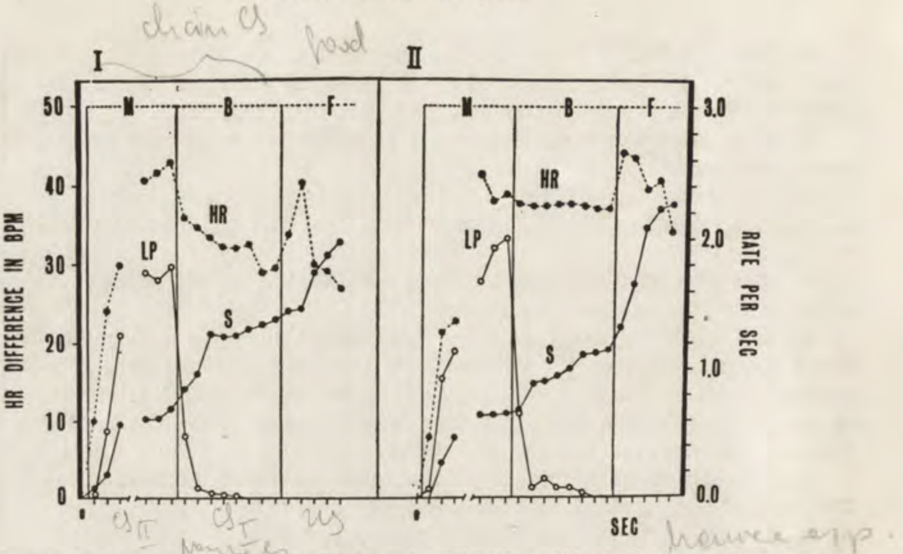


Fig. 1. Mean rate of lever presses (LP) and salivation (S), and mean increase of heart rate (HR) during the CS_{in} (M, metronome) and the CS_{cl} (B, buzzer). F, food. The duration of CS_{in} varied from trial to trial and therefore the responses to it are shown in the first three and in the last three seconds. Left ordinates refer to heart rate and right ordinates refer to salivation (number of drops per second) and lever presses. I, data collected from 6 dogs and five consecutive daily sessions at the beginning of the experiment. II, data collected from the same dogs at the end of the experiment, i.e., after the dogs were subjected to all the tests

The conditioned salivation, however, appeared during the CS_{in}. True, its rate was more than doubled during the CS_{cl} but even this result disagrees with Ellison and Konorski's data which shows virtually no salivation during the light CS_{in}. Heart rate increased sharply during the CS_{in} and gradually decreased after the onset of CS_{cl}. This decrease continued during eating, except for the first two seconds after presentation of food what coincides with the approaching and seizing the food.

This picture was slightly changed after the animals were subjected to various tests mentioned above. The result is shown on the right side of Fig. 1. The main differences are: (i) slightly increased rate of lever pressing during the CS_{cl}, (ii) decreased salivation during the CS_{cl}, and (iii) higher heart rate during the CS_{cl}; practically no decrease in heart rate is seen during the buzzer. The explanation of these changes is given in the discussion. In Fig. 2 the responses of two yoked animals are presented. On the right side the responses of the experimental dog H are shown in the same way as in Fig. 1, and on the left side are plotted the salivary and cardiac responses of the dog Ak which had the same training (i.e. number of trials and duration of stimuli) except for lack of instrumental responses. In other words the yoked dog Ak was classi-

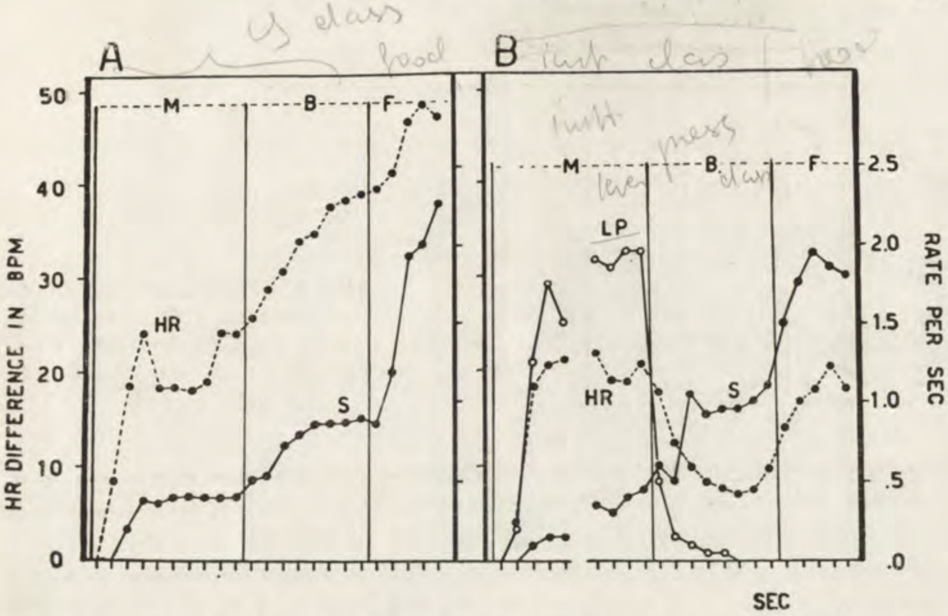


Fig. 2. Comparison of cardiac and salivary responses in two yoked dogs. A, no instrumental responses were trained in this dog and thus both metronome (M) and buzzer (B) constituted a chain classical CS. B, this dog was trained by Ellison-Konorski separation method, i.e., metronome was the CS_{in} and buzzer was the CS_{cl}. Except for the lack of instrumental responses in the former dog, both animals received exactly the same training. HR, heart rate increase above the prestimulus level. S, salivation; mean number of drops per second. LP, mean number of lever presses per second. Left ordinates refer to heart rate and right ordinates refer to salivation and lever presses

cally conditioned to the "chain" CS consisting of metronome and buzzer. There are certain differences in salivary and cardiac curves in both dogs. Although in both dogs salivation increases after the onset of buzzer, this increase is much steeper in the dog trained according to Ellison-Konorski procedure. But the dramatic difference is seen in the cardiac curve. During the metronome the increase of heart rate is quite similar in both dogs, the buzzer elicits further increase of heart rate in the control yoked dog instead of a typical slowing down seen in the experimental animal.

In order to further analyze the mutual influence of the CS_{in} and CS_{cl} the following two tests were performed. In one the presentation of the CS_{cl} was delayed for 8 sec, and in the other the CS_{in} was prolonged for 30 sec. In Fig. 3 the effects of termination of the CS_{in} without simultaneous presentation of the CS_{cl} are shown. There is a clearcut drop in the rate of both lever presses and heart rate, however the lever presses are still performed at the rate of one press in two seconds and they

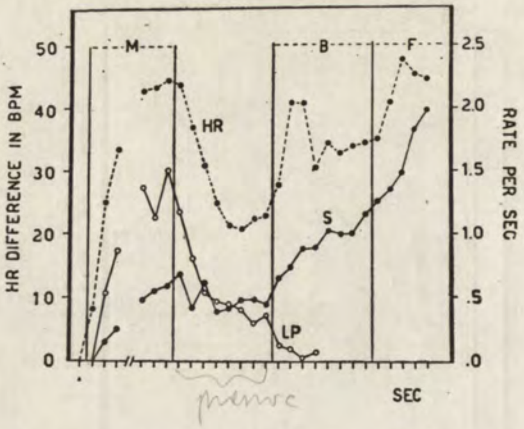


Fig. 3. Cardiac, salivary and instrumental CRs in trials where the CS_{in} and CS_{cl} were separated by pause of eight seconds

disappear only after the CS_{cl} is presented. The onset of the CS_{cl} elicits also a sudden though short-lasting increase of the heart rate.

The salivation tends to decrease slowly during the pause and increases immediately after the onset of the buzzer. Fig. 4 presents the

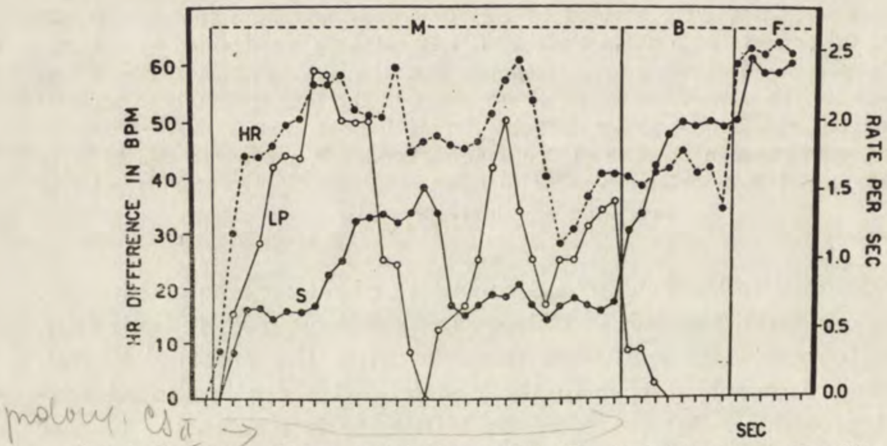


Fig. 4. Cardiac, salivary and instrumental CRs in trials where the CS_{in} was presented for 30 sec

responses during prolonged action of the metronome. The dogs continued to press a lever with a high rate but soon they started to pay more attention to a food-tray and stopped pressing the lever, while their salivation increased. After a few seconds they resumed the pressing and at the same time the rate of salivation decreased. The animals looked disturbed and barked at the metronome or at the silent buzzer. There was striking parallelism in the rate of lever presses and the heart rate, especially in the second half of the prolonged CS_{in}. In Fig. 5 are shown

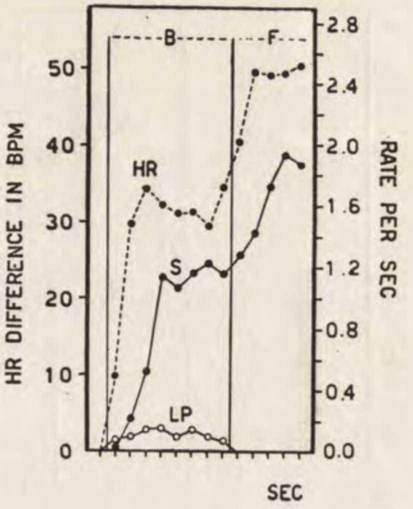
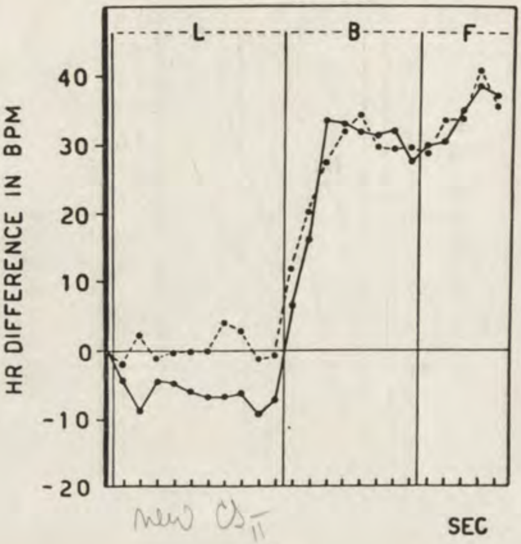


Fig. 5. Cardiac, salivary and instrumental CRs in trials where the CS_{cl} was presented alone

the responses in trials where the CS_{in} was omitted. The trial started with the presentation of the buzzer which as usually was followed in 8 sec by food. Salivation started promptly and was continued at a good rate throughout the CS-US interval. Heart rate also increased rapidly but after some three seconds started slowing down. There were some sporadic lever presses during the whole duration of the buzzer. Thus, despite the unexpected omission of the CS_{in}, the animals responded appropriately to the CS_{cl}.

Transfer of the CR_{in} to a new stimulus

On one or two of four trials in a daily session the light stimulus was presented for 10 seconds and followed by the CS_{cl} and food reinforcement. 42 such trials were administered in each dog. On the first trials the animals reacted to the light with a marked orienting (targeting) response. This response habituated gradually and at the end of this series of sessions virtually no attention was paid to this stimulus. No transfer of the lever pressing was observed at either stage of this experiment. Also salivation appeared very rarely to light, showing that no conditioning has taken place despite systematic pairing with the CS_{cl} and food. Fig. 6 shows the heart rate changes observed during the lst and 42nd application of this stimulus (L). The first application elicited a definite deceleration of the heart rate which was absent on the last trial. The CS_{cl}, i.e. the buzzer elicited immediate increase of the pulse rate and after 3—4 sec a gradual deceleration. This course of the pulse curve resembles that shown on Fig. 5 where the buzzer was presented without the preceding CS_{in}. It is worth while to point out that the CS_{in}



new CS_{II}

Fig. 6. Cardiac response to a new stimulus (L, light) paired 42 times with the CS_{cl} (B, buzzer) and food-US (F). Solid line: the first presentation of light. Broken line: the last, 42nd presentation of light

elicited cardioacceleratory response which continued until the onset of the CS_{cl}. During the buzzer (see Fig. 1) there was only gradual cardiodeceleration. When the buzzer was presented alone (Fig. 5) or after the light (Fig. 6) both acceleratory and deceleratory responses appeared in succession, the former lasting only 3 sec and followed by the deceleration during the remaining 5 sec of the stimulus.

Extinction

Acute extinction was performed three times in each dog. The extinction session consisted of 20 non-reinforced presentations of CS_{in} lasting 10 sec and followed by the CS_{cl}. After each extinction the responses were retrained to the previous level of performance. Three successive trials with no lever presses were taken as the criterion of extinction.

As shown in Table I in the first extinction session none of the dogs has reached the criterion within 20 trials. However, during the second extinction session one dog reached the criterion, and at the third session four animals were able to extinguish their CRs_{in}. Thus, the gradual decrease of the resistance to extinction was found in consecutive extinction sessions, despite of the interposed reconditioning sessions. Fig. 7 was plotted from the results obtained on the extinction sessions in which the criterion was not attained. Gradual decrease of the lever press rate, salivation rate and heart rate response was observed as a function of the extinction trials.

The general behavior of the dogs changed as the extinction trials proceeded, especially later from the 15th to 20th trial, when the dogs

Table I
Number of the extinction trials given in each test

Dog	Extinction (1)	Extinction (2)	Extinction (3)
T	20	8	20
H	20	20	6
K	20	20	4
S	20	20	10
Q	20	20	5
Tk	20	20	20
Mean	20	18	10.8

were extremely excited, attempting to escape from the stand, particularly during the presentation of the CS_{cl}. This is seen in the heart rate curve from the last 5 trials (open circles in the bottom graph of Fig. 7) which has the highest peak at the very end of the buzzer.

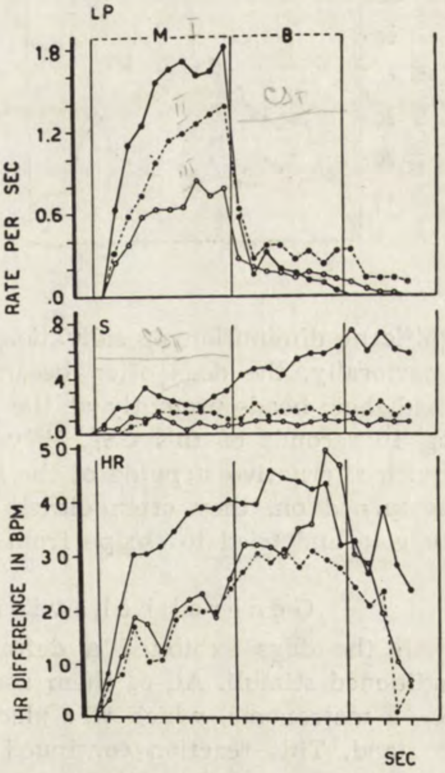


Fig. 7. Extinction of the instrumental (LP), salivary (S) and cardiac (HR) conditioned responses. Twenty extinction trials were divided into five blocks. Solid line with filled circles refers to the first block of four trials; broken line with filled circles refers to the middle block (trials 9—12), and solid line with open circles shows the responses in the last four trials

Finally, on Fig. 8 presented are responses from the first trial of extinction (upper curve of each graph) and from the first trial on which no instrumental response occurred (lower curve). It is clear that parallelly with the complete extinction of the lever presses (LP) there was significant diminution of salivation (S) and heart rate response (HR). Behaviorally, the dogs often became drowsy between trials, but they raised their heads promptly at the presentation of the metronome. During 10 seconds of this CS_{in} they seemed excited, showing restlessly a quick alternative stepping of the forelegs. But when the CS_{cl}, (buzzer) was turned on, they often either became quiet, or, on the contrary, struggled and tried to escape from the stand.

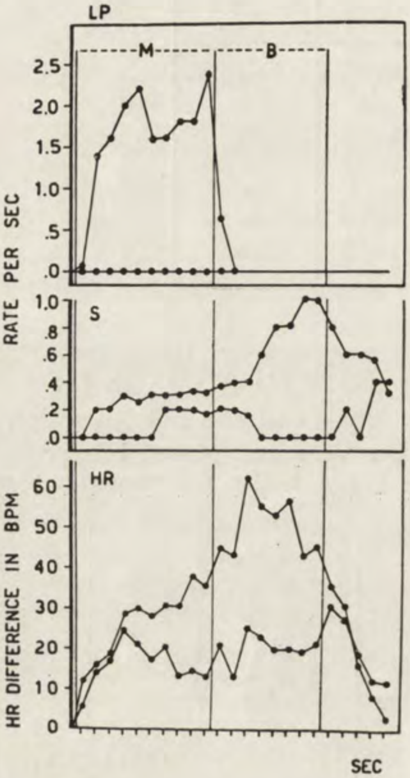


Fig. 8. The first extinction trial (upper curve on each graph) is compared with the trial on which no lever presses occurred for the first time (lower curve on each graph). LP, lever presses. S, salivation. HR, heart rate. M, metronome. B, buzzer. (Mean from five dogs)

General behavior during the trial

All the dogs exhibited a definite orienting responses toward the conditioned stimuli. All of them used to turn a head backwards at the CS_{in}, a metronome, which was placed behind and on the right side of the stand. This reaction continued throughout the entire experiment.

They showed, however, different patterns of responses which are summarized in Table II. For example, the dog Q, while pressing the lever looked at the metronome and barked violently. The dog S on the contrary looked and barked at the buzzer during the CS_{in}. After the onset of CS_{cl} (the buzzer) the dogs took a glance at it and then attentively looked at the food-cup.

