

Lecture delivered at Symposium "The frontal granular cortex and behavior"
held in Jablonna near Warszawa
August 1971

EFFECTS OF PREFRONTAL LESIONS ON AVOIDANCE AND ESCAPE REFLEXES

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Abstract. Retention of the avoidance and escape reflexes after removal of preorear and orbital gyri has been studied in adult cats. The ability to perform short-latency avoidance responses was severely impaired after prefrontal lesions, whereas no effect was found either on avoidance responses executed with longer latencies or on escape responses. Severity of impairment of the avoidance reflex was related to the pre-operative level of performance of the short-latency avoidance responses, which depend on the CS intensity, duration of the CS-US interval, and the type of inhibitory training. The post-operative retraining of the avoidance reflex performance was exclusively due to the increase in the proportion of avoidance responses executed with longer latencies. On the basis of neurophysiological and behavioral data it is postulated that different physiological mechanisms are responsible for execution of short-latency avoidance responses and avoidance responses with longer latencies. Only the first mechanism is destroyed after prefrontal lesions in cats.

Analysis of published data shows that effects of prefrontal lesions on the retention of the defensive conditioned reflexes are, in contradistinction to effects of similar lesions on alimentary reflexes, less definite, more changeable, and sometimes — unpredictable. However, from the short review of respective data (Zieliński 1966) it follows that good retention or even enhancement of the conditioned responses after frontal lesions were observed in tasks involving the application of a noxious stimulus in each trial, as it is in case of classical defensive reflexes and escape reflexes. In contrast, performance in different variations of the conditioned avoidance reflexes was as a rule impaired. The effect of frontal lesions on the acquisition of the avoidance response

was often more pronounced than on its retention. Further experimental progress did not change this general picture and we still are not able to predict the degree of severity of post-operative changes observed in different experimental situations and to analyse the reasons for exceptions.

Many discrepancies in results obtained so far may be related to differences in species, extent of lesions, experimental procedures, properties of stimuli, length of training and so on. Unfortunately, our knowledge of interaction of different variables of the experimental situation with the effects of frontal lesions on defensive behavior is very limited. To enlarge our understanding of such interactions, a series of

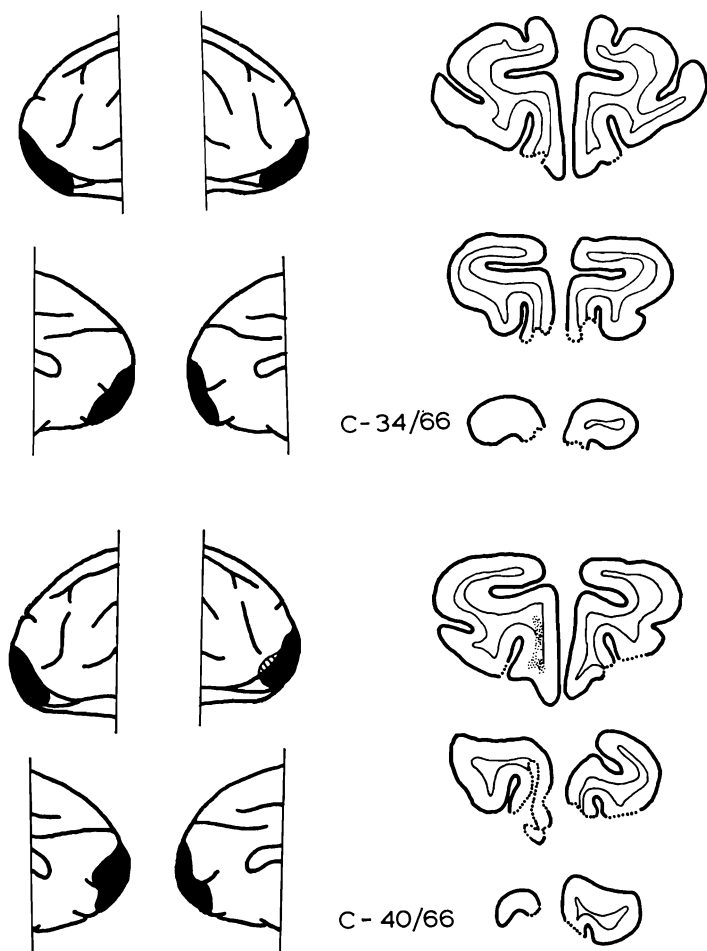


Fig. 1. Reconstruction of the typical prefrontal lesions (cat C-34/66) and the most extended lesion (cat C-40/66).

experiments was performed in recent years in which we studied the effects of the removal of proreus and orbitalis gyri on instrumental defensive reflexes. The same apparatus was used in all experiments — a box with a grid-floor and a bar. The subjects were 56 male adult cats. Lesions were done by suction, bilaterally in one stage, under Nembutal anesthesia. The extent of typical lesions is seen on the upper part of Fig. 1. In some cats superficial lesions on the lateral border of the sulcus presylvius were observed (lower part of Fig. 1), however, the post-operative performance of such animals did not differ from the others. In all experiments which will be reported below, the post-operative training began 10 days after surgery, and the same procedure as just before the operation was used.

*Initiation and execution of the instrumental
defensive responses in frontal cats*

In the first experiment (Zieliński 1966) an avoidance bar-pressing response was trained in eight cats. A tone, of 2000 cycle/sec frequency and 60 db intensity, served as the conditioned stimulus (CS), and electrification of the grid-floor was the unconditioned stimulus (US). The CS-US interval was of 5 sec duration. Pressing the bar with latency shorter than 5 sec, which was scored as avoidance response, terminated the CS and prevented electrification of the grid-floor. Pressing the bar with latency longer than 5 sec from the CS onset terminated the CS and the US simultaneously and was scored as escape response. Ten trials daily were given until reaching the criterion of 90 avoidance responses in 100 consecutive trials. Then, as a control, a 10 day pause in experimental sessions followed. As seen from Fig. 2, this pause had no effect

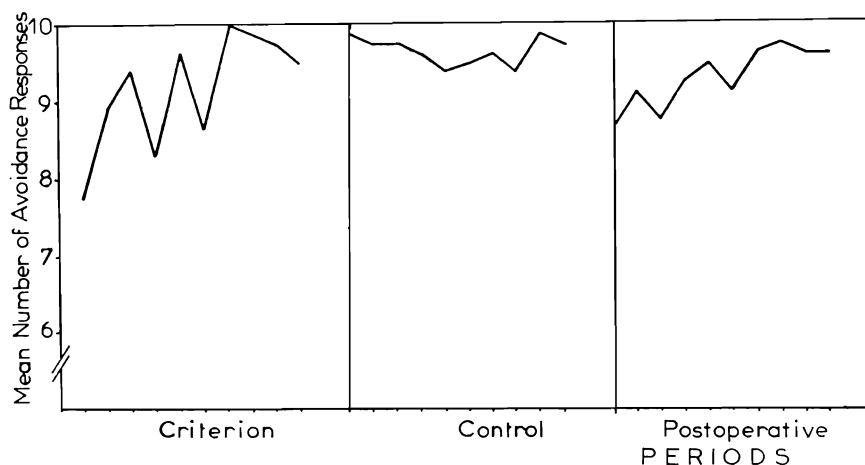


Fig. 2. Avoidance reflex performance in consecutive sessions in the criterion, control, and post-operative periods.

on the level of performance. In contrast, the removal of proreus and orbitalis gyri after the control period resulted in some impairment of the avoidance performance. This effect, although statistically significant at $p < 0.01$ level (analysis of variance), was small and transient, lasting only a few days.

The effect on the latencies of instrumental defensive responses was more pronounced and longlasting. In Fig. 3 the median latencies of bar-

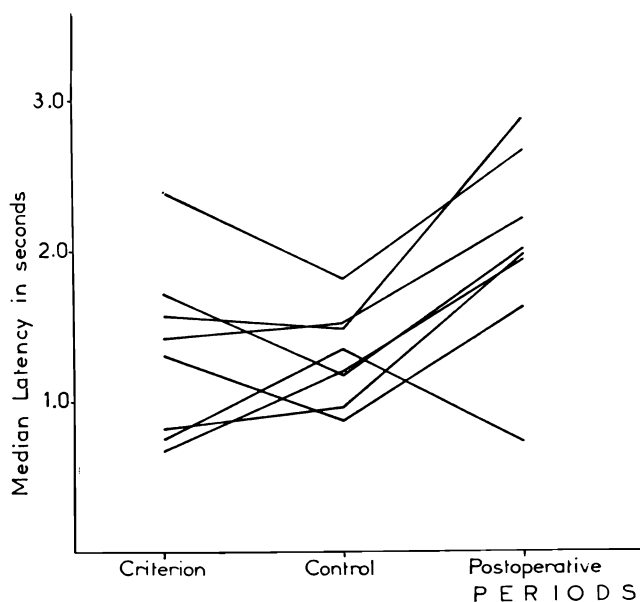


Fig. 3. Median latencies of the instrumental responses for individual cats in the criterion, control, and post-operative periods.

pressing responses for each individual cat are given in three consecutive 100 trial blocks. As seen, changes in latencies between criterion and control periods were unsystematic, whereas the prefrontal lesion resulted in lengthening the median latencies in 7 out of 8 cats. This result was statistically significant at $p < 0.001$ level (analysis of variance).

Comparison of the median latencies of instrumental responses is not a very sensitive measure. Detailed analysis of the effects of prefrontal lesions on the instrumental response latencies is possible, when pre-operative and post-operative distribution of latencies are compared. Cumulative frequency distribution of responses with different latencies indicate (Fig. 4) that after prefrontal lesions there is a definite decrease in the frequency of short-latency avoidance responses. The two cumu-

relative frequency distributions shown on Fig. 4 differ at the $p < 0.001$ level (Kolmogorov-Smirnov two-tailed test).