Table II

The type of reactions to CSs during pressing a lever

Dog	Instr. CS	Class. CS	Food-cup
T		Looking	
H	Looking		Looking
K		Looking	
S		Looking and barking	
Q	Looking and barking		
Tk			Looking

DISCUSSION

Spectacular as they are, the results of Ellison and Konorski (1964, 1965) remain open to criticism. They used as a CS_{in} a light and as a CS_{cl} an auditory stimulus. This arrangment proved to be extremely successful in separating the instrumental and salivary CRs. However, would it be so if the CS_{in} and CS_{cl} were selected from the same analyzer, or if the CS_{in} were auditory and CS_{cl} visual? It is well known that visual stimuli are much "weaker" as salivary CSs than auditory ones. If the visual stimulus is followed by the auditory and food, the lack of salivation to the "weak" visual CS migh be explained by masking or inhibition of delay. Considerations of this sort led us to investigate further the Ellison-Konorski separation procedure using auditory stimuli for both the CS_{in} and CS_{cl} and testing their properties under several conditions.

The first fact to be discussed is the obvious failure to separate fully salivation from instrumental motor responses. Although the CS_{cl} produced almost exclusively salivary responses with no concommittant lever presses, the CS_{in} elicited both salivation and motor CR_{in}. True, the rate of salivation was less than 50% of that during the CS_{cl} but nevertheless it was a consistent response coexisting with the lever presses. How could it be explained?

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First of all, some degree of generalization between both CSs could be expected for both were the auditory stimuli. But why there was only one-way generalization, from buzzer to metronome and not in the reverse direction? Several factors might contribute to this assymetry of generalization.

a. Salivary conditioning preceded instrumental. The CS_{in} was introduced after the CS_{cl} had been well conditioned and, of course, the generalization was from the well trained to a new stimulus and not in the opposite direction.

b. If any generalization or transfer was due to associations between both stimuli, again the associations were in favor of forward conditioning of the salivary CR as compared with the backward conditioning of the instrumental CR.

c. The CS_{cl} certainly cannot be a pure "consummatory" CS because, as shown in paper of Kiryłowicz et al. (1968) the normal feeding elicits both drive (i.e., preparatory) and consummatory responses. The dog not only salivates but also awaits for food and prepares himself to approach and seize it. This motor responses, which could be considered as very natural instrumental CRs, compete successfully with the ontogenetically young instrumental CRs like lever presses.

d. Finally, it is feasible to assume that there is an inherent assymmetry in mutual relationship between drive and consummatory reflexes. While the consummatory reflex inhibits more or less completely the preparatory activity, there is no need to suppress fully the consummatory reflexes during preparatory behavior, especially, if there is no struggle for the common final path, as in the case of lever pressing (the preparatory, or drive behavior) and salivation (the consummatory reflex). The strong inhibitory influence of a consummatory reflex upon the preparatory one was shown by Konorski and Wyrwicka (1950) in an experiment where the former classical CS eliciting good salivary CR was transformed into a CS_{in} evoking an instrumental CR. The transformation was difficult and the CR_{in} was weak and much inferior to CR_{in} elecited by other CSs which had not been used as classical salivary CSs. It would be interesting to test the opposite transformation: of a CS_{in} into a CS_{cl}. According to the presented above view, no such difficulty in transformation is expected, and the resulting salivary CR should be as good as the salivary CR to primarily classical CSs.

It is interesting to note, that after all the tests, which included repeated acute extinction, applying the CS_{cl} alone, prolonging the duration of the CS_{in} and others, the cardiac and salivary CRs to buzzer (a CS_{cl}) have undergone a significant change. As shown on the right graph of the Fig. 1, there was a decrease of salivation as compared with the salivary CR measured before the tests (see the left graph on the Fig. 1). The general rate of salivation was not only decreased but also the initial increase of salivation was reduced during the first three seconds of the buzzer. At the same time an even more striking change was seen in the cardiac response. The definite deceleratory response during the buzzer found before the tests (left graph on Fig. 1) was virtually absent after the tests (right graph on Fig. 1). Undoubtedly the tests had a deteriorating effect mainly upon the CS_{cl}. This would be in keeping with the general concept of drive and consummatory CRs (Sołtysik and 1966 Konorski ~~1967~~). The drive CRs are believed to be more resistant to extinction and to the increase of CS-US interval. But in our present case the differential effect of extinction (and other tests) might be simply explained by the fact, that while the CS_{cl} was subjected to full nonreinforcement, the CS_{in} was at least secondarily rewarded by the CS_{cl}.

The other tests were performed mainly to investigate the properties of both CS_{in} and CS_{cl}, and also to find out what are the relations between instrumental (i.e., drive), salivary (i.e., consummatory) and cardiac responses. We were particularly interested in the possibility of finding a correlation of heart rate and drive and antidrive (Konorski 1967) states. Let us review the obtained relevant data.

First of all, the curve of heart rate in Fig. 1 seemed to confirm our expectations. The CS_{in} elicited a prompt and substantial (up to over 40 beats per minute on average from 6 dogs!) increase of heart rate, whereas the CS_{cl} produced a gradual cardiodeceleration. Even more convincing was the result from our "pure" classical yoked dog (Fig. 2) in which heart rate steadily rose during both metronome and buzzer. Obviously the dog exhibited a natural instrumental reaction of approaching and preparing to seize, and the intensity of this reaction increased approaching the moment of presenting the food. In the dogs that had to press a lever during the metronome i.e., when the intensity of instrumental activity was higher during the metronome, also the heart rate was higher during this CS. It could, of course, reflect simply the amount of muscular effort. In fact, in tests where the metronome and buzzer were separated by the 8 sec pause, or where the metronome was prolonged to 30 sec (Fig. 3 and 4), there was a good parallelism of heart rate and the rate of lever presses, except for the sudden increase of heart rate after the onset of a buzzer (a CS_{cl}) as seen in Fig. 3 and 5. In both cases the onset of this stimulus was unexpected and separated from the end of the metronome. And in both cases there was no increase of lever presses. However, the very first reaction to any meaningful stimulus is an orienting response, turning the head towards the stimulus or at least giving a glance at it. This response might belong to the category of preparatory responses even if the stimulus is a CS_{cl}. If so, the initial increase of heart rate could be still interpreted as a drive CR. Perhaps, as the innate instinctive behavior always starts with preparatory activity and ends with the consummatory or "goal" response, also the conditioned consummatory reflexes must be preceded by some short preparatory response, at least in the form of orienting reflex necessary to recognize the stimulus. By the way, it should be stressed again, that the CS_{cl} in the Ellison-Konorski procedure is not a pure classical-consummatory stimulus. Ellison et al. (1968) have recently shown that the electromyogramme from the neck muscles is quite active during the CS_{cl}, proving how tense are dogs awaiting for food. Since Kieryłowicz et al. (1967) have shown that presenting food directly into the mouth gives better consummatory CRs than presenting it in the bowl, an improvement in separation procedure might be expected by combining the Ellison-Konorski method with mouth-feeding. Konorski et al. (1968), using five of our dogs and recording the EEG observed that the heart rate was highly correlated with the hippocampal theta rhythm. Both heart rate and theta rhythm accelerated during CS_{in} and CS_{cl} and decelerated during the food-intake.

The next point for discussion is our negative result in the test for a transfer of instrumental CR. Whenever in a well trained dog an instrumental CS is replaced by a new stimulus in a series of trials a transfer of the CR_{in} is expected. There are usually two mechanisms of such a transfer. Either the new stimulus is somehow similar to the old CS and thus the CRs appear due to stimulus generalization, or even if there is no generalization the CRs appear after the new stimulus is several times reinforced with food. This transfer due to classical food conditioning was described by Wyrwicka long ago (1952). However, one of us (Sołtysik 1960, unpublished experiment) found that if a new stimulus is presented for one or two seconds and then reinforced, and this CS-US interval is gradually but slowly extended to 10 or 20 seconds, the transfer of instrumental CRs does not occur, despite of good salivary conditioning. On the other hand, it was possible to "provoke" the instrumental CR by unexpected prolongation of this new CS. The animal seemed excited, the salivation ceased and the instrumental movement was performed. This and similar observations led to the formulation of a concept in which the instrumental food rewarded movements is mediated by the hunger drive „center", and the salivary CR has a separate reflex arc (Sołtysik 1960). In the present experiment the metronome which elicited a vigirous instrumental activity was replaced by a flashing light. This combination was repeated 42 times in each dog but neither lever presses nor salivation was conditioned to the light. There was a cardiodeceleratory response of first trials but it habituated quickly and the stimulus was perfectly disregarded by our animals. Was it masked by a much stronger buzzer? Or is an analogous case to that, where a new stimulus is "reinforced" by the aversive CS eliciting an avoidance movement (Konorski, unpublished observation). In such a training no "secondary" avoidance response could be obtained. Further experiments are needed to elucidate these puzzling results.

The results of the extinction although it was not completed within 20 trials show an interesting picture. The typical change in the motor responding was pressing the lever which appeared during the classical CS and after its cessation. This was observed most often, as shown in Fig. 7, on the third block of the extinction. Since the classical CS was not followed by the food, the connection once formed between the classical CS and the food began to weaken. Therefore the inhibitory effect on the drive CR, responsible for the lever-pressing was diminished. The rate of salivation decreased as the extinction proceeded, but has not reached the zero level. The cardiac rate showed a high resistance to extinction; especially in the third block, when it increased remarkably at the classical phase. The dogs were very much excited and restless, attempting to escape from the stand. This prompts us to assume that the extinction itself produces a certain kind of foreign emotional drive. Another common symptom was yawning regularly observed after the onset of the instrumental or the classical CS.

When the motor response was completely extinguished, the salivation occurred slightly just before and after the classical CS, and the cardiac rate still showed some increase.

The more detailed account of the problems on the drive and consummatory CRs will be brought about in our second paper, including the data and discussion concerning food-deprivation and satiation.

SUMMARY

1. According to the Ellison-Konorski's separation method, six dogs were trained to perform fourteen lever-presses in response to the metronome (the instrumental CS), which was followed by the buzzer (the classical CS) and food-reinforcement. In distinction from the original Ellison-Konorski's study we used the auditory stimuli as both, the instrumental and classical CSs. Besides the salivary and instrumental CRs the cardiac responses were recorded. Two other dogs were run especially as control subjects.

2. The instrumental CS elicited lever-pressing but also a fair rate

of salivation. Thus we failed to obtain a strict separation between the motor and salivary responses to the instrumental CS.

3. The classical CS, on the other hand, inhibited strikingly the instrumental response and produced a copious salivation.

4. The cardiac rate increased during the instrumental CS but slowed down during the classical CS.

5. In several tests the properties of either CS were studied. It was concluded that neither the first stimulus is a pure instrumental CS nor the second one could be considered a pure classical CS.

6. Acute extinction was performed three times in each dog. None of six dogs in the first extinction, one in the second, and four in the third could reach the criterion of three consecutive trials without lever pressing. Even when the instrumental CR was extinguished, some salivation was still observed and the cardiac rate remained at a relatively high level. As extinction developped, the dogs showed yawning on some earlier trials. But they became very nervous and restless, trying to jump down from the stand at the later stage of the extinction session.

7. Each dog expressed a different pattern of the orienting reaction toward the instrumental and classical CSs. Some looked at the instrumental CS and barked at it while pressing a lever, and others preferred to watch the classical CS.

8. From the results mentioned above, the interrelationship between the drive and consummatory CRs was discussed.

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THE INSTRUMENTAL ALIMENTARY-AVOIDANCE DIFFERENTIATION IN DOGS

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It was shown by numerous authors that if signals for avoidance and alimentary reactions were applied in the same experimental environment, a "conflict" between alimentary and defensive tendencies (drives) occurred and neurotic disturbances resulted (Erofeeva 1913, Cook 1939a, Dimmick et al. 1939, Maier 1939, Masserman 1943, Liddell 1947, Mowrer 1950, Dollard and Miller 1950, Wolpe 1952, and others).

In most experimental studies devoted to the problem of neuroses the so-called "clash" of alimentary and defensive signals was considered as the most effective neurogenic method. Similarly, several authors working with other problems noticed accidentally that if a test possessed both alimentary and defensive features, then various unwished disturbances in behavior may occur. For example, many years ago Konradi (1932) produced an experimental neurosis when he aimed to elaborate three different conditioned reflexes reinforced, respectively, by food, acid and electric shock. Similary, Konorski and Szwejkowska (1956) reported that the transformation of the alimentary reactions into avoidance and vice versa may be neurosogenic.

Therefore it existed the general opinion that test composed of defensive and alimentary elements should be avoided in order to prevent neurotic disturbances.

However, for some purposes it seems very usefull to establish alimentary-avoidance differentiation. Everyone studying the effect of lesions on behavior knows that it is very difficult to obtain exactly the same lesions in different subjects. Therefore, in order to compare impairments in avoidance and alimentary responses after lesion, a great number of subjects should be used for each group to have a probability of obtaining twin lesions in different subjects.

The alimentary-avoidance differentiation gives us an opportunity to compare the effect of a lesion on either avoidance or alimentary reactions in the same subject and, in addition may furnish some information about the discriminative abilities of the subjects. The only objection against this method was it's neurosogenic character.

The aim of this paper was to show that the alimentary-avoidance differentiation may be used as a perfect behavioral test without producing any abnormal reactions.

EXPERIMENT I

Procedure. The experiments were performed on 4 male mongrel dogs. They were trained to perform instrumental alimentary reactions to a tone of 1000c/sec. The instrumental movement consisted in putting the right fore leg on the food-tray and this reaction was reinforced by food (Konorski and Miller 1933). The experimental sessions were carried out every day, 20 trials during each session, intertrial intervals being one minute. All dogs were trained to the criterion of 100% of positive reactions during 20 consecutive experimental sessions (400 positive reactions without error). Therefore the alimentary reactions were overtrained. When the criterion was reached, the experiments with alimentary reactions were stopped and the avoidance training started. Avoidance reactions were trained by the method of passive movements described by details in our previous work (Fonberg 1958). It consisted in putting the right hind leg on the platform to the sound of buzzer. The avoidance conditioned stimulus was purposely chosen to be very different from the tone, in order to make the discrimination of conditioned stimuli for alimentary and avoidance reactions as easy as possible. The experiments were performed in the same reflex chamber as was the alimentary training, and they were carried out every day, ten trials during each experimental session, with intertrial intervals of one minute. The dogs were trained to criterion of 100% of correct reactions during ten experimental sessions and at least 95% of correct reactions during 25 consecutive experimental sessions. In this way the avoidance reaction was overtrained. As soon as the criterion was reached, avoidance and alimentary stimuli were combined during the same experimental session. Experiments were performed every day, each experimental session consisting now of 20 trials, ten alimentary and ten avoidance, interspersed in a random order, with one minute intertrial intervals.

Results. The results are shown on Fig. 1. We see that when the well-trained avoidance reactions were combined with well-trained alimentary reactions, this procedure did not produce any disturbances. In spite of the fact that the stimuli for both reactions were separated by short intervals, and applied in a random way, the dogs performed the proper reaction in 100%, without any mistake. Also general behavior of the dogs was not changed, besides of some orienting reaction to the first few interchanged avoidance and alimentary stimuli. Slight effect was only noticed on the latency of avoidance reactions (Fig. 2). In two dogs the lenghtening of the latencies was statistically significant ($p < 0.01$). The latencies of the alimentary reactions were not changed in three dogs ($P > 0.05$),

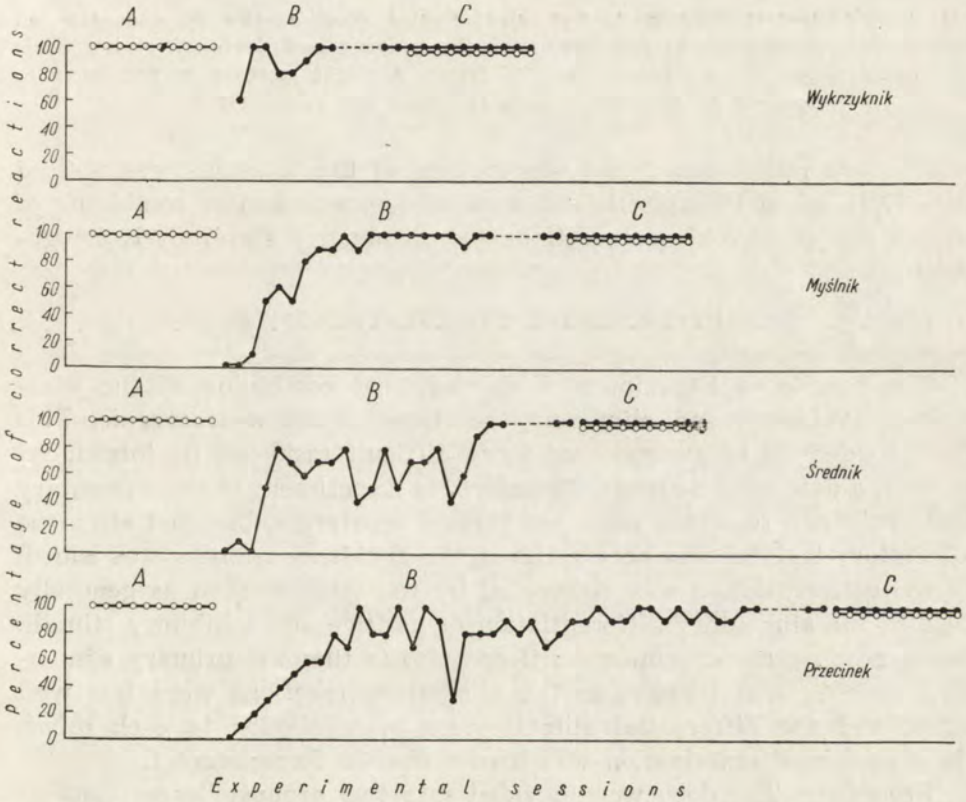


Fig. 1. Combining of evertrained instrumental alimentary and avoidance reactions. The graph shows the course of training for each dog during the last ten experimental sessions of alimentary training (A) of avoidance training (B) and during the first ten sessions of combined test (C). Ordinates, percentage of correct reactions in each experimental session. Abscissae, successive experimental sessions. We can see that the performance of avoidance and alimentary reactions is not changed when both reactions are combined

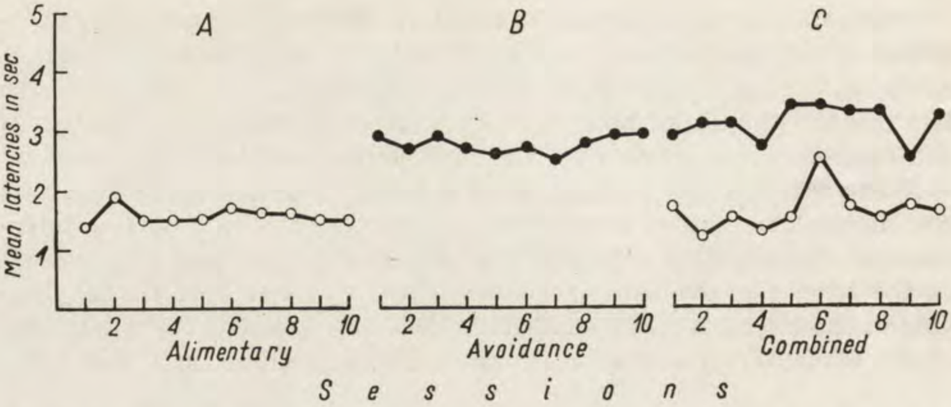


Fig. 2. The mean latencies of the instrumental reactions during the last ten sessions of alimentary (A) and avoidance (B) training and during first ten trials of combined test (C) are plotted on the graph. A slight increase of the latencies can be noticed when both reactions are combined (C)

and in one dog a significant shorthening of the latencies was noticed ($p < 0.01$), when 10 experimental sessions before and after combining of alimentary and avoidance reactions were compared (Smirnov-Kolmogorov test).