In order to test whether the prefrontal lesions affected similarly an escape bar-pressing response, a second experiment was performed (Zieliński 1970), in which no CS was used and electrification of the grid-

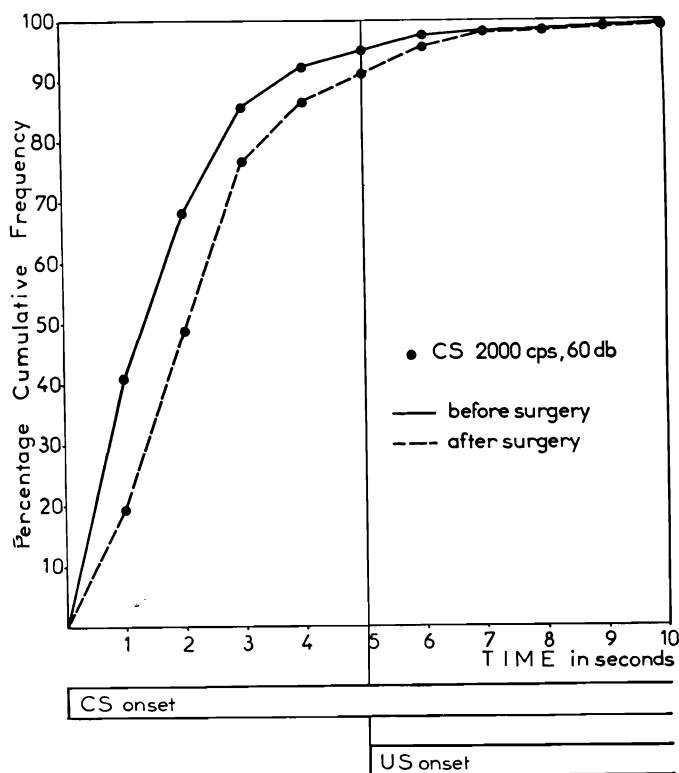


Fig. 4. Cumulative frequency distributions of the latencies of bar-pressing responses before and after prefrontal lesions in cats trained to the 2000 cycle/sec tone of 60 db intensity with the 5 sec CS-US interval.

floor started the trial. Pressing the bar terminated the shock application. After the 21st experimental session, one group of cats underwent prefrontal lesions whereas the control group rested in their home-cages for 10 days.

In this experiment no systematic changes in median latencies calculated for 100 trial blocks were observed, either after prefrontal lesion, or after 10 days rest period in the control group. From the cumulative distribution curves presented in Fig. 5 one can see that in the course of post-operative training the proportion of short-latency instrument-

al responses was even increased, but the same process took place in the control group. An analysis of variance based on median latencies data has shown that the interaction between 100 trial blocks and groups (i.e. treatments) was statistically not significant.

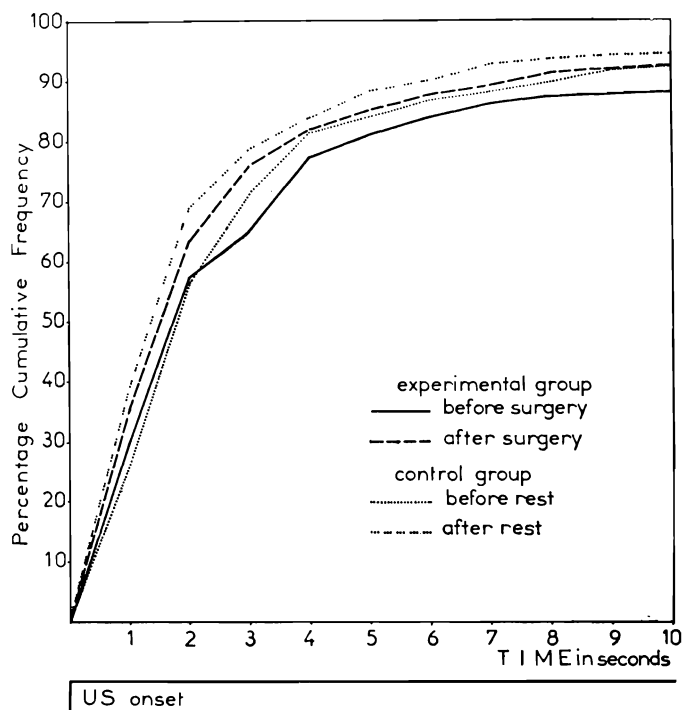


Fig. 5. Cumulative frequency distributions of the latencies of bar-pressing escape responses in cats before and after pause in experiments and/or prefrontal lobectomy.

Thus, prefrontal lesions in cats have no effect on performance of the bar-pressing escape responses. Since in the previous experiment the same motor response was used, the transient impairment of the avoidance reflex and the decrease in the frequency of short-latency avoidance responses cannot be the effect of prefrontal lesions on the motor part of the reflex arc. Comparison of the results of the two experiments show that after prefrontal lesions there is no deterioration of the ability to perform the motor act, pressing the bar, which is the instrumental response.

Another question, which had to be answered, was whether or not the prefrontal lesions change the sensitivity of animals to painful stimulation. In the second experiment, using the escape reflex, it was

found that there was no difference between the operated and control animals in responding to different shock intensities applied in test sessions (Zieliński 1970). This indicates that in both groups the threshold of the escape response to shock was similar. Thus, we may conclude that prefrontal lesions do not affect the reactivity to shock, when the cat can terminate its application by performing the escape response. In typical avoidance procedures this opportunity to terminate the shock also exists, and in the case of post-operative impairment of avoidance reflex activity, the escape responses are performed with normal latencies and efficiency (Brady et al. 1954, Thompson 1963, 1964, Zieliński 1966, Dąbrowska and Jarvik 1970, Warren et al., this Symposium).

The problem arises: why reactivity to the CS, which is a signal for the shock application after the CS-US interval, is diminished by the same lesion?

As was shown in the first experiment, the main and longlasting evidence of the diminution of reactivity to the CS consists in a decrease of the percentage of short-latency avoidance responses. From other experiments concerning the effect of conditioned stimulus intensity in avoidance conditioning, which were performed recently in our Laboratory, we know that the intensity of the CS and its relation to the background intensity level are important factors determining the proportion of short-latency avoidance responses (Zieliński 1971). When a white noise was used as the CS, the CS intensity had very little effect on the length of training necessary to reach the 90% level of avoidance performance, but reflected on the distribution of the avoidance response latencies.

Results obtained in one such experiment are presented in Fig. 6. Inspection of the data for pre-operative criterion sessions (when cats performed at least 90% avoidance responses) shows that the percentage of responses with latencies shorter than 1.1 sec was five times lower in the group trained to 50 db CS than in the group of cats trained to 70 db CS.

After reaching the performance criterion, cats from both groups received prefrontal lesions. As seen from Fig. 6 the two effects: small percentage of short-latency avoidance responses due to weak CS, and diminution of the percentage of such response after prefrontal lesions — are additive. In spite of the fact that after lesions the curves for both groups are moved to the right, which reflects prolongation of response latencies, the largest post-operative differences between two groups are observed in the percentage of responses with short latencies (less than 1.1 or 2.1 sec).

According to the contemporary view on stimulus intensity effect, the intensity of the CS determines the strength of the conditioned

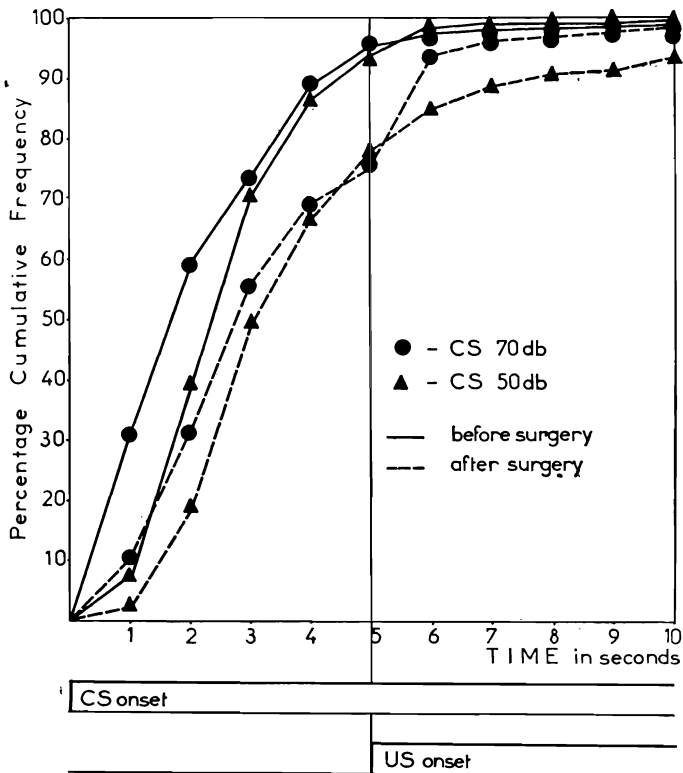


Fig. 6. Cumulative frequency distributions of the latencies of bar-pressing responses before and after prefrontal lesions in two groups of cats, one trained to the 70 db white noise CS and the second trained to the 50 db white noise CS, both with the 5 sec CS-US interval.

response, and latency of the response is one of the indices of this strength.

The strength of the conditioned response can be influenced by other independent variables of the experimental procedure. One of such variables is duration of the CS-US interval. In order to test how this variable interacts with the prefrontal lesions effect, E. Jakubowska and I (in preparation) carried out an experiment in which during the acquisition stage a 2×2 design was used, one factor being the CS intensity (50 db white noise versus 70 db white noise) and the second factor the duration of the CS-US interval (3 sec vs. 9 sec). After reaching the criterion of 90 avoidance responses in 100 consecutive trials, each cat received prefrontal lesion.

Results obtained from groups trained with the 3 sec CS-US interval (Fig. 7) resemble those presented before for groups trained with