EXPERIMENT II (DIFFERENTIATION)

The results of Experiment I showed, that combining of the well-trained avoidance and alimentary reactions is not neurosogenic. This fact alouded us to assume that more difficult task can be introduced without a danger of neurosis. Therefore, in Experiment II the alimentary and avoidance reactions were not trained separately, but just after the alimentary training was accomplished, the avoidance training was added, so the differentiation was elaborated by the same method as generally used in the alimentary differentiation of positive and inhibitory stimuli. The procedure of experiments differed also in that the primary alimentary training was shorter, so the alimentary reactions were less well fixed, and the differential stimuli were more similar to each other, therefore the discrimination was harder that in Experiment I.

Procedure. The dogs were devided into two groups: "experimental" and "control", four dogs in each. Both groups were first trained to perform the alimentary reactions. The general procedure was similar to that in the Experiment I. The only difference concerned the criterion which in Experiment II consisted in 15 sessions with at least 95% of proper reactions, whereas in Experiment I it was 20 sessions with 100% performance.

When the criterion for alimentary reactions was reached the alimentary-avoidance differentiation was trained in such a way that the tone 500 c/sec was introduced and interspersed randomly among the trials with tone 1000 c/sec (alimentary). Tone 500 c/sec was followed after 10 sec by an electric shock (100 V) delivered through electrodes connected to the palm of the right hind leg. The shock evoked leg flexion. If the dog performed similar flexion of the hind leg during 10 sec of tone duration then the shock was not applied, and the tone was stopped immediately after the avoidance movement.

The control group was trained in the same way, with the only difference that tone 500 c/sec was not reinforced, either by food, or by electric shock.

In both groups 20 trials were applied during each experimental session. Ten trials with positive alimentary conditioned stimulus (tone 1000 c/sec) and ten trials with either avoidance or inhibitory stimulus (tone 500 c/sec). The trials with tone 1000 c/sec and tone 500 c/sec were interspersed randomly, with intertrial intervals of one minute.

Results. Mean numbers of experimental sessions to criterion for differentiation of two groups are plotted on Fig. 3. And on Fig. 4 the course of training in both groups is shown. In two dogs only, one belonging to the experimental group and the other — to the control group, during first experimental sessions of the differentiation, a slight disturbance in the alimentary performance was noticed. It was due either to the orienting reaction to new situation or to reciprocal inhibition from

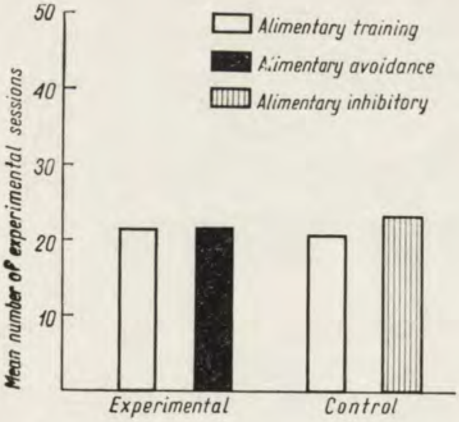


Fig. 3. Comparison of the numbers of experimental sessions necessary to achieve criterion. White blocks represent mean numbers of sessions (for each group), for alimentary training in experimental and control group. Black blocks represent mean numbers of sessions for alimentary-avoidance differentiation; stripped blocks, mean numbers of sessions for alimentary positive-inhibitory differentiation

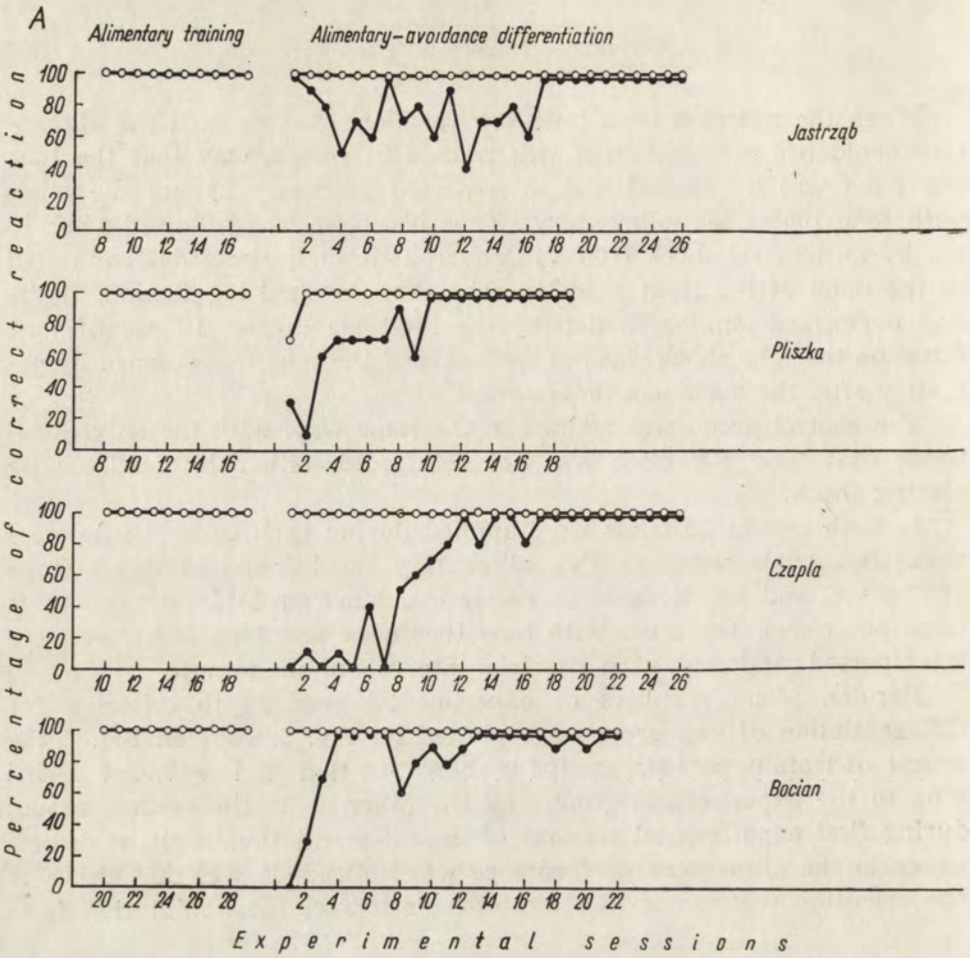
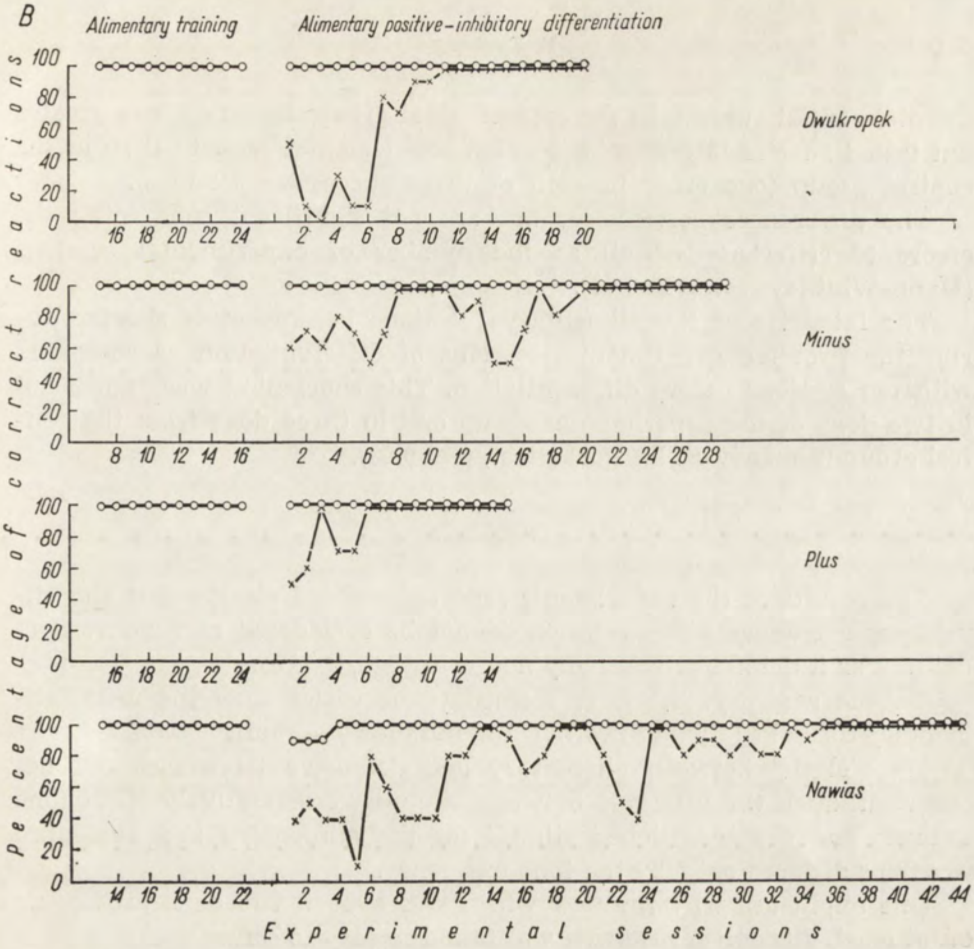
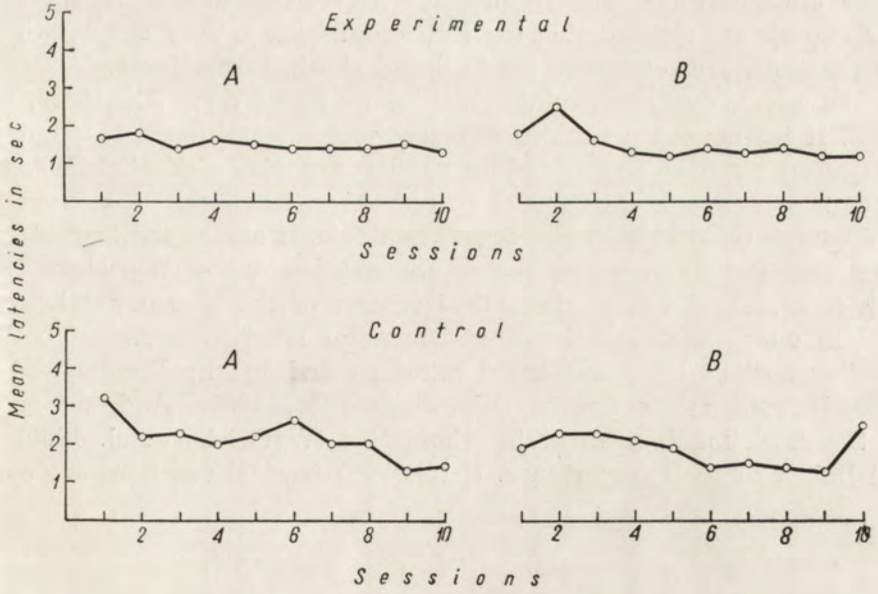


Fig. 4. Graph represents the course of alimentary-avoidance differentiation in the experimental group (A) and alimentary positive-inhibitory differentiation in the control group (B). Each dog is represented separately. First part of each graph represents the last ten trials of alimentary training (100% performance); second part represents, respectively, the avoidance-alimentary differentiation (A) and alimentary positive inhibitory differentiation (B) for each dog. Abscissae; successive experimental sessions. Ordinates, percentage of correct reactions

→

Fig. 5. Latencies of instrumental alimentary reactions (mean for each group) during last ten experimental sessions of alimentary training (A) and (B) first ten sessions of the avoidance-alimentary differentiation (experimental group) or alimentary positive-inhibitory differentiation (control group)


B
Alimentary training
Alimentary positive-inhibitory differentiation
Percentage of correct reactions
Dwukropek
Minus
Plus
Nawias
0
20
40
60
80
100
Experimental sessions


Mean latencies in sec
Experimental
A
B
Control
A
B
Sessions
Sessions
1
2
3
4
5
2
4
6
8
10

the differential stimuli. In the experimental group the effect was greater but lasted shorter (3 errors in the first experimental session) than in the control group (one error in each of three successive sessions).

The differences between groups are not significant concerning the errors to criterion as well as the number of experimental sessions (Mann-Whitney test, $p > 0.05$).

The latencies of the alimentary reactions became even shorter during the first ten experimental sessions of differentiation as compared with ten sessions before differentiation. This shortening was significant in two dogs of the experimental group and in three dogs from the control group (Smirnov-Kolmogorov test, $p < 0.05$).

DISCUSSION

The results of the experiments reported showed clearly that the alimentary-avoidance differentiation cannot be considered as a neurosogenic task as it did not produce any neurotic disturbances.

On the contrary, this task seemed to be easier than the usual alimentary differentiation of positive and inhibitory stimuli.

The "clash" between alimentary and defensive tendencies did not occur although the intervals between stimuli were relatively short (one minute) and the conditioned stimuli for the alimentary and avoidance reactions differed only by the tone frequency.

One might ask why the task which was expected to be neurosogenic or, at least, difficult for the dog was found so easy to solve?

We know that differentiation of two different motor reactions reinforced by food is by itself difficult for the dog if conditioned stimuli differ only in their tone frequencies (Dobrzecka and Konorski 1967). Our experiment showed that such differentiation is easy if the two motor reactions are reinforced by food and shock, respectively.

These facts could be explained by the theory of Wyrwicka (1952, 1960, 1966). It is known that if two different motor conditioned reactions are reinforced by food and tested in similar experimental situations, then there is often a mutual transfer of responses (Konorski 1928, Wyrwicka 1952). Such transfer does not occur, as a rule, if one of the instrumental reactions is alimentary and the second one avoidance (Wyrwicka 1958). This is explained by the theoretical scheme of the instrumental "reflex arc" in which the conditioned instrumental reaction is linked both to the "center" of the conditioned stimulus and to the "center" of the unconditioned reinforcement (Wyrwicka 1952, 1960). And, as proved by the experiments with brain stimulation (Wyrwicka et al. 1960) this last link is of great importance. If two instrumental reactions are conditioned to two different stimuli reinforced by food, they have the common "route" through the alimentary center an therefore these two reactions may mix.

On the other hand, if one reaction is connected with the alimentary "center" and the second — with the defensive "center", the reflex arcs are separated and the instrumental reactions do not mix.

On the ground of Wyrwicka's hypothesis we expected that only in the case if the particular instrumental reactions were strongly "linked" to the particular unconditioned reinforcement, then the alimentary avoidance differentiation could be established. Therefore we performed the Experiment I, in which both the alimentary and avoidance reactions were overtrained separately.

The results showed, however, that our care was unnecessary and that the introduction of the conditioned stimulus reinforced by shock among the alimentary stimuli was amazingly not more disturbing that an introduction of the inhibitory stimulus.

Why then several authors had difficulties with the mixed avoidance and alimentary test and observed neurotic disturbances which we did not noticed at all?

The main reason seems to be that in our experiments strict rules were observed and that our animals were never uncertain about the meaning of the differential stimuli i.e. which kind of reinforcement they had to expect. This permitted us to avoid the neurosogenic clash. In the experiments of other authors the competition of opposite tendencies, due to both alimentary and nociceptive stimuli acting stimultaneously (Maier 1939, Masserman 1943, Dollard and Miller 1950, and others) or due to variability of tests (Erofeeva 1913, Konradi 1932, Cook 1939b, and others) could be pointed out as the cause of neurosis. On the other hand, it was shown previously (Fonberg 1961) that it is possible to elaborate two different instrumental avoidance reactions to two conditioned stimuli even if they are reinforced by two noxious agents provided the experiments are very regular. However, when any unexpected or unpleasant stimuli were applied, sometimes only once in the beginning of the experimental session is resulted in a chaotic mixture of both instrumental reactions to both conditioned stimuli and an avalanche of intertrial reactions appeared during the subsequent part of the session. This proves how important are the strict rules of experimental procedure for sustaining normal behavior of the dog, especially in sophisticated tests or situations.

Nevertheless, the fact that even in our conditions first experimental sessions with the shock did not produce evident disturbances in the alimentary reactions and in general behavior of the dog was rather unforseen.

In conclusion we can say that the alimentary-avoidance differentiation is not neurosogenic in normal subjects. As will be shown in the next paper (Fonberg, in preparation), this method was found to be very useful to detect changes after lesions within the limbic system.

SUMMARY

The alimentary-avoidance differentiation was established in dogs. It was shown that combining of alimentary and avoidance procedures during the same experimental session is not neurosogenic and, furthermore, that the alimentary-avoidance differentiation is not more difficult for the dogs than the usual alimentary differentiation between positive and inhibitory stimuli.

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THERMOSENSITIVE BAR-PRESSING BEHAVIOR OF THE RAT WITH UNILATERAL LESION IN THE HYPOTHALAMUS AND DURING CORTICAL SPREADING DEPRESSION

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As was demonstrated by a number of authors (Carlton and Marks 1958, Laties and Weiss 1959, Weiss and Laties 1960, 1961, Panuska and Popovic 1963, 1965), rats are able to press a bar to get radiant heat while staying in a cool environment. We used this technique in order to see whether the change of excitability, occuring in the hypothalamus and other cerebral structures during cortical spreading depression (SD) (Rüdiger et al. 1962, Burešova et al. 1962, Rüdiger and Fifkova 1963), is expressed by a change of the bar-pressing rate during a radiant heat reinforcement schedule. Since bilateral cortical SD eliminates instrumental conditional reflexes whereas bilateral lesions of the preoptic area interfere with thermoregulation, we combined unilateral hypothalamic lesion with ipsi- or contralateral cortical SD thus preserving associative and motivational components which both are necessary for the performance of this behavior.