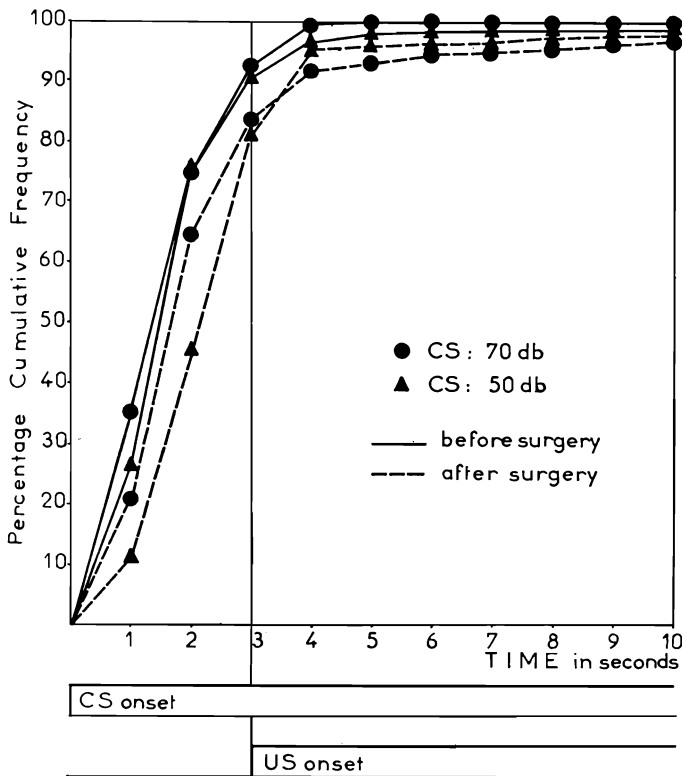


Fig. 7. Cumulative frequency distributions of the latencies of bar-pressing responses before and after prefrontal lesions in two groups of cats, one trained to the 70 db white noise CS and the second trained to the 50 db white noise CS, both with the 3 sec CS-US interval.

5 sec CS-US interval, except for a more rapid increase of the cumulative distribution curves both before and after operations and a smaller effect of the prefrontal lesions on the level of avoidance performance.

In Fig. 8 data for groups trained with the 9 sec CS-US interval are presented. Due to the long CS-US interval the proportions of short-latency responses were considerably smaller in these groups than in groups trained with 3 or 5 sec CS-US intervals. However, the data for the pre-operative period shows the usual stimulus intensity effect on the proportion of short-latency avoidance responses. After lesions, the group differences are clearly visible for a much greater part of the CS-US interval.

In each case the group differences in distribution of response latencies were increased after prefrontal lesions, and animals trained with

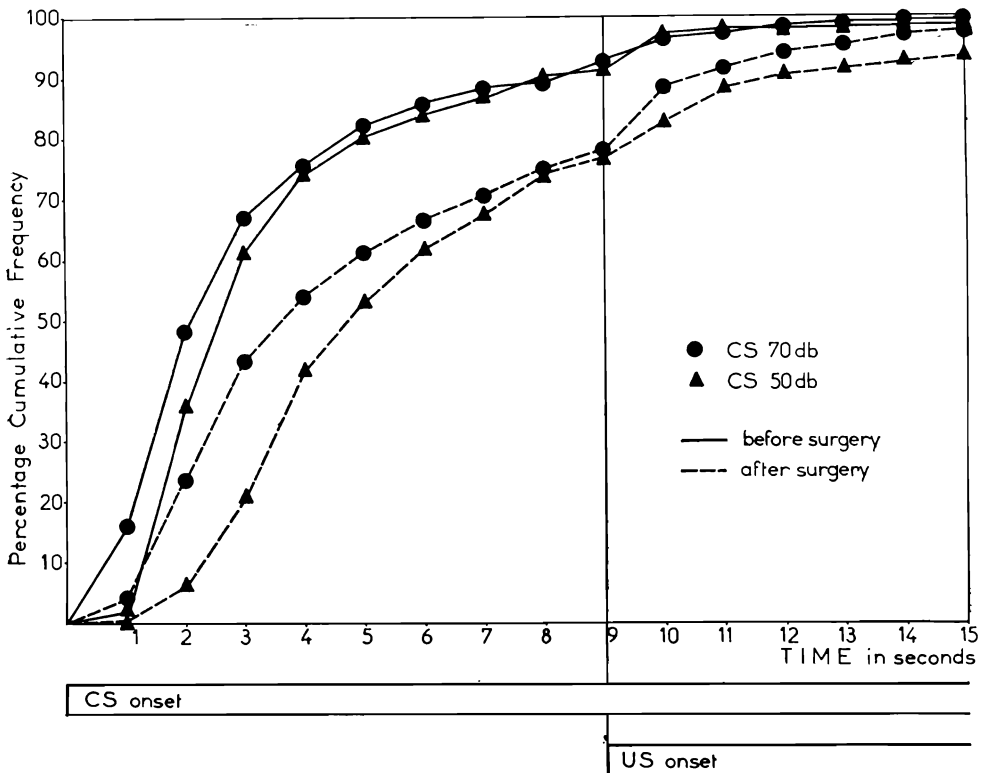


Fig. 8. Cumulative frequency distributions of the latencies of bar-pressing responses before and after prefrontal lesions in two groups of cats, one trained to the 70 db white noise CS and the second trained to the 50 db white noise CS, both with the 9 sec CS-US interval.

weaker stimuli were more impaired than animals trained with stronger stimuli. Similarly, when median latencies, or, more exact, the distributions of response latencies are taken into account, the animals trained with longer CS-US intervals were more impaired after prefrontal lesions than animals trained with shorter CS-US intervals. Thus, we may draw a conclusion that such variables as the CS intensity and the duration of the CS-US interval, which determine the avoidance response strength, have an important influence on the degree of impairment of the avoidance reflex after removal of prefrontal cortex. As a rule, the smaller the proportion of short-latency avoidance responses observed before operation the greater the post-operative impairment of the avoidance response.

During post-operative training of the avoidance reflex some shortening of instrumental response latencies was observed. However, this compensation is related mostly to an increase in the proportion of

avoidance responses in the second half of the CS-US interval, whereas only small changes were observed in the proportion of responses with very short latencies. This is illustrated in Fig. 9 and 10, in which cumulative frequency distributions of response latencies for groups trained with the 9 sec CS-US interval for the three 100 trial blocks are compared. As seen from the Figures, the frequency distribution curves estimated for the post-operative criterion period, when animals reached the 90% level of avoidance performance, in the first part of the CS-US interval resemble the slope of the curves for the first post-operative 100 trial block, whereas toward the end of the CS-US interval they are very similar to the pre-operative frequency distribution curves.

Comparison of the cumulative frequency distributions of response latencies for the same level of avoidance reflex performance (during criterion sessions) before and after prefrontal lesions shows that after

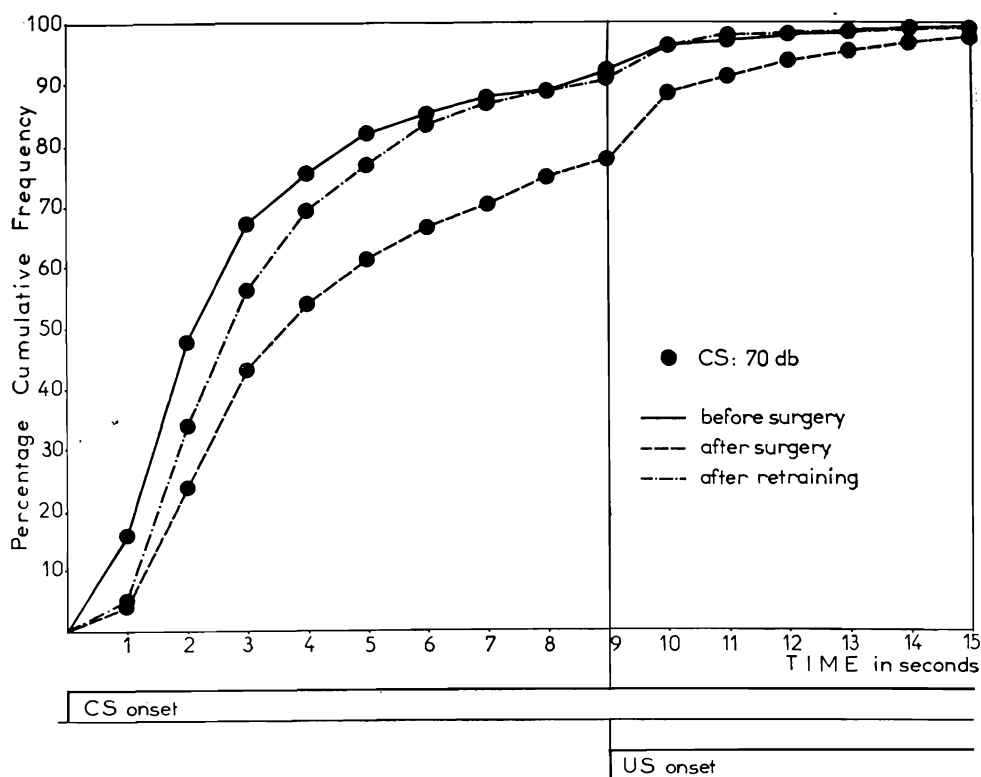


Fig. 9. Comparison of the cumulative frequency distribution curves before and after prefrontal lesions and the distribution obtained after post-operative relearning of the avoidance reflex in cats trained to the 70 db white noise CS with the 9 sec CS-US interval.