MATERIAL AND EXPERIMENTAL PROCEDURE

Experiments were performed on 10 male rats of the Wistarstrain, 3—4 months old, weighing 250—300 g. The fur on the back was shaved in an area of 7×12 cm. Before each trial the rats were cooled rapidly to a rectal temperature of 29—30°C. Then they were put in a Skinner-Box like apparatus (Fig. 1). The environmental temperature of —2 to —4°C was maintained by a refrigerator. Each bar-press activated for 2 sec a heating coil (44 watts) mounted above the animal's back. The lever presses were sampled by a counter and registrered by a cumulative recorder.

Rectal temperatures were measured immediately before and after the trials. When the instrumental conditional reflex was firmly established we performed a unilateral lesion in the hypothalamus using the stereotaxic coordinates AP = 0,5—1,0 mm, L = 1,0 mm, T = 7,6 mm (after the atlas from Fifkova and Maršala 1960). This means that the area preoptica and nucleus lateralis anterior of the hypothalamus were destroyed which was proved by the histology after end of the experiments.

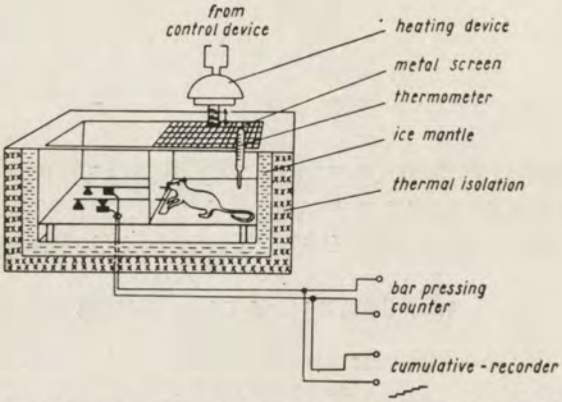

Fig. 1. Modified Skinner-Box for self-heating by thermal radiations in a cold environment

The experimental procedure consisted in trials before the unilateral hypothalamic lesion, after the lesion, and during ipsi- or contralateral cortical SD produced by application of filter paper soaked with 25% KCl solution on the intact dura mater.

Additional experiments were performed in animals without hypothalamic lesion but with unilateral SD, and in animals with lesions outside the hypothalamus.

RESULTS

1. General observations. The lowering of body temperature to 29—30°C did not impair the ability to press the lever.

Already in the first trials the instrumental conditional reflex of bar-pressing for radiant heat could be established. Without the previous cooling we failed to elaborate this operant behavior.

Within a period of 120 min the rats pressed the bar on an average number of 490 ± 73. Towards the end of this period the bar-pressing rate became slower. When the body temperature had reached control levels, what occured within the following hour, the bar-pressing rate became very rare in most of the experiments.

2. Self-radiation after unilateral hypothalamic lesion. The bar-pressing rate remained within the range observed in the intact animals. In the 2-hour-period the lever was pressed 480 ± 63 times. The body temperature reached values the animals had before cooling.

3. *Self-radiation in hypothalamically lesioned rats with ipsilateral cortical SD.* There was only a transient but short-lasting impairment of the operant heating. The total number of bar-presses remained the same as in the former procedure without cortical SD (495±42).

4. *Self-radiation in hypothalamically lesioned rats with contralateral cortical SD.* In contrast to the above mentioned procedures the animals pressed the lever much more, as could be seen in Fig. 2, column 4 from the left. The average number of bar-presses came to 715±110 in 120 min. At the end of the trials the body temperature had reached previous values. Fig. 3 presents a typical course of events during the experiments mentioned above. Note that the bar-pressing rate is highest in the combination of hypothalamic lesion and contralateral cortical SD.

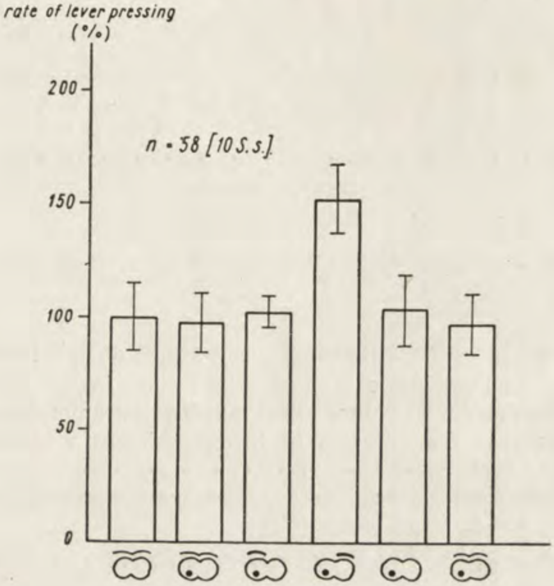

Fig. 2. Lever-pressing rates in 10 rats. 1st column, before lesion, 2nd column, with lesion in area preoptica, lat. ant., 3rd column, with hypothalamic lesion and ipsilateral cortical SD, 4th column, with hypothalamic lesion and contralateral cortical SD, 5th column, hypothalamic lesion, trephine holes in skull, dura uncovered, no KCl-application, 6th column, hypothalamic lesion, trephine holes in skull, skin closed, no KCl-application

5. *Control experiments.* For these experiments another group of rats was used. In one series the skull was trephined on both hemispheres but without application of KCl — solution on the dura mater. The presence of the trephine holes and the contact of the dura mater with the open air had no effect on the normal self-heating behavior (Fig. 2, first co-

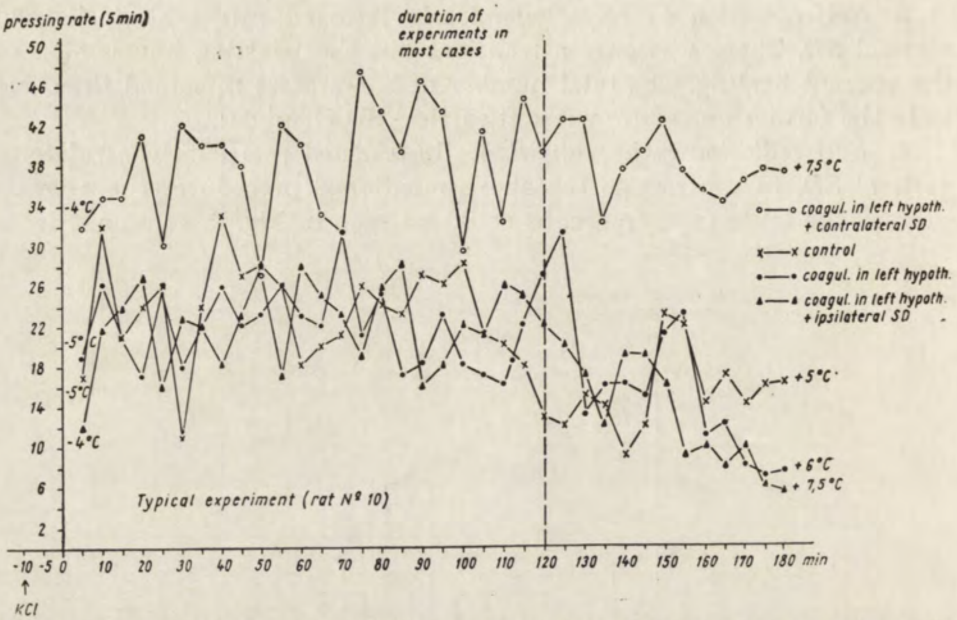

Fig. 3. Lever-pressings (self-readiations) every 5 min during typical experiment in four different arrangements (see inset on right side) in the same rat. Unilateral KCl application on the dura 10 min before putting the animal in the Skinner-Box. In this case the duration of the experiment was 180 min

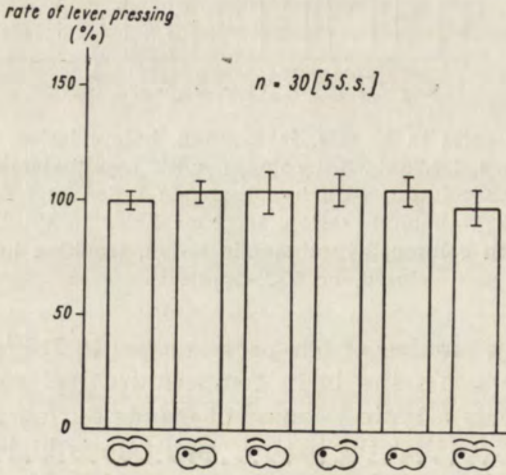

Fig. 4. Control experiments in 5 rats with unilateral lesion of same extention but just above hypothalamus. For further explanation see legend of Fig. 2

lumn). In another series a lesion was made in one hemisphere outside the hypothalamus. Neither ipsilateral SD nor the contralateral one inhibited or facilitated the self-radiation (Fig. 4, Table I).

Table I

Statistically significant rise in lever-pressing rate in hypothalamus-lesioned rats during contralateral SD (4th row). In controls and in all other combinations of SD and lesion the changes in leverpressing rate ranged within initial level (1st row)

Experimental series animals intact	Lever pressing rate (% of controls) ± s 100	n 15
Unilateral lesion in hypothalamus	98 ± 13	10
Unilateral lesion in hypothalamus + ipsilateral SD	101 ± 8,4	10
Unilateral lesion in hypothalamus + contralateral SD	150 ± 15	10
Control experiments		
Unilateral lesion in hypothalamus trephine holes opened, without KCl	102 ± 15,8	9
Unilateral lesion in hypothalamus trephine holes closed by skin suture, without KCl	97 ± 12	9
Unilateral lesion outside of hypothalamus	104 ± 4,7	5
Unilateral lesion outside of hypothalamus + ipsilateral SD	104 ± 8,7	5
Unilateral lesion outside of hypothalamus + contralateral SD	105 ± 7,2	5
Unilateral lesion outside of hypothalamus trephine holes opened, without KCl	105 ± 6,5	5
Unilateral lesion outside of hypothalamus trephine holes closed by skin suture, without KCl	98 ± 7,5	5

DISCUSSION

Recent results of several investigators using implanted thermodes have strengthened the assumption that the anterior-lateral regions of the hypothalamus are involved predominantly in the initiation and maintenance of bar-pressing for radiant heat in cold environments (Satinoff 1964, Baldwin and Ingram 1966, 1967, Baldwin 1966, Carlisle 1966). There is further agreement in that the rats aquire this bar-pressing behavior easely when their body temperature just before the trials and during the early period of the trials was below the normal level. The body temperature most suitable for the fast acquisition of the performance was reported to be 29—30°C, the critical temperature lying at 25°C (Panuska and Popovic 1963). This is in agreement with observations of Buresova and co-workers (1964) pointing out that rectal temperatures of 30°C do not interfere with the acquisition and re-activation of memory traces in the rat.

Since hypothermic rats which were prevented to self-radiate nevertheless recovered their initial temperatures within 2 h in the cold environment, the rewarding effect seems to be due to the excitation of skin thermoreceptors at each onset of the radiations.

Previous experiments with a shuttle-box technique have shown that normal rats react very sensitively upon temperature changings in their environment, i.e. lowering or rising the temperature in one of the two compartments with respect to the other one (Rüdiger and Seyer 1965, Seidel 1968). Thus the thermosensitive locomotion from a warm environment as well as from a cold one to an environment of neutral temperature proved to be a suitable indicator for alterations of the thermoregulatory behavior after lesions in various regions of the brain and during "functional decortication" by means of the KCl-induced SD. As could be demonstrated in this laboratory (Rüdiger and Seyer 1965) in rats with unilateral lesion in area preoptica and nucleus lateralis anterior of the hypothalamus, cortical SD in the contralateral hemisphere inhibited the thermosensitive locomotion selectively. Since cortical SD is correlated with a remarkable decrease in firing rates of hypothalamic neurones (Rüdiger et al. 1962), it was concluded that the excitatory state of this hypothalamic areas (and maybe of other structures not investigated so far) is lower during SD. That a decrease of drive could result from the influence of the cortical SD on the hypothalamus was shown by Burešova and co-workers (1962) in rats with unilateral lesion of the s.c. hypothalamic drinking centre: Cortical SD contralateral to the lesion reduced drinking activity significantly.

The rise in bar-pressing rate during cortical SD seems to be in contradiction to the results reported above. Since the increase of instrumental responding is generally considered to be due to increased drive, an explanation of our findings on thermosensitive bar-pressing simply on the basis of the drive mechanism meets with difficulties. Whether the increase of responding is merely the consequence of a rise in the threshold to the sensation of pain due to overheating of the skin or it is an expression of a releasing phenomenon in regions of the brain-stem other than the hypothalamus could not be answered at present. Further investigations should explain the different results obtained by the two different methods in studying the action of cortical spreading depression on thermosensitive behavior.

SUMMARY

The influence of cortical spreading depression (SD) upon the excitability of hypothalamic areas was investigated in rats with unilateral lesion in the area preoptica and the nucleus lateralis anterior. An instrumental (operant) conditioning procedure on the basis of a thermal reward (radiant heat) in a cold environment was used for the elaboration of an instrumental conditional reflex (lever pressing for radiant heat) which could easely be subjected to quantitative evaluation. When the cortical SD was produced in the hemisphere contralateral to the lesion in the hypothalamus the lever pressing rates became higher than in the other possible combinations of cortical SD with hypothalamic or extrahypothalamic lesions. The results are discussed in terms of the drive theory of instrumental responding.

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DEGENERATION IN THE THALAMUS FOLLOWING MEDIAL FRONTAL LESIONS IN THE DOG

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The frontal lobes of the dog are relatively fairly large, but the boundary of the prefrontal cortex has not yet been definitely marked out. Many authors, e.g., Pribram et al. (1953) and Rose and Woolsey (1948a), gave definitions of the prefrontal cortex, regarding its range as a projection of the thalamic nucleus medialis dorsalis. The projection of the dorsomedial nucleus to the prefrontal cortex is well differentiated in primates, in which three systems connecting particular parts of the nucleus with definite portions of the cortex can be distinguished (Brutkowski 1965). Akert's (1964) observations were based on the amputation of a large portion of the prefrontal cortex in the dog brain. Although the study carried out by Narkiewicz and Brutkowski (1967) on the projection of the dorsomedial nucleus to the prefrontal cortex in the dog manifested its basic organization to a great extent, the posteromedial portion of this formation has not been explored as yet. The results of these authors suggest that the lateral area of the dorsomedial nucleus remains undegenerated even after the most extensive lobectomy (dogs D101 D22). In our experiment operative lesions were located caudally to the medial lesions of the abovementioned authors. The objective of this paper has been to describe the connections of these caudomedial regions of the frontal cortex with the thalamus and to classify this area in the premotor or prefrontal cortex according to the results obtained.

The myeloarchitectonic division of the frontal cortex in the dog brain has been worked out by Kreiner (1961). He marked out the posterior boundary of this cortex along the caudal margin of the prorean gyrus and, on the medial side of the frontal lobe, across the pregenual sulcus, from where it descends ventrally. The cortical areas sited caudodorsally to the frontal region described by Kreiner have been identified by him as sensorimotor cortex (1964). According to this author, the extent of the myeloarchitectonic areas agrees with his observations of the cytoarchitectonic pictures. In the dog brain it is however difficult to define the prefrontal cortex cytoarchitectonically for lack of a distinct inner granular layer IV (Narkiewicz and Brutkowski 1967), which in the monkey brain is well developed and thus characteristic of the prefrontal cortex (Walker 1940a).

The nucleus medialis dorsalis of the dog is a large mass sharply demarcated by the lamina medullaris interna on the ventral and lateral sides. Medially it touches the nuclei of the median line, dorsally borders upon the parataenial nucleus and, where this last nucleus vanishes, extends upwards and neighbours upon the stria medullaris. The posterior surface of the dorsomedial nucleus reaches the habenula, centrum medianum and parafascicular nucleus. On the basis of myeloarchitectonic sections the dorsomedial nucleus can be divided into two parts, a medial and a lateral. Most of the bundles of fibres that spread in the dorsomedial nucleus come from the anterior radiation of the thalamus and only part of them derive from the intermediate thalamic radiation. The systems of fibres from the anterior thalamic radiation penetrate through the ventral and lateral surfaces of the dorsomedial nucleus and assume a dorsocaudal direction. Part of these fibres turn more towards the medial portion of the nucleus, the others keep their dorsal direction and scatter in the lateral area. In addition, the lateral portion of the dorsomedial nucleus receives bundles from the intermediate thalamic radiation. The direction of these systems extending from the lateral boundary of the nucleus is still dorsocaudal. Cytoarchitectonically the dorsomedial nucleus can also be divided into two parts: the magnocellular part situated medially and the parvocellular part, which lies in the lateral portion of the nucleus.

MATERIAL AND METHOD

The material used for this study consists of 18 brains of dogs which were previously examined in behavioral experiments (Stępień et al. 1967). All the dogs were male mongrels, with their weight ranging from 8 to 16 kg.

Description of surgical procedures. Surgical procedures were made under aseptic conditions in general anaesthesia (Nembutal — 35 mg/kg). One-stage bilateral cortical lesions were performed by subpial aspiration. Care was taken to avoid excessive bleeding from vessels going to the sinus longitudinalis superior. The dura, muscles, subcutaneous tissue and skin were sutured in layers.

The post-operative period was uneventful. The general condition of the animals operated on was excellent; no epileptic fits were observed.

The dogs lived for a period from several weeks to half a year after the operation, next they were sacrified and their brains were fixed in formalin. Blocks embedded in paraffin were sectioned serially at 20 micra, and every fifth section was stained by the Nissl and Klüver-Barrera methods. Such sections were used to determine the extent of the operative lesion and the size of degeneration in the thalamus. The absence or a reduction in the number of cellular bodies and a poor or marked gliosis were taken into account in estimation of degenerated nerve cells in a manner similar to that in the descriptions of degeneration presented by Walker (1936).

OBSERVATIONS

With respect to extent the operative lesions may generally be divided into three groups (Fig. 1). One of them (Fig. 1a), the most numerous, consisted of 11 specimens with the most extensive lesions which involved the cortex situated on the medial side, frontally to the cruciate sulcus, i.e., according to Kreiner's (1964) nomenclature, the central, posterior, and medial precruciate areas (XC, XP, and XM, respectively), and in the front reached to the pregenual sulcus FPG, called also the ectogenual sulcus by Dziurdzik (1965). In the second group (Fig. 1b) we numbered 4 specimens which had lesions covering the medial precruciate area XM and, partly, some small adjacent cortical fields. The third group (Fig. 1c) consisted of 3 dogs with lesions of a small cortical region by the cruciate sulcus, on the medial and, partly, dorsal surfaces, i.e., the central precruciate area XC.

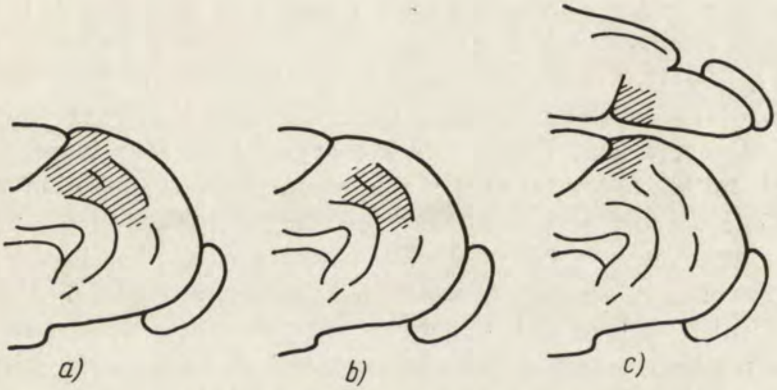


Fig. 1. The extension of the lesions presented on the schematical drawing of the left hemisphere. a) group I; b) group II; c) group III

Individual differences between paritcular specimens of the first group (Fig. 2a, b, c, and d), i.e., that with the most extensive lesions, were small. The lesion sometimes ascended the posterior portion of the prorean gyrus or encroached upon the dorsal portion of the precruciate gyrus or, lastly, it did not involve some of the marginal regions of the extent intended (Fig. 2c, and d). The lesions were not very deep; in most of the dogs the cortex alone was destroyed completely and only within the medial precruciate area the destruction was deeper and affected the white matter under the cortex (dogs: D8, S3, D4, D12, D13, Fig. 2a and b). Some dogs, e.g. S2 (Fig. 2b), had so shallow lesions that the white matter under the gyri remained intact.

All these lesions induced degeneration of nerve cells in the laterodorsal part of the lateral (parvocellular) portion of the dorsomedial nucleus. The degeneration extended from the oral pole of the nucleus to the posterior part of the middle region. It was most intense in the middle portion of the nucleus. Slight differences in degeneration of this nucleus between particular specimens were dependent on the depth of the lesion.

In the dogs showing deeper operative lesions (Fig. 2c and d — dogs D16, S7, D7, D1, S1) the degeneration was heavier and covered a larger portion of the nucleus, whereas the dogs with shallower lesions had poorer degenerations. Degenerative changes were also found in other thalamic nuclei. In all the dogs of this group slight degeneration appeared in the laterocaudal portion of the ventrolateral nucleus of the thalamus. In some specimens in which the lesion was sited farther to the rear, in the gyrus cinguli, degeneration included the posteromedial portion of the anteromedial nucleus and, sometimes, also the anteroventral nucleus.

The second group (Fig. 2e) was composed of 4 dogs with individually differentiated lesions of the cortex of the medial precruciate area. The dog S11 had a bilaterally symmetrical superficial lesion of the cortex of the medial precruciate area, and only in its central portion destruction affected the underlying white matter. In this dog the degeneration of the dorsomedial nucleus occurred in the anterior part of its lateral portion, whereas in the medial portion it concentrated in a small dorsal region and there it also dwindled.

In the dog S9 the lesion was bilaterally shallow and asymmetrical. In the left hemisphere it covered the posterior portion of the proreal gyrus, the posterior precruciate area and, medially, the central precruciate area. On the right side the lesion of the medial precruciate area extended also to the rear, over the posterior precruciate area. The degeneration of the dorsomedial nucleus was observed in its anterolateral portion and was present in the form of islets in the lateral part of the middle portion, where it disappeared. The more extensive lesion in the left hemisphere of this dog resulted in a more intense degeneration in the left dorsomedial nucleus.

In the dog S10 the extent of the lesion was like that in the dog S9. The lesion of the left side was more extensive and, in addition to the medial precruciate area designed for ablation, the destruction included also the medial portion of the prorean gyrus, the posterior precruciate area and the medial portion of the central precruciate area. In the right hemisphere the lesion was somewhat smaller than that on the left side; only a large portion of the posterior precruciate area was destroyed in addition to the medial precruciate. The lesions of both sides were shallow, involving the cortex and only in their central regions also the white matter. In the thalamus degeneration was present in the orodorsal portion of the dorsomedial nucleus. It was heavier on the left side, which was only natural in view of the larger lesion in this hemisphere.

Dog S8. The lesion in this dog was large and fairly deep. In the left hemisphere it occupied the ventral portion of the medial precruciate area, the anterior part of the genual gyrus and, farther caudad the posterior precruciate area. On the right side the lesion was remarkably deeper and wider. Destruction affected also the pregenual and genual gyri, the posterior precruciate area, and the medial portion of the central precruciate area. The degenerative changes in the dorsomedial nucleus of this dog were very intense and included a larger area of the nucleus than in the previous dogs of this group; they extended especially over the posterior region of the nucleus. This extensive degeneration may have resulted from the destruction of the projection fibres from the anterior regions of the prefrontal cortex. As in the dogs of the previous group, all the dogs of this group showed also other sites of degeneration in the thalamus, namely, in the posterior portion of the nucleus ventralis lateralis. In the dog S8 there appeared, in addition, a degeneration in the ventral and medial anterior nuclei, induced probably by the greater extent of the lesion in the genual gyrus.

The third group (Fig. 2f) consisted of three dogs (S4, S5, S6) with narrow lesions in the central precruciate area. The lesions in these dogs resembled each other in area and depth. In all these dogs the cortex was destroyed, whereas the white matter remained unaffected. Only the dog S4 had its lesion somewhat larger in the right hemisphere. The dog S5 showed additional destruction of the cortex in the dorsal postcruciate gyrus on both sides. The lesion brought about slight insular degenerations in the caudal part of the middle portion of the dorsomedial nucleus. No degenerative changes were observed in other thalamic nuclei.

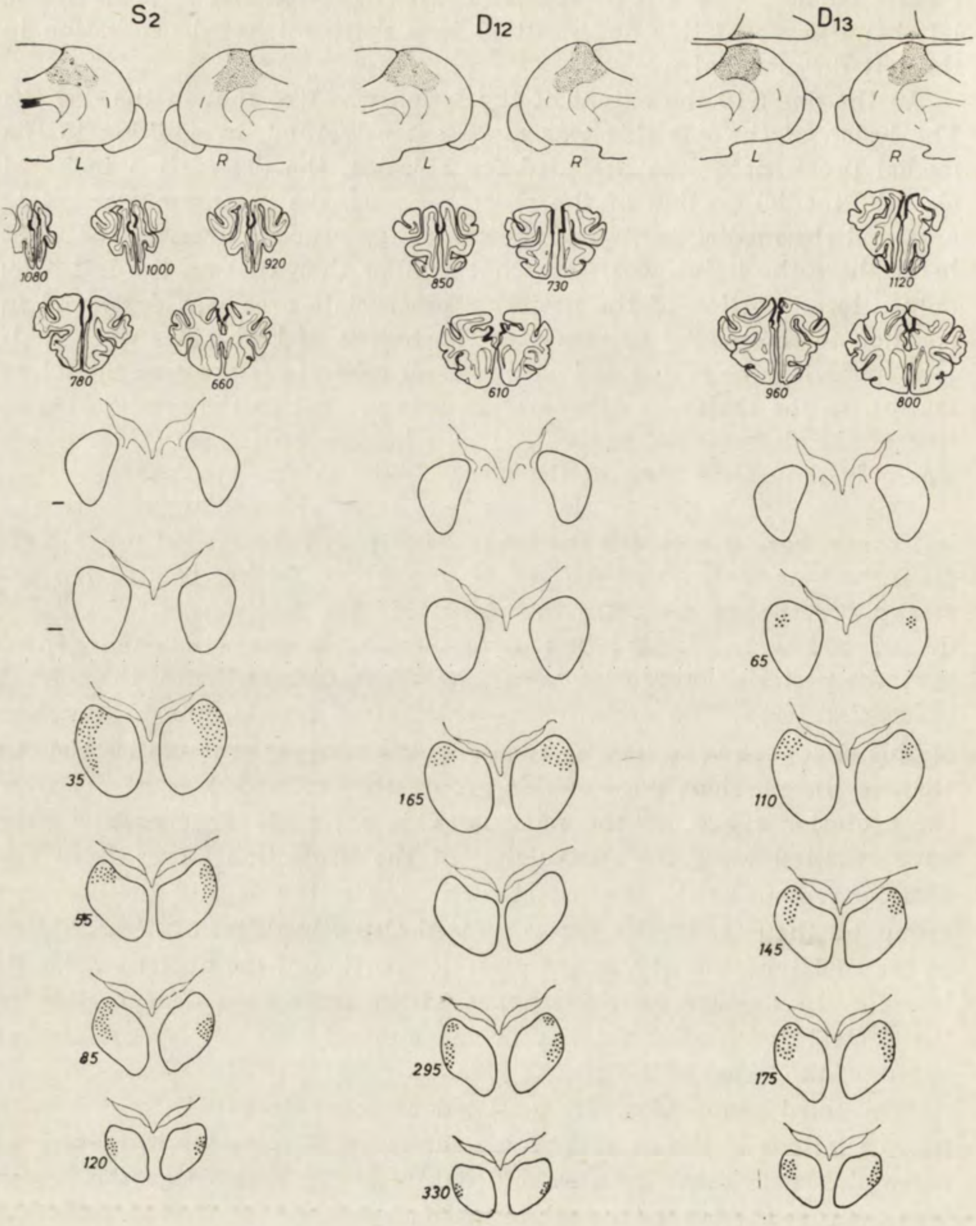


Fig. 2a

Fig. 2. The extension of the lesions and degenerations in the particular animals. a, b) The animals with the shallow lesions belonging to the group I; c, d) The animals with the deep lesions belonging to the group I; e) The animals of the group II; f) the animals of the group III

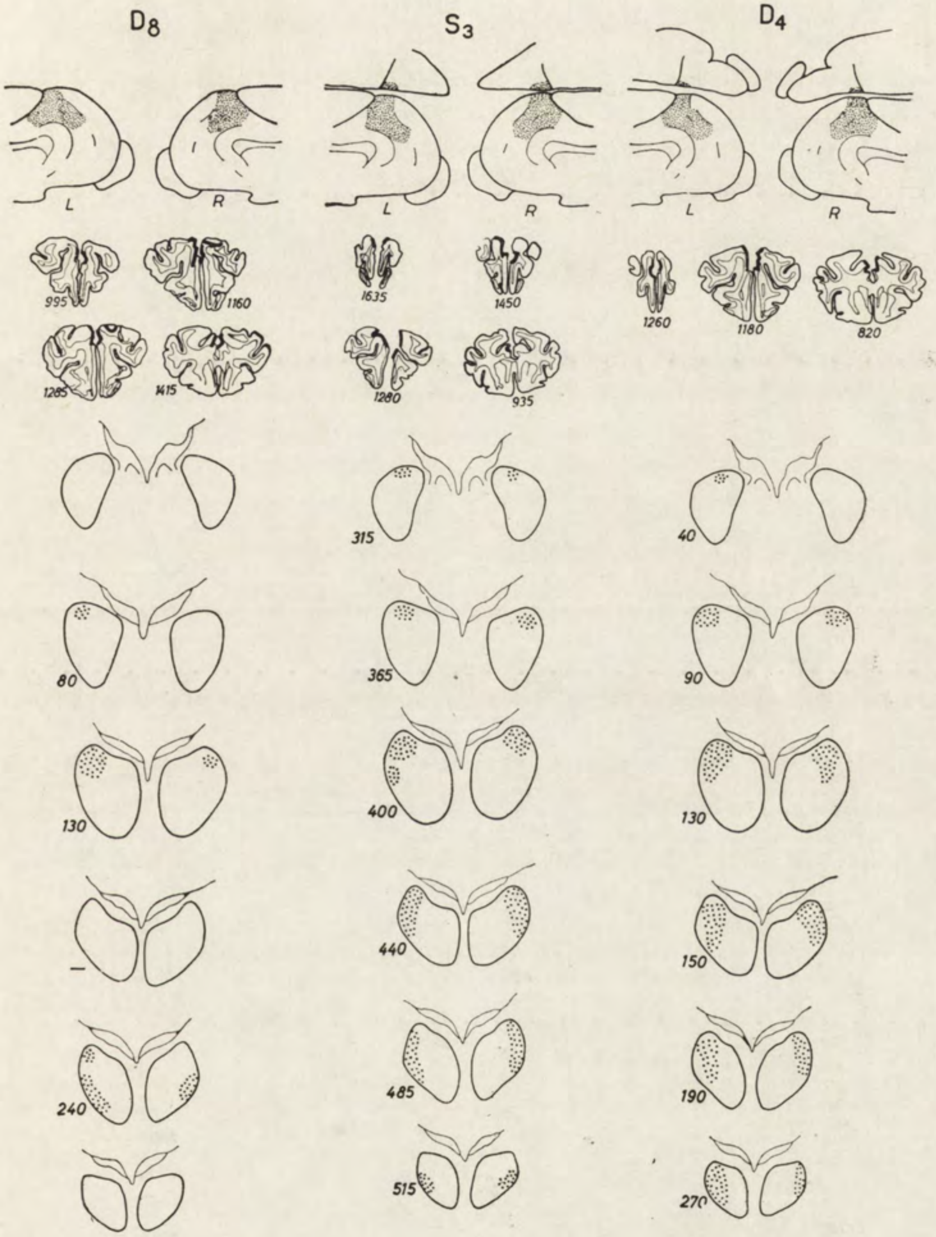

D8
S3
D4
L
R
L
R
L
R
995
1160
1285
1415
1635
1450
1280
935
1260
1180
820
315
40
80
365
90
130
400
130
440
150
240
485
190
515
270

Fig. 2b

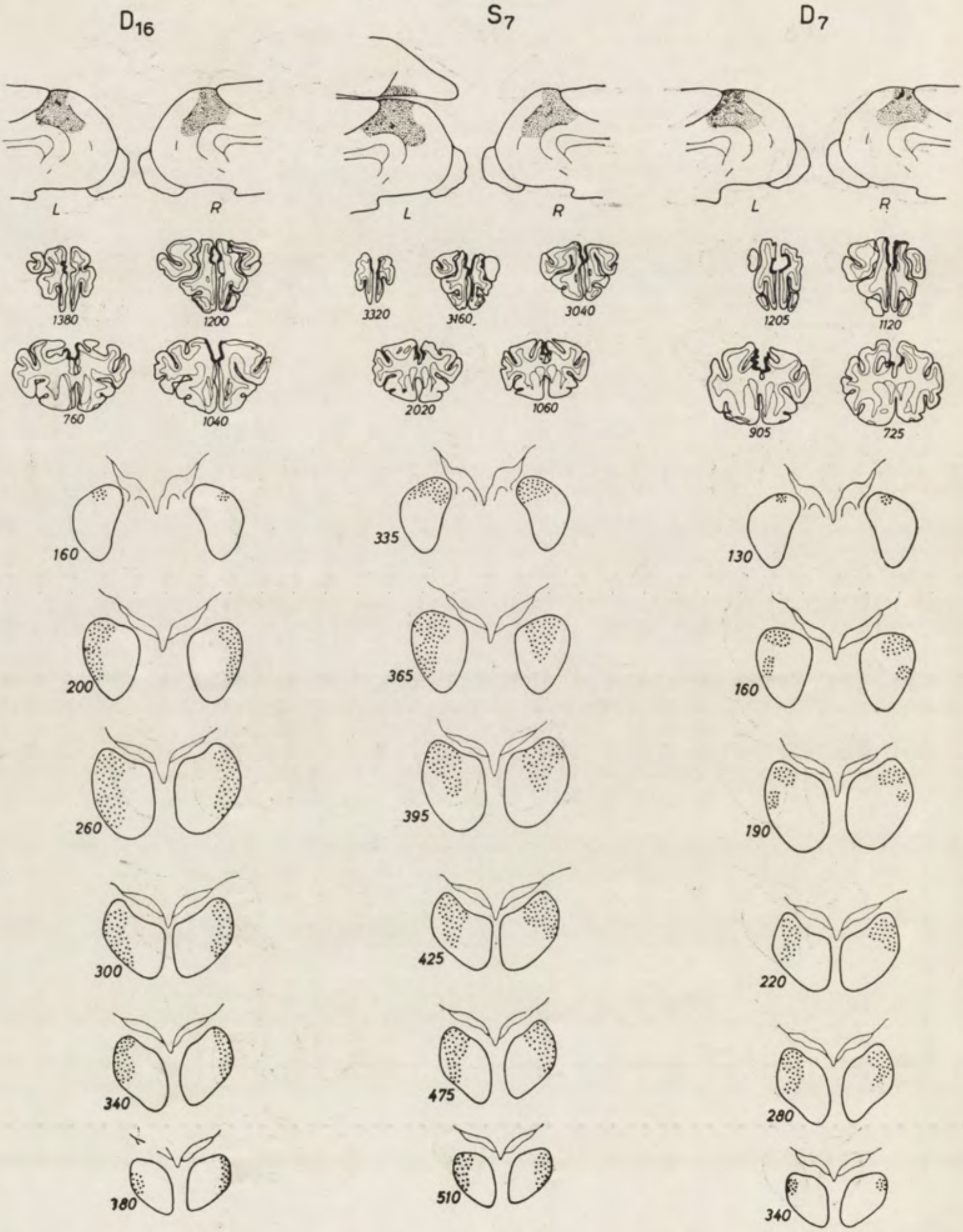

D16
S7
D7
L
R
L
R
L
R
1380
1200
3320
3160
3040
1205
1120
760
1040
2020
1060
905
725
160
335
130
200
365
160
260
395
190
300
425
220
340
475
280
380
510
340