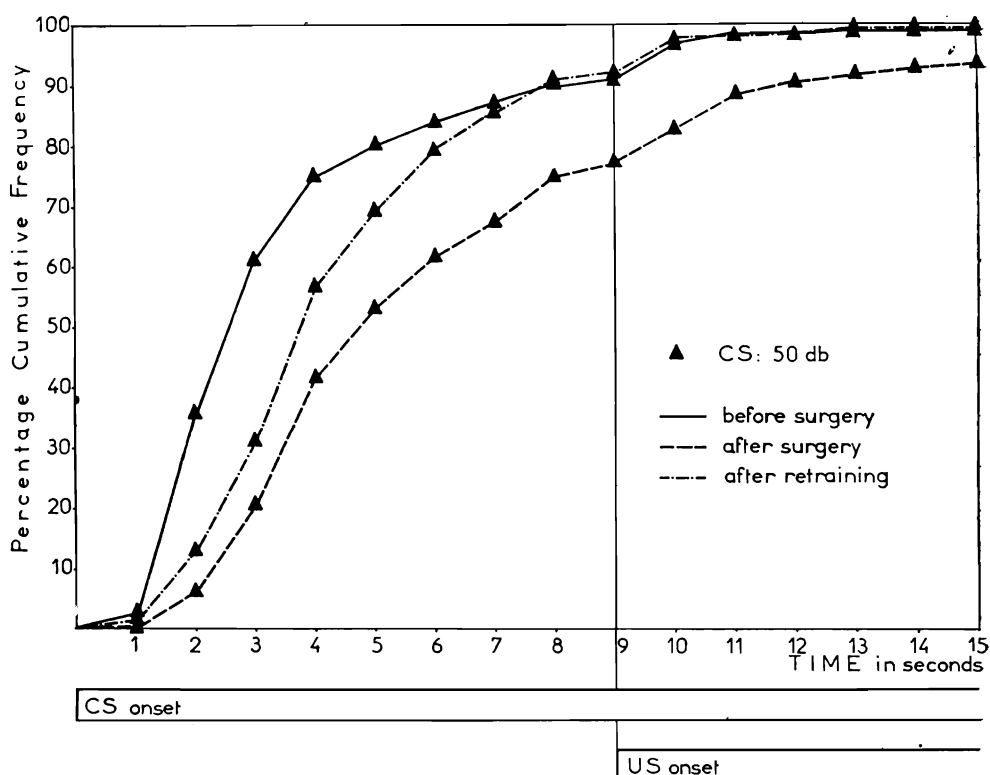


Fig. 10. Comparison of the cumulative frequency distribution curves before and after prefrontal lesions and the distribution obtained after post-operative relearning of the avoidance reflex in cats trained to the 50 db white noise CS with the 9 sec CS-US interval.

lesions the curves are flatter at the beginning of the CS-US interval and steeper in the middle and toward the end of the CS-US interval.

This indicates that the ability to perform the short-latency avoidance responses does not recover and the post-operative retraining of the reflex is due to the augmentation of the avoidance responses executed with longer latencies. Prefrontal cats resemble normal cats in the transitional stage of training, when avoidance responses are executed more often than escape responses, but the short-latency avoidance responses are observed only exceptionally.

So, we may draw a conclusion that initiation, not execution of the avoidance response is impaired after prefrontal lesions in cats.

Inhibition of the avoidance responses in frontal cats

Introduction of inhibitory trials is an experimental variable which may influence the strength of the avoidance response. Our results con-

cerning the effects of prefrontal lesions on the retention of positive and inhibitory avoidance reflexes were reported for the first time at the International Congress in Leyden (Zieliński et al. 1962).

The course of pre-operative training in this experiment has been reported in detail before (Sołtysik and Zieliński 1962). Briefly, it consists in shaping the bar pressing avoidance response to the 2000 cycle/sec tone of 60 db intensity using the 5 sec CS-US interval. After reaching the criterion of 90 avoidance responses in 100 consecutive trials the avoidance reflex was extinguished during 10 sessions and then retrained to the same criterion. Then inhibitory trials were introduced. A click with a rate 5/sec was used as the conditioned inhibitor (CI). On the first stage the inhibitory trials were of 15 sec durations, in the first 5 sec the click was given alone and during the next 10 sec overlapped the tone. No shock was given in inhibitory trials and duration of this inhibitory compound was independent of the animals' behavior. In each daily session 10 regular avoidance trials (positive trials with the tone as the CS) and 10 inhibitory trials were given. This discrimination task was easily mastered by all cats after 5 to 14 sessions of training. Then in four cats a more difficult form of the inhibitory compound was introduced. In this case the inhibitory compound lasted for 10 sec only, but there was no overlap between the CI and the CS: the click was acting for 5 sec and simultaneously with its offset the tone alone started for another 5 sec. As before, no shock was given in inhibitory trials and duration of this compound was not related to the animals' behavior. Cats extinguished responding to this inhibitory compound only after prolonged training (40-52 sessions).

In Fig. 11 there are given cumulative frequency distributions of response latencies to the tone presented in regular avoidance trials at different stages of training for the last four cats. Changes in the frequency distribution curves indicate that the "easy" form of inhibitory training had no effect on the strength of the avoidance reflex. On the contrary, the "difficult" form of inhibitory training resulted in a reduction in the proportion of short-latency avoidance responses to the tone presented in regular avoidance trials, which indicates a weakening of the avoidance reflex. Thus, it may be expected that after prefrontal lesions impairment of the avoidance performance will be greater in cats in which the "difficult" form of the conditioned inhibition has been established than in cats which received lesions at the end of the "easy" inhibitory task training.

The results of the experiment were in agreement with this hypothesis. The impairment of performance in the regular avoidance trials in cats trained in the "easy" form of the inhibitory task reminds one

of the results presented before for cats trained to the tone alone (the first experiment). No marked post-operative changes in the amount of bar-presses to the inhibitory compound was observed, either.