Fig. 2c

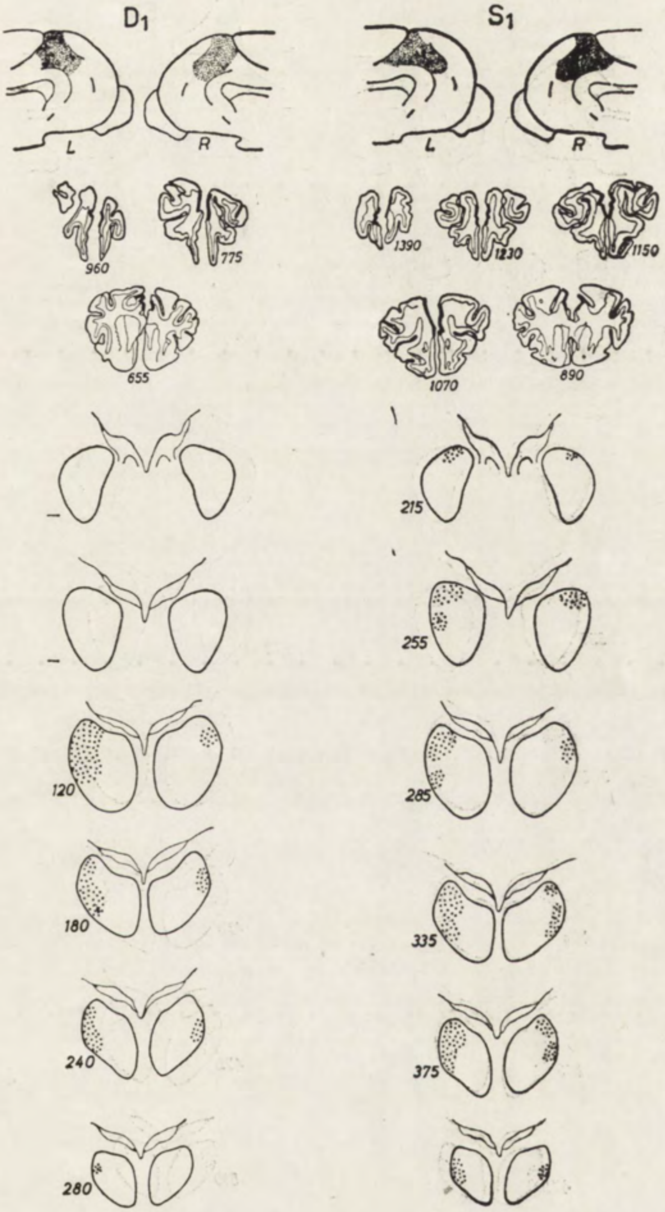

D1
S1
L
R
L
R
960
775
1390
1230
1150
655
1070
890
215
255
120
285
180
335
240
375
280

Fig. 2d

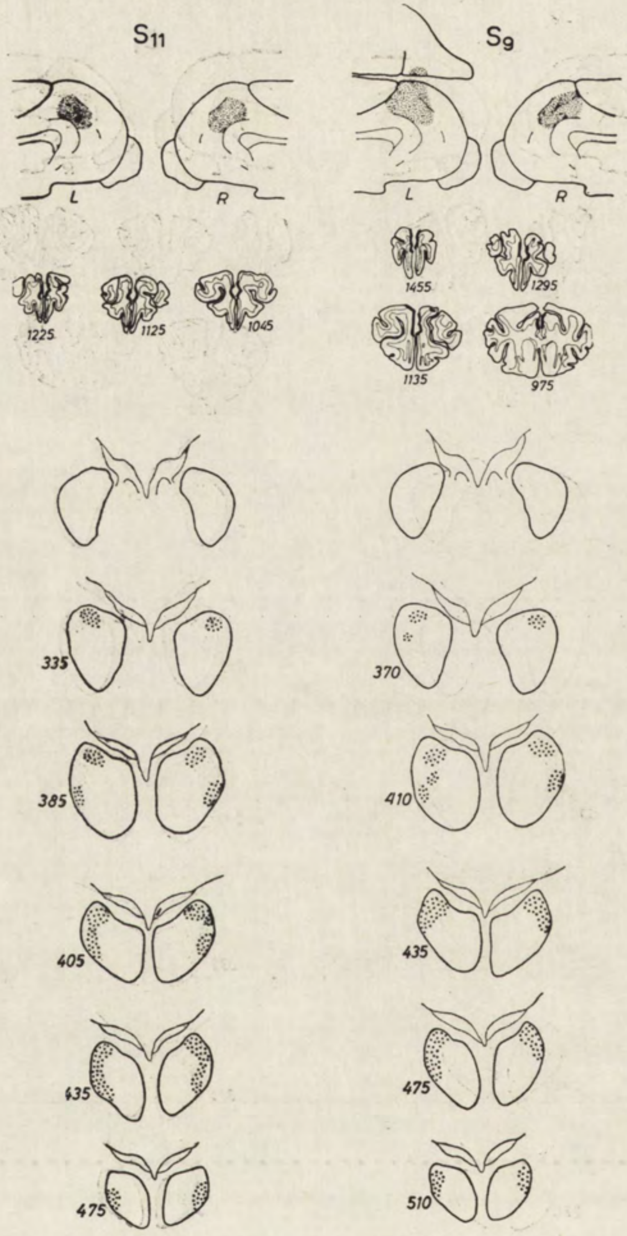

S11
S9
L
R
L
R
1225
1125
1045
1455
1295
1135
975
335
370
385
410
405
435
435
475
475
510

Fig. 2e

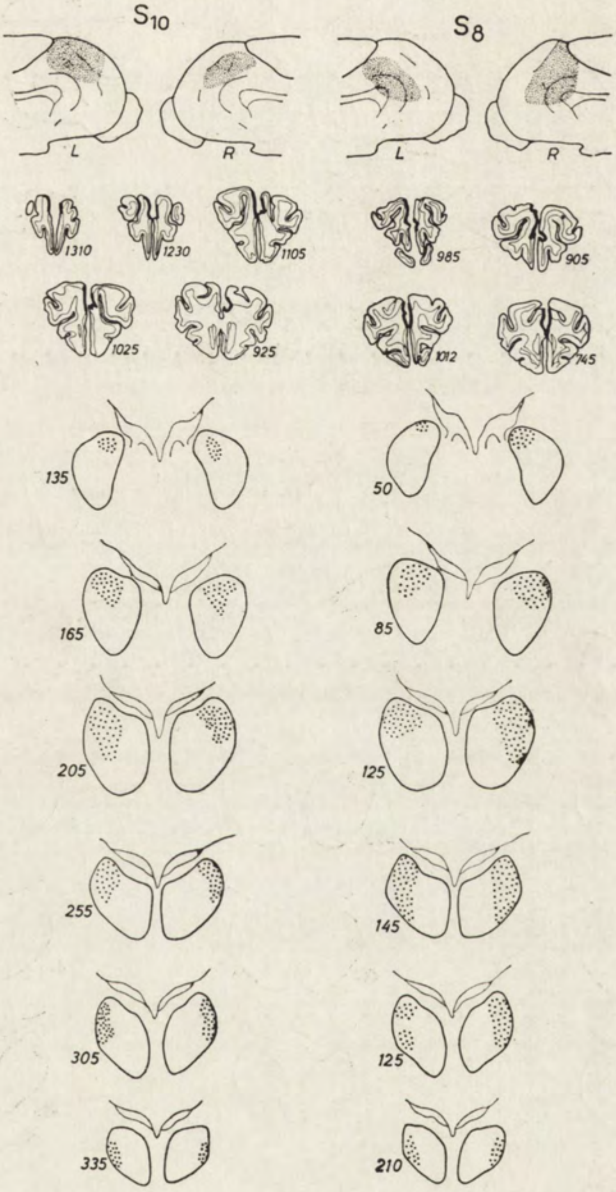

S10
S8
L
R
L
R
1310
1230
1105
985
905
1025
925
1012
745
135
50
165
85
205
125
255
145
305
125
335
210

Fig. 2e

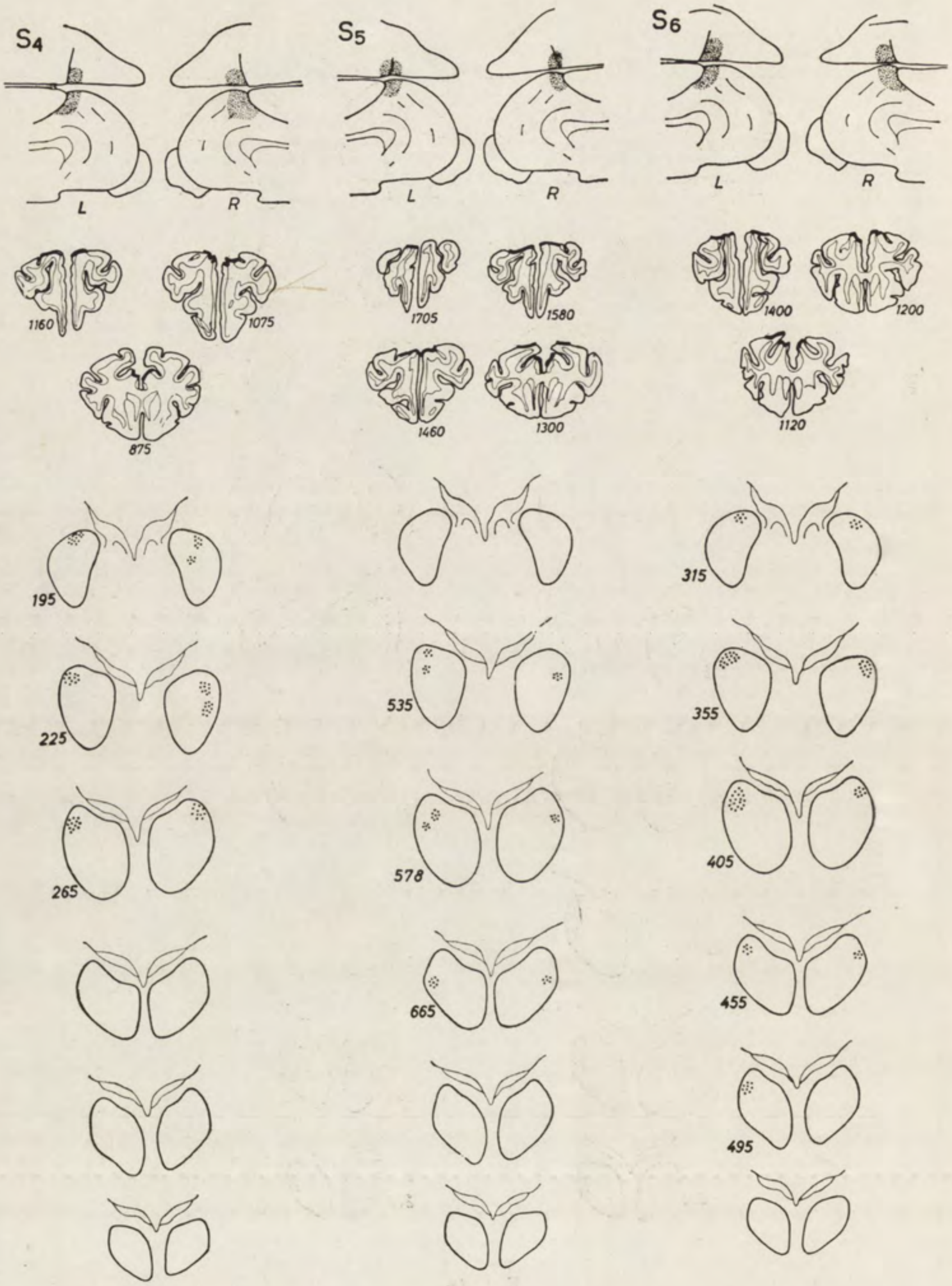
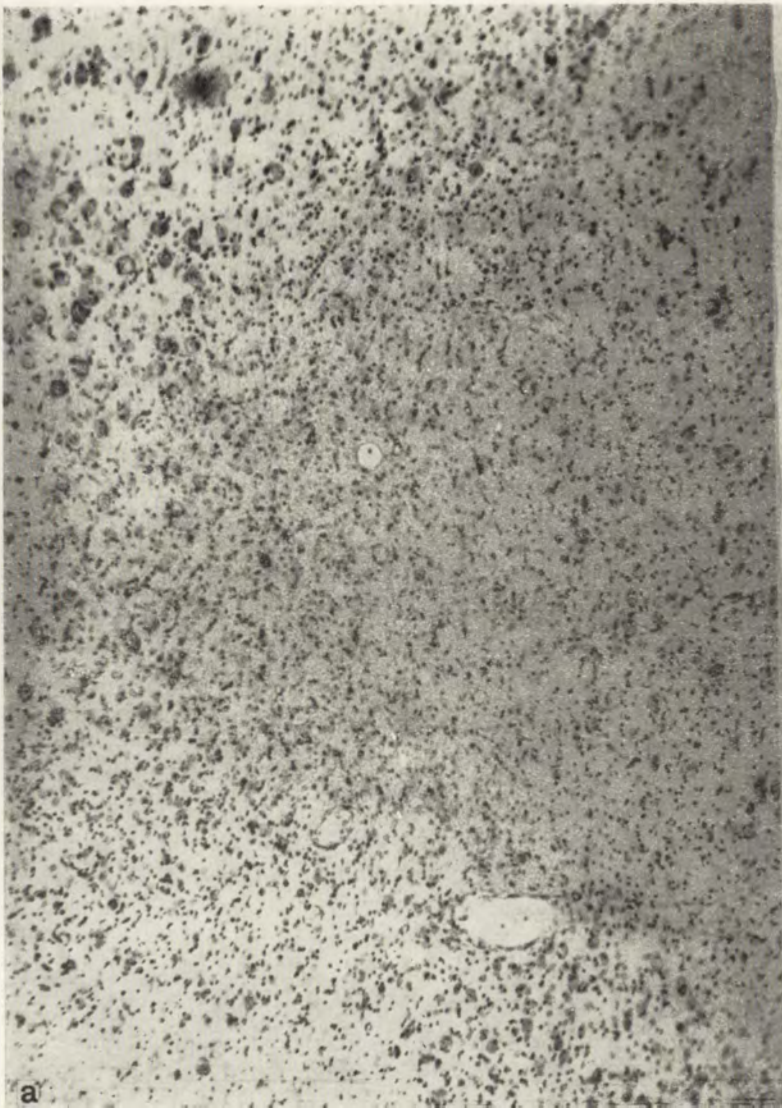

S4
L
R
1160
1075
875
195
225
265
S5
L
R
1705
1580
1460
1300
535
578
665
S6
L
R
1400
1200
1120
315
355
405
455
495

Fig. 2f


a


b

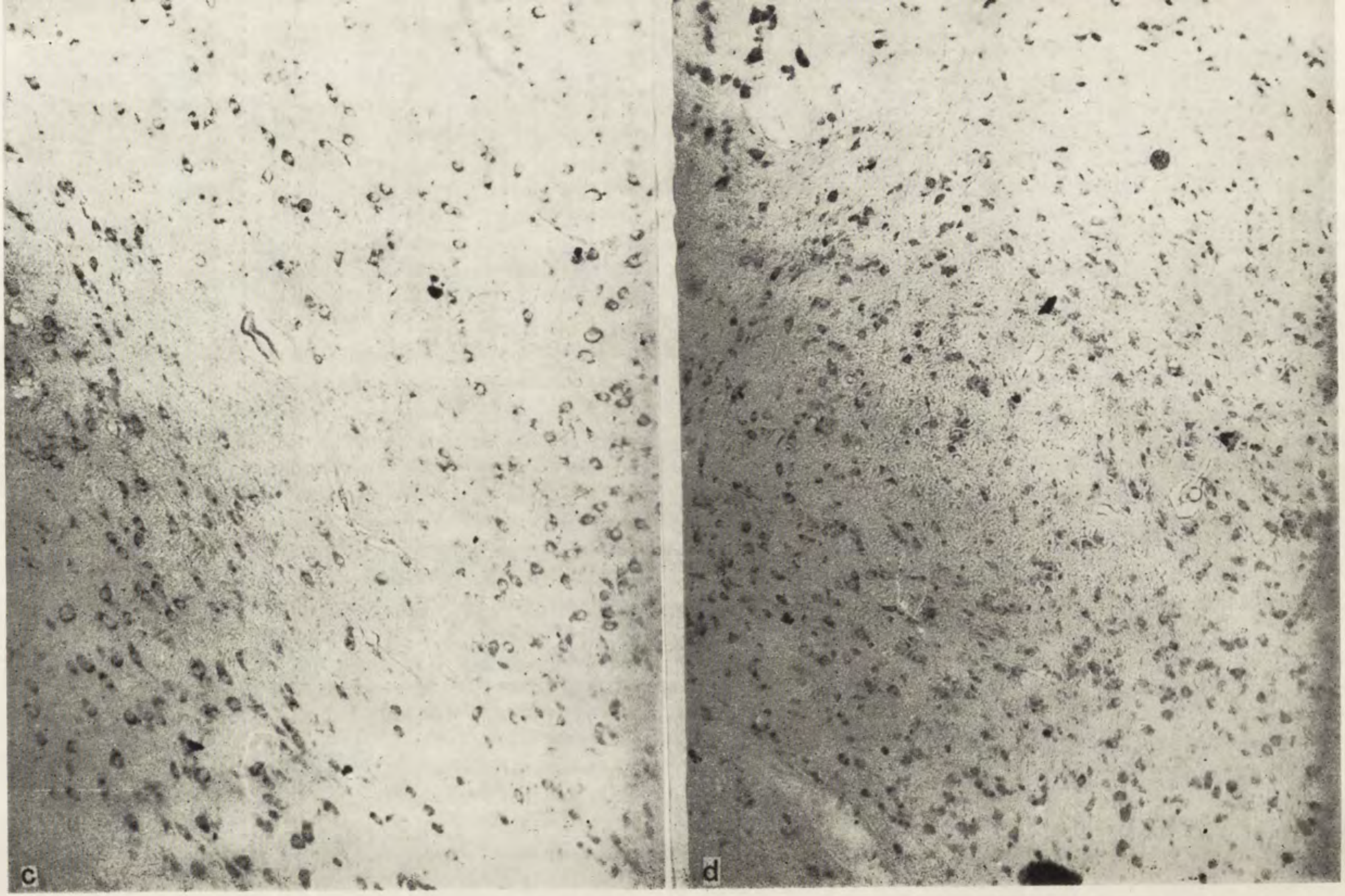


Fig. 3. Microphotographs of the laterodorsal region of the dorsomedial nucleus. a) Dog S7, The resulted degeneration after the deep lesion (group I); b) Dog S2, The resulted degeneration after the shallow lesion (group I); c) Dog S11 (group II); d) Dog S4 (group III)

DISCUSSION

The boundary of the prefrontal cortex and the projection fields connecting it with different parts of the dorsomedial nucleus in the primate brain have already been studied by many workers (Waller 1940, Pribram et al. 1953, Bonin 1948, Akert 1964). It is hard to define the boundary of the prefrontal cortex of the dog precisely. Unlike the characteristic granular cortex of primates, the prefrontal cortex of the dog shows no clear-cut boundary of the internal granular layer. The definition of the extent of this cortical region must, therefore, be preceded by close investigation consisting in the performance of partial ablations and the studies of retrograde degenerations in the projection to the dorsomedial nucleus, which would make it possible to refer it to the prefrontal cortex. Narkiewicz and Brutkowski (1967) presented the projection of the prefrontal cortex except for its posterior portion, which has become the object of our present experimental study so as to complement the picture of this region.

There are no definite opinions of anatomists on the question to what region the medial precruciate area belongs. On the basis of the myeloarchitectonical studies of the cortical areas, Kreiner (1964) included the region in question in the sensorimotor area. Presenting the area PrC_2L_2, corresponding to the medial precruciate area in the cytoarchitectonics of the dog cortex, Adrianov and Mering (1959ab) do not mention exactly in which region they include this area. On the other hand, Swietuhina (1956) defines this field as the pregigantopyramidal area. However, Adrianov (personal communication) assumes that the lesions of the area PrC_2 give rise to the degeneration of the lateral portion of the dorsomedial nucleus.

In our earlier papers on the functional role of the XM cortex the area under discussion was called the premotor cortex (Stępień et al. 1960; 1963). The anatomical results of the present study indicate that the area XM receives the projection from the lateral portion of the dorsomedial nucleus. Taking into consideration the generally accepted definition of the prefrontal cortex (Krieg 1954, Pribram et al. 1953, Rose and Woolsey 1948a, Walker 1940a, Warren et al. 1962), which states that it receives projections from the dorsomedial nucleus, and our results, one may concluded that the area XM belongs to the prefrontal region (Fig. 4).

Having used extensive frontal and prefrontal lesions, Waller (1940) determined the extent of the prefrontal cortex in the cat. However, he did not perform such partial lesions as those described in this paper. Judging from his material, only the lesion in cat no. 117 is comparable with those in our experiment. It was confined to the posterior part of the mediodorsal portion of the prefrontal cortex and followed by degeneration in the lateral portion of the dorsomedial nucleus. A study by Auer (1956) shows that the lesion of the precruciate gyrus induces degeneration in the lateral portion of the dorsomedial nucleus (cat 73), which is confirmed in accordance with our results. Akert (1964) observed the appearance of degeneration in the parvocellular part of the dorsomedial nucleus in the dog after an extensive frontal lobectomy. In our material, however, changes occurred in its lateral portion, which was obviously degenerated. Our lesions were situated caudally to Akert's lobectomy and for this reason Akert's results and ours complete each other.

Fig. 4. The extension of the medial prefrontal cortex in dog

The results obtained from behavioral experiments performed on dogs with alimentary CS magnetoreaction also seem to indicate that the medial precruciate area belongs to the prefrontal region and not to the premotor area (Stępień and Stępień 1965; Stępień et al. 1966). Similarly, behavioral studies conducted with monkeys show that, as in dogs, the destruction of the cortical area round the arcuate sulcus is followed by disturbances analogous to those in dogs with cortical lesions in the medial precruciate area (Stępień and Stamm, in preparation).

The posterior and central precruciate areas do not seem to be associated with the prefrontal cortex. This opinion may be supported by the fact that lesions in this region resulted in slight insignificant degeneration in the dorsomedial nucleus, whereas in the case of essential connections with the prefrontal cortex one should expect a more intense degeneration after its removal. For this reason it might be supposed that this field belongs to the premotor region. However, in our material concerning the third group of dogs, i.e., those with small and shallow lesion, no degeneration was found in the lateroventral nucleus. True enough, the degeneration in the lateroventral nucleus may demand the removal of a larger cortical field than that ablated in this group. Slight degeneration in the caudolateral portion of the lateroventral nucleus after extensive and deeper lesions (group I) suggests that the cortical area removed is connected with this nucleus and, consequently, constitutes a part of the premotor cortex. On the other hand, the lack of degeneration after lesions in the XP and XC areas may have resulted from the fact that too small an area of the cortex was destroyed. Besides, the cortical fields situated orally to the premotor and motor regions have, according to Krieg (1954), poor connections with the lateroventral nucleus in the monkey. It should be kept in mind that de Vito and Smith (1964), using the Nauta technique, found connections of the dorsomedial nucleus after prefrontal lesions. Their findings indicate the existence of anterograde cortico-thalamic connections, which enter the parvocellular part of the dorsomedial nucleus through the anterior radiation of the thalamus (see also Crosby et al. 1962). As will be gathered from our observations and also from the views presented by Rioch (1931), the cortical projection of the dorsomedial nucleus runs in two separate thalamic radiations, the anterior and the intermediate. Only two parts, a magnocellular and a parvocellular, can be distinguished in the cytoarchitectonic pictures of the dorsomedial nucleus in the dogss brain, whereas the distinction of a part corresponding to the paralamellar region in the monkey is difficult (Olszewski 1952, Walker 1940b).

In the dogs in which the lesion was shifted to the rear, to the gyrus cinguli, degeneration occurred in the posterior portions of the anterior thalamic nuclei, i.e., the anteromedial and anteroventral nuclei. This seems only natural, since a somewhat wider lesion in the gyrus cinguli can induce such degeneration (Rose and Woolsey 1948b, Yakovlev et al. 1960).

Heavier and more extensive degeneration obtained in the dorsomedial nucleus of dogs may have resulted from the destruction of white matter under the lesion during the operation.

SUMMARY

Examination of the thalamo-cortical connections in the dog brain was made using the method of partial operations in the posterior region of the prefrontal cortex. An analysis of retrograde degeneration on the basis of brain sections stained by the Nissl and Klüver-Barrera methods allowed the conclusion that the medial precruciate area (denomination after Kreiner 1964) belongs to the prefrontal cortex, whereas the posterior and central precruciate areas should be referred to the premotor region. Degeneration in other thalamic nuclei has also been discussed in the light of the present findings and the data from literature.

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STUDIES ON THE PERCEPTION OF COLOURS IN SOME *PAPILIONIDAE (LEPIDOPTERA)*

II. INBORN PREFERENCES FOR COLOURS IN THE STATE OF FEEDING

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The capacity for colour discrimination in the three Papilionid species *Papilio demoleus, Polydorus aristolochiae* and *Graphium agamemnon* has already been demonstrated (Vaidya 1968). The present series of experiments deals with another aspect of the colour perception of these insects, viz., the nature of their inborn colour preferences in the state of feeding.

Knoll (1922) offered coloured papers to a few individuals of the hawk-moth *Macroglossum stellatarum* and found that even freshly emerged imagines of this insect, who could not have had any experience with colour, showed definite responses to colours. Some preliminary experiments with *Papilio demoleus* (Ilse and Vaidya 1956) have also indicated that this species shows definite inborn colour preferences in the state of feeding. A detailed study of this aspect of colour vision in the three Papilionid species was therefore of interest from the point of view of comparative physiology.

MATERIAL AND METHOD

The material used as well as the general plan of experiments were similar to those adopted in previous investigations on the colour perception of these species and have already been described in details (Vaidya 1968).

The experiments were performed in a large outdoor cage (4 m × 4 m × 2 m). Here, the freshly emerged hungry imagines were offered artificial flowers made out of papers of the standardized Ostwald saturated colour series (pa series) and the Bauman grey series. An Ostwald paper represented a coloured surface, while a Bauman paper represented a neutral surface.

All the insects used in these experiments were reared from eggs in the laboratory so as to ensure that none of them had any previous experience with colour.

On the artificial flowers, the imagines showed a characteristic feeding response. Each one approached the artificial flower in flight, landed on it, unrolled its tongue and performed probing and sucking movements with it on the flower surface. Conclusions regarding the colour preferences were then drawn on the basis of number of responses obtained by each of the papers.

EXPERIMENTS AND OBSERVATIONS

On account of the limited field of vision to be expected in these insects, all the 24 types of papers of the Ostwald saturated series were not offered simultaneously. Thus, 3 different experiments were performed by subdividing the series of Ostwald colour papers into 3 groups of 8 papers each. Each group in itself covered the whole range of colours as can be seen from Table I. For each experiment 25 flowers were taken which included 2 from each of the 8 colours of the Ostwald series and 9 different grey shades of the Bauman series. These 25 flowers were arranged horizontally in 5 rows of 5 flowers each. This arrangement was offered to the inexperienced unfed imagines.

Table I

Distribution of coloured papers of the standardized Ostwald series

Colours	Experiment I	Experiment II	Experiment III
Yellow	pa 1	pa 2	......
Yellow orange	.....	......	pa 3
Orange	pa 5	pa 4	......
Red	......	pa 7	pa 6
Reddish purple	pa 8	......	......
Purple	pa 11	pa 10	pa 9
Blue	pa 14	pa 13	pa 12 pa 15
Blue green	pa 17	pa 16 pa 19	pa 18
Green	pa 20	......	pa 21
Yellowish green	pa 22	pa 23	pa 24

The possibility that the imagines might be attracted to a coloured paper due to its particular position in the whole arrangement was minimised by offering two models of each colour and furthermore, almost excluded by frequently turning the whole arrangement through 90° during the course of the experiments.

The experiments were conducted separately with each of the three species. The results are represented in Table II.

Table II

Inborn preferences for colours (number of responses and their equivalent in percentages are given)

Experiment	Artificial Flower	*Papilio demoleus*	*Polydorus aristolochiae*	*Graphium agamemnon*
I	pa 1	5 (2.0)	9 (4.1)	3 (1.4)
	pa 5	14 (5.6)	38 (17.3)	12 (5.7)
	pa 8	27 (10.8)	21 (9.6)	14 (6.7)
	pa 11	76 (30.4)	53 (24.2)	27 (12.9)
	pa 14	98 (39.2)	51 (23.3)	111 (52.8)
	pa 17	12 (4.8)	14 (6.4)	28 (13.3)
	pa 20	1 (0.4)	12 (5.5)	7 (3.3)
	pa 22	4 (1.6)	12 (5.5)	1 (0.5)
	Greys	13 (5.2)	9 (4.1)	7 (3.3)
		250 Total	219 Total	210 Total
II	pa 2	5 (1.9)	34 (14.3)	11 (5.6)
	pa 4	17 (6.6)	41 (17.3)	8 (4.1)
	pa 7	18 (3.1)	6 (2.5)	6 (3.0)
	pa 10	69 (26.8)	44 (18.6)	38 (19.3)
	pa 13	82 (31.9)	54 (22.8)	87 (44.2)
	pa 16	66 (25.7)	33 (13.9)	34 (17.3)
	pa 19	5 (1.9)	8 (3.4)	3 (1.5)
	pa 23	1 (0.4)	9 (3.8)	4 (2.0)
	Greys	5 (1.9)	8 (3.4)	6 (3.0)
		258 Total	237 Total	197 Total
III	pa 3	26 (16.5)	46 (21.4)	16 (7.4)
	pa 6	1 (0.6)	7 (3.3)	5 (2.3)
	pa 9	29 (18.4)	26 (12.1)	11 (5.1)
	pa 12	78 (49.4)	86 (40.0)	96 (44.6)
	pa 15	5 (3.2)	18 (8.4)	68 (31.6)
	pa 18	5 (3.2)	9 (4.1)	3 (1.4)
	pa 21	2 (1.3)	7 (3.3)	4 (1.9)
	pa 24	4 (1.5)	8 (3.7)	5 (2.3)
	Greys	7 (4.5)	8 (3.7)	7 (3.3)
		157 Total	215 Total	215 Total

In every experiment, the grey papers obtained a few responses. However, these were restricted to the paler or to almost white papers. This shows that the Ostwald papers were visited because of their colour quality and not because of their particular degree of brightness.

A study of the combined graphic representation (Fig. 1) of the three experiments with each of the three Papilionid species shows the following important characteristics.

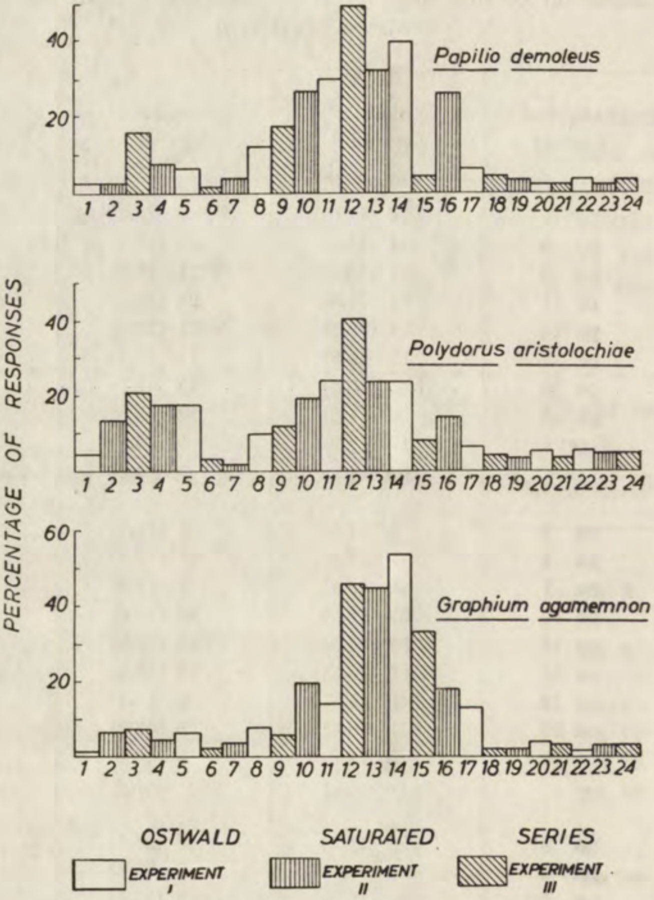

Fig. 1. Combined graphic representations showing the trend of spontaneous colour preferences in the state of feeding

i) For all the three species, the purple and blue colours were the most attractive. This range is represented by the Ostwald papers pa 8 (reddish purple), pa 9 to pa 11 (purple), pa 12 to pa 15 (blue) and pa 16 to pa 17 (blue green).

ii) In addition, the yellow and orange colours represented by the Ostwald papers pa 2 (yellow), pa 3 (orange yellow) and pa 4 to pa 5 (orange) were also attractive, though to a lesser extent as compared to the abovementioned purple-blue range of colours.

iii) In case of *Papilio demoleus,* the major peak of attractiveness seems to be in the blue region (pa 12). The minor peak is situated in the yellow-orange region (pa 3). The Ostwald paper pa 15 has gained a surprisingly less number of visits, probably because of the simultaneous presence of a large number of highly attractive colours in the same set.

iv) In the case of *Polydorus aristolochiae,* though the general trend of colour preference is the same as shown by *Papilio demoleus,* there is an indication of a considerable increase in the minor peak (yellow-orange region) at the expense of the major peak (purple-blue region). This shows that the wide difference in attractiveness between the yellow-orange region and the purple-blue region that prevailed in *Papilio demoleus* has diminished.

v) *Graphium agamemnon* also shows the same general trend of colour preferences as the above two species. However, a careful comparison indicates that in the case of *Graphium agamemnon* the major peak of attractiveness in the purple-blue region has shifted further into the blue area (pa 14). A comparison of the two peaks of attractiveness in this insect indicates that the difference between them is wider than that in the case of *Papilio demoleus* and *Polydorus aristolochiae.*

vi) The blue-green, green and yellow-green colours represented by the Ostwald papers pa 18 to pa 24 were neglected while feeding by all the three species. This is not surprising, since observations in nature show that they are not the appropriate feeding colours for *Lepidoptera.*

DISCUSSION

Papilio demoleus, Polydorus aristolochiae and *Graphium agamemnon* devoid of any previous experience with colours show marked "inborn" or "spontaneous" preferences for certain colours in their feeding responses. For feeding they prefer purple and blue colours and to a lesser extent yellow and orange colours. The spontaneous feeding responses to colours by the European swallowtail *Papilio machaon (Papilionidae), Pieris brassicae* and *Gonepteryx rhamni* (*Pieridae*) investigated by Ilse (1928) by means of the Hering series of coloured papers are very similar to those given by the three Papilionid species investigated here.

On the whole, it seems that among *Lepidoptera,* there exist the following three types of spontaneous colour preferences in the feeding state.

(i) The Papilionids and Pierids both show a high peak in the blue and only a small one in the yellow region.

(ii) Quite an opposite type of preference is shown by a comparatively primitive Nymphalid, *Vanessa polychlorus* (Ilse 1928) which shows a high peak in yellow and only a very small one in blue.

(iii) Other Nymphalids, e.g., *Vanessa io* (Peacock), *Vanessa urticae* (Ilse 1928) and *Eumenis semele* (Tinbergen et al. 1942) show two peaks, one in yellow and the other in blue, both of almost equal heights.

The above comparison of the spontaneous feeding responses to colours in different Lepidoptera is of interest since it has been found that primitive insects show more preference for the yellow colour when they are in the feeding state. For example, flower visiting *Diptera* (Ilse 1949; Kugler 1952), Aphids (Moericke 1950 and 1955) and also the white flies *Aleyrodes* (Weber 1931) respond to the yellow colour while feeding.

The present series of experiments with *Papilio demoleus, Polydorus aristolochiae* and *Graphium agamemnon* clearly show that all three of them possess the first of the abovementioned types of spontaneous colour preferences in the state of feeding. However, within this type considerable variations have already been noticed. Among the three species, *Graphium agamemnon* seems to show a somewhat typical spontaneous colour preference with a small peak in the yellow region. On the other hand, *Papilio demoleus* and *Polydorus aristolochiae* tend to exhibit successively increasing though slight tendencies towards the type of spontaneous colour preferences shown by the majority of Nymphalids while feeding, i.e., the type (iii) described above.

SUMMARY

1. Imagines of *Papilio demoleus, Polydorus aristolochiae* and *Graphium agamemnon* which had no previous experience with colour were kept in a large outdoor cage. They were offered artificial flowers made out of the papers of the Ostwald colour series and the Bauman grey series.

2. On these flowers, the imagines showed a characteristic feeding response: they approached the artificial flower in flight, landed on it and unrolled their tongues with which they performed probing and sucking movements on the paper.

3. On the basis of the number of responses gained by each of the coloured papers, conclusions were drawn regarding the spontaneous preferences for colours shown by the feeding imagines of each of the three species.

4. All the three species preferred for feeding the purple and blue colours, and also (to a lesser extent) the yellow and orange colours.

5. Thus, the spontaneous preferences for colours shown by the feeding Papilionids are found to be alike to those of the Pierids, but quite distinct from those shown by the Nymphalids.

6. Though the colour preferences during feeding in the three Papilionids investigated here belong to the same general type, they show certain individual variations.

The author is grateful to Professor Dora Ilse for her encouragement and valuable suggestions during the early part of this work.