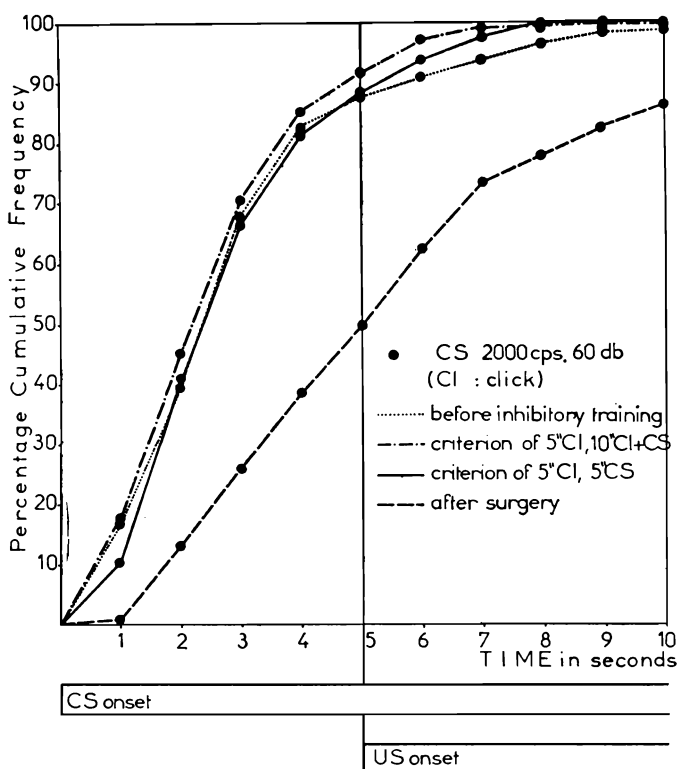


Fig. 11. Cumulative frequency distributions of the latencies of bar-pressing responses to the CS at different stages of inhibitory training in cats.

The situation was drastically changed when prefrontal lesions were done after the "difficult" form of the conditioned inhibition training. The post-operative distribution of response latencies to the tone presented in positive trials shown in Fig. 11 indicate severe impairment of the avoidance reflex activity in these cats. In this case the performance in regular avoidance trials was so impaired that in three cats out of four it was necessary first to reestablish the avoidance reflex to the tone alone, before the inhibitory trials were again introduced (Fig. 12).

It is interesting to add that in Cat 13 and in Cat 8, in which prolonged post-operative training of avoidance reflex was necessary, the greatest changes during "difficult" inhibitory training in cumulative frequency distributions of response latencies were observed. Introduction

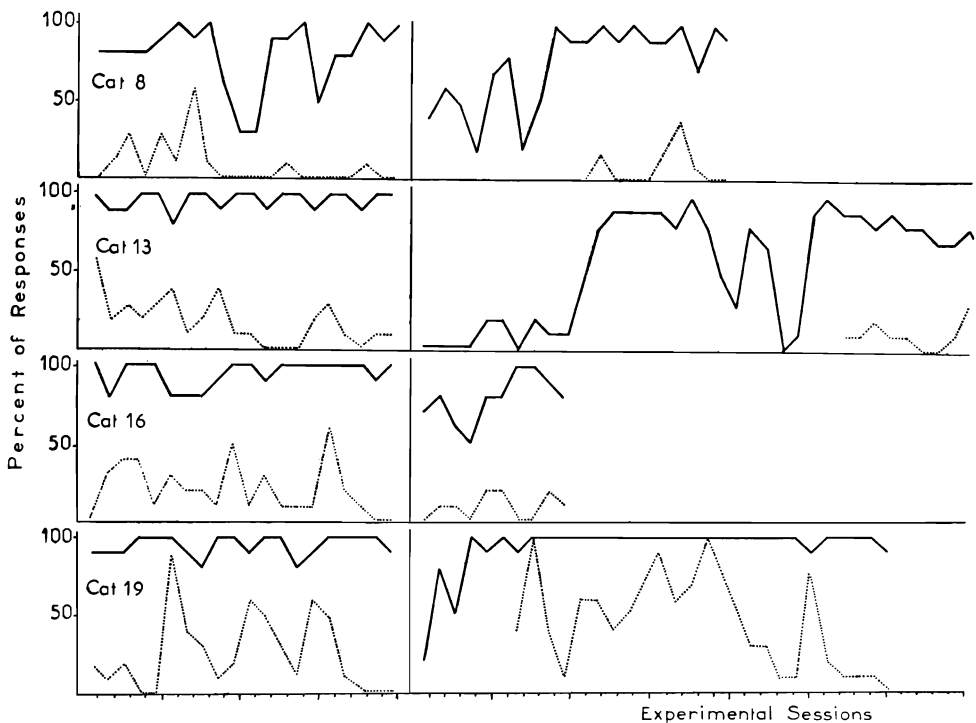


Fig. 12. Performance of bar-pressing responses to the CS (solid line) and to the inhibitory compound (dotted line) in individual cats before and after prefrontal lobectomy. Vertical line on each graph denotes the prefrontal lesion.

of inhibitory trials after retraining of the avoidance reflex shows that the retention of inhibition was not impaired in these cats. Signs of "disinhibition syndrome" were observed only in Cat 19. This cat was the only one in which distribution of response latencies was not changed during training of the "difficult" form of conditioned inhibitory task.

This example tells us how strongly the effects of prefrontal lesions are dependent on changes in the avoidance performance during pre-operative training. In contrast to previous discussions of the results of this experiment (Soltyśik and Jaworska 1967), much more attention has to be paid to changes in avoidance response latencies which occur during the pre-operative inhibitory training. In the light of results presented in the first part of this paper showing that prefrontal lesions in cats affect initiation of the avoidance response, full retention of inhibitory effect of the conditioned inhibitor