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A POWER BOOSTER FOR STIMULUS ISOLATION UNITS

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(Received May 17, 1968)

Those stimulus isolation units which are generally available usually have low output power. They are good for electrical stimulation of biological preparations with high impedance or during stimulation with microelectrodes. Their power is often not sufficient when stimulation of larger muscles or nervous tissue or saline-shunted preparations is required. If a stimulus isolation unit has not sufficient power, a significant decrease of stimulus voltage will be observed. When metal electrodes are used this decrease will be especially high with stimulus onset (Fig. 1b).

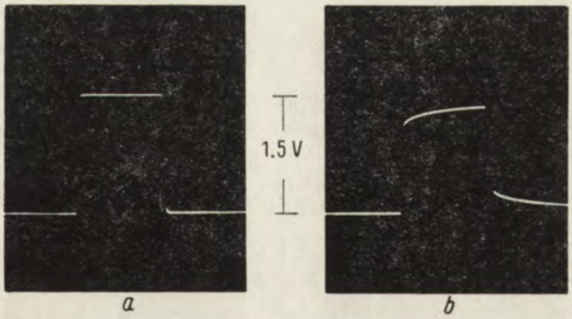

Fig. 1. Comparison of voltage pulse shapes on the output of ISA Isolator Bioelectric Instruments Inc.-type stimulus isolation unit (This isolation unit is a low power device ideally suited for intracellular stimulation through microelectrodes or with other preparations requiring little power): a, with open output circuit, b, during electrical stimulation through permanently implanted subcortical platinum electrodes in the rabbit's brain. The contact area: electrode — brain tissue about 1 mm^2. Distance between electrodes, 1 mm. Pulse duration. 1 ms

This fact may be explained by the change of the impedance of the electrode — biological preparation interface during current flow (Schwan 1963, Weinman and Mahler 1964).

The increase of output power of the Schmitt-type isolation unit can be achieved by application of a power booster in the output circuit of the isolation unit (Richardson and Werman 1966).

A new simple power booster was constructed, the principle of which is similar to that of Richardson and Werman-type (see diagram, Fig. 2).

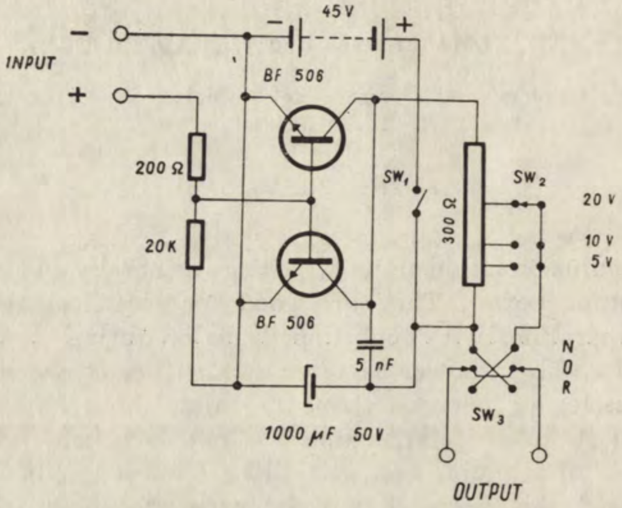

Fig. 2. Schematic diagram of the power booster for stimulus isolation unit

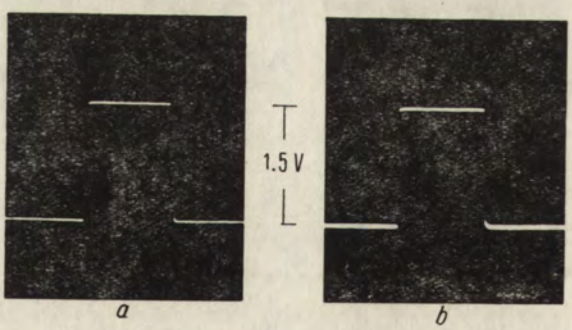

Fig. 3. Comparison of voltage pulse shapes on the output of ISA Isolator-type stimulus isolation unit with power booster: a, with open output circuit, b, during electrical stimulation through permanently implanted subcortical platinum electrodes in the rabbit's brain. The contact area: electrode — brain tissue about 1 mm². Distance between electrodes, 1 mm. Pulse duration, 1 ms

The operating principle of this system is very simple. Two BF 506 silicon npn transistors[1] connected in parallel are triggered externally by rectangular pulses from an isolation unit. In this system the transistors act as an electronic relay switch. Normally they do not conduct current, but a trigger pulse causes the transistors to conduct. The BF 506 transistor is capable of handling collector to emitter voltages of up to 45 V with 50 mA current. Two transistors with similar parameters should be selected. The electronic relay switch is powered by a 45 V battery shunted by an 1000 μF electrolytic capacitor. This shunting capacitance is necessary to minimize the internal resistance of the power supply. The three position output attenuator (SW_2) sets maximal voltage values of 20, 10 and 5 volts. Each of these voltages can be continuously varied from zero to maximum by changing the pulse amplitude of the driver. The output resistance for 20-V range is 200 Ω, and for 10-V, 5-V ranges 100 Ω and 50 Ω respectively. The radio-frequency component at the output is adequately compensated by the 5 nF capacitor placed in

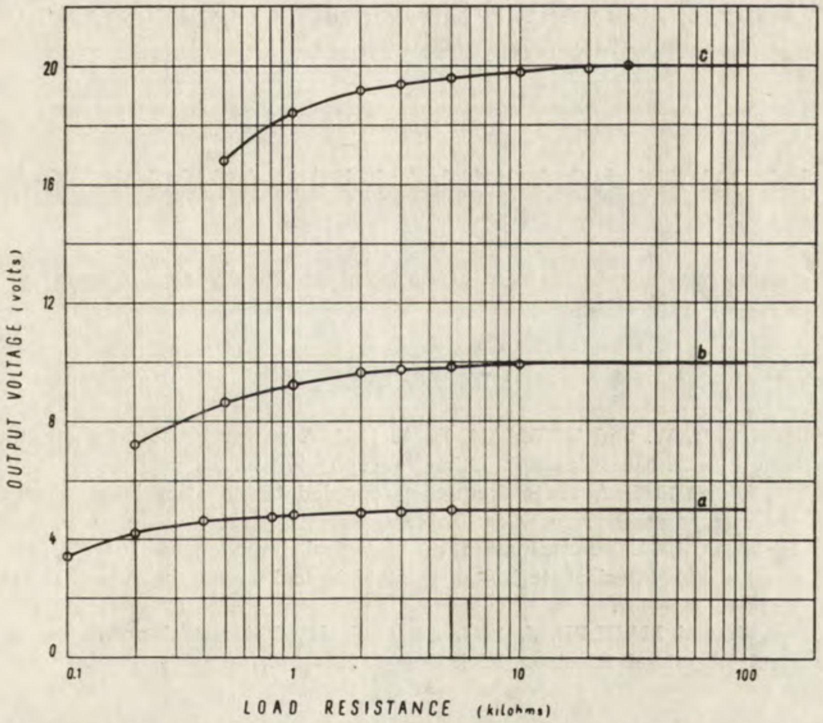

Fig. 4. Diagrams illustrating output voltage decrease of ISA Isolator with power booster in relation to load resistance. Output resistances: a, 50 Ω; b, 100 Ω; c, 200 Ω

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[1] Manufactured by TEWA — Warsaw.

the collector circuit. A double pole, three position switch (SW_3) permits the changing of the output pulse polarity or to switch it off [normal polarity (N), off (O), reverse polarity (R)]. SW_1 switch enables one to cut off the power supply (45 V battery).

The comparison of Fig. 1 and 3 shows that when employing the power booster for stimulus isolation unit neither the γ the shape nor the amplitude of the voltage pulse changes during stimulation. Fig. 4 shows the output voltage of the power booster as function of the load resistance.

A stimulus isolation unit with a power booster works on constant voltage when the load resistance in over 20 kΩ for the 20 V range and when the load resistance is over 10 kΩ and 5 kΩ for 10 V and 5 V ranges, respectively. The application of described previously circuit increases the output power 20—70 times. The power gain of the transistors varies from item to item in each particular case. Such important parameters of the stimulus isolation unit as the capacitance to ground, and the output leakage resistance are not changed by the use of the power booster. DC output voltage in the intervals between 20-V pulses is less than 0.5 mV and radio-frequency interference is not marked.

SUMMARY

A power booster for the Schmitt-type stimulus isolation units which increases the output power 20—70 times is described.

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PROF. DR. JANINA HURYNOWICZ
(1894—1967)

Prof. dr. Janina Hurynowicz, an eminent Polish neurophysiologist, for many years Head of the Department of Neurophysiology and Comparative Physiology at the Nicholas Copernicus University, Toruń, died on 2nd October, 1967.

Prof. Hurynowicz was born on 10th November, 1894, in the district of Wilno. She finished secondary school in Wilno in 1911 with a gold medal award and graduated with distinction as a physician at the Women's Medical Institute in St. Petersbourg (Leningrad), in 1918. From 1917—22 she was director of different war hospitals and worked as surgeon, epidemiologist, neurologist and psychiatrist.

With her brilliant intelligence and keen mind she was predestined for scientific work. From 1922—33, without interrupting her clinical practice, she became assistant, adjunct and finally deputy director of the Neurological Clinic at the Stefan Batory University in Wilno. In 1938 she was appointed adjunct at the Department of Physiology, Stefan Batory University, where she directed the neuro-physiological laboratory.

She obtained her doctorate in medical sciences in 1927, at the Stefan Batory University, Wilno. In 1927—30 she worked at the Sorbonne University in the Department of prof. Lapicque, in Salpetrière in prof. Bourguignon's, and in the Collège de France with prof. Gley.

During her stay in France, in collaboration with A. B. Chauchard, she worked out a new chronaximetric method of measuring the excitability of the vasomotor system, which constists in differentiating the excitability of the two components of this system: the vasomotor nerves and the wall of the vessel. This method was approved by the Paris Academy of Sciences.

As a result of these studies she continued her research work in Poland and obtained her docent's degree at the Stefan Batory University in 1930.

During the occupation she was deputy director of the Municipal Neurological Hospital in Wilno and acted as scientific director of the hospital.

From 1945—65, i.e. from the moment of her arrival at the Copernicus University in Toruń, to the day when she retired, prof. Janina Hurynowicz dedicated all her knowledge and her inexhaustible energy first to the organization of the Department of Neurophysiology and Comparative Physiology in very difficult post-war conditions, and then to its development and to the education of the younger generation of her co-workers. By the decree of 6th May, 1949 she was appointed professor at the Department of Neurophysiology and Comparative Physiology. On 27th November, 1953 she was awarded the degree of doctor of biological sciences.

Very consistently in her research work she improved and modernized, in collaboration with her physicists-assistants, the method of investigating the excitability of iterative nerves and continued researches on the chronaxy of vestibular reflexes, by means of her own method of the determination of the excitability of the vestibular system. This method became an interesting instrument in the research work of her students and Ph. d. candidates.

Since 1938 prof. J. Hurynowicz investigated the role of the nervous system in anaphylactic shock. She continued this work at the Nicholas Copernicus University with her co-workers. She discovered a number of functional changes within the nervous system in prolonged anaphylactic shock, as well as certain side effects connected with the type of preserving substances in the injection applied.

Her work in collaboration with her assistants on the disturbances of the coordination of the excitability of the vasomotor system and the balance of nervous processes in the states of fatigue and exhaustion was a continuation of earlier investigations.

Her research work on the physiology of the pilomotor reflex started in 1928, which constitutes the basis of an interesting suggestion of the existence of a specific, separate sense of feeling, is today continued in the Department of Neurophysiology at the Nicholas Copernicus University, by means of the microelectrode technique of recording elementary bioelectric phenomena which accompany the irritability of sensory piles in insects.

Prof. Janina Hurynowicz had 91 scientific works published, out of which many are quoted in the Polish and foreign scientific literature.

On 17th December, 1959 she was awarded a prize by the Minister of Higher Education for the organization of complex research work in neurophysiology and in 1964 — by the same Minister — for outstanding achievements in scientific work.

She did not interrupt her contact with clinical practice — first as organizer and director, then since 1953 to her retirement — scientific consultant of the Psychic Health Centre in Toruń.

Prof. Janina Hurynowicz organized in Toruń a section of the Polish Physiological Society, of which she was president for many years. In 1947 she reactivated the Medical Society in Toruń, a section of the Polish Medical Society, and became the first president of the Toruń section after the war.

In 1957 at the plenary session of the Society she was elected its honorary member.

Prof. Janina Hurynowicz was an active member of numerous other scientific societies as well as of the Scientific Council of the Nencki Institute of Experimental Biology, Polish Academy of Sciences; of the Institute of Physiology and Alimentation of Animals, Polish Academy of Sciences, of the Scientific Council of the Physiology Department, Polish Academy of Sciences in Łódź, and of the former Shock Commission, Polish Academy of Sciences, she was also deputy president of the Neurophysiological Commission of the Committee of Physiological Sciences, Polish Academy of Sciences.

In 1960, on the anniversary of the liberation of Bydgoszcz, the National Council of the Province awarded her an Honorary Medal for special services rendered to this territory. In recognition of her merits in scientific activity she was elected honorary member of the Polish Physiological Society and the Polish Zoological Society.

She was decorated with the 10th Anniversary Medal of People's Poland, the Officer's Cross of Polonia Restituta, the Cross of the Valiant and the Silver Cross of Merit with Swords for participation in the Underground Movement.

She educated a generation of Polish physiologists. Active almost to the last days of her life, she was a person of noble character and great heart, always ready to serve with advice and moral support. Her death is a severe blow to all who knew her.

Pupils

Acta Biol. Exp. (Warsaw), vol. 28, no. 4, p. 415—416, 1968

Book review

An introduction to animal behaviour by A. MANNING. E. ARNOLD (Publishers) Ltd., London, 1967, pp. VIII + 208, illustrated.

Students of biology have just obtained a new book from the field of contemporary biology. It is important for those who are interested in the animal behavior.

The subject is treated here in an up-to-date manner, that is, behavior is considered not as a happening, a phenomenon to be described or even to be classified from the functional point of view, but as a complex process, the causal analysis of which and conditions under which it tends to appear are to be investigated. This means that the reader should not look in the book for such behavioral units as ingestive, eliminative, reproductive behavior, or for detailed information of various kinds of social behavior. An approach of the author is rather physiological and psychological than biological. I mean by this that an adaptive rôle of behavior is engaging comparatively less attention. In this book, much more than in the others similar, ethology stands far from her sister-science, ecology. The author deals, as he says himself in preface, with the problems which he considers to be important. On the other hand, he was limited in his work by the restricted volume of the book. Therefore the book reflects in a perhaps higher degree the personal interest of the author than occurs usually with textbooks. This is reflected well in the chapter about the evolution of behavior where twelve pages are devoted to genetic works on *Drosophila*, a topic especially familiar to the author. On the contrary, one hardly finds a brief remark about the orientated behavior where only tropisms are mentioned (and even they are neglected in the subject index). There is no discussion on animal migrations; neither homing nor navigation are taken into account.

Dr Manning has begun the book with a short description of certain aspects of reflexes and of complex behavior. The content of the first chapter can be estimated from the titles of its paragraphs: "Latency", "After-discharge", "Summation", "Warm-up", "Fatigue", and "Inhibition". Following these lines, the author gave a basis for an analysis of the complex behavior.

Second chapter, "The development of behavior", apart from the discussion on the inherited responses, their growth and maturation as well as on the ability to modify behavior under individual experience, includes information on a post-war situation in the study of animal behavior, that is, mainly on ethology and American psychology.

If the latter chapter deals with forms of adaptivity of behavior, the next ones entitled "External stimuli", "Motivation", „Conflict behavior", and „Hormones and behavior" concern the sources of behavior.

Here, in the first chapter of them, the reader finds encyclopaedical information bout diverse sensory capacities of animals; the releasing rôle of stimuli is discused along with the problem of stimulus filtering. It is a pity that one does not find here even a slight influence of cybernetics, found so valuable in recent times. I mean a short general remark on the control of behavior by external stimuli which should sum up an information, scattered in the text, about their sensitizing, eliciting and orientating rôle, the latter one almost completely neglected in the book. One should find here at least a single example of the feedback control of stimuli, as described in form of the re-afference principle. However, in the section on stimulus filtering, some data about adaptative value of psychical features are given instead. It seems that the parsimony concerning this problem, i.e.,. taking into consideration the biological role of behavior, arises rather from the caution not to give examples which have not been proved sufficiently in the scientific way, than from the lack of its appreciation. Who of the ethologists ignores how scarce such data are in literature, as, for instance, evidences of the biological importance of colouration and of the so-called frightening postures? On the other hand, it should be pointed out that the book of Dr Manning belongs to those few ones where the notion of homeostasis is applied. And this may serve undoubtedly as a prove of an up-to-date approach to biology.

The chapters about motivation are completing the information on instinct. In the chapter 4, "Motivation", one finds the fundamental notions of appetitive behavior and consummatory action. Displacement activities and their role as signals as well as of the vacuum activity are discussed in the chapter 5, on "Conflict behavior". Most of space, however, is devoted to the methods of estimating actual motivation, measuring motivation, and, in first place, to the concept of drive. Apart from the discussion of ethological models of motivation, Dr Manning gives a substantial selection of data about physiological studies of it. Out of forty four pages which constitute these two chapters, ten pages give the neurophysiological basis of motivation. There are still eighteen pages of the subsequent, sixth chapter, "Hormones and behavior", which contribute to the problem of the physiology of motivation from the biochemical aspect.

Chapter 7, "Evolution", gives not so much comparative collections of diverse homologous behavioral patterns in various animals, as it contains discussion of the nature of evolutionary changes and their mechanism. As it was mentioned before, Dr Manning pays attention to genetics in the first place. He does not disregard, however, a rôle of sexual isolation or the natural selection. The problem of ritualization of behavior is discussed here in one of the sections.

The final two chapters are treating of learning. The first of them gives classification and description of various types of learning. There is also here a concise account on the comparative study of learning. The last chapter is concerned with the mechanism of learning. Apart from the "classic" data on the neural mechanism, the reader finds here a modern biochemical approach although, as the author says himself, "we seem to have facts which are ahead of theories".

In spite of the criticisms which have been put forward to some particular aspects of the book, it is worthy of a warm recommendation to all those who intend to engage in studies of animal behavior. It is very readable, the style being not too "scientific" (what may happen even with an English text!) Illustrations, although relatively not numerous (2 plates and 54 text figures) are well chosen and constitute an integral part of the book. References, 291 in number, include more important books and review articles besides original papers, when necessary. In this way, the reader may have here an introduction to the behavioral literature. The book is completed with 4 pages of the subject index.

J. A. Chmurzyński, Warsaw, Poland

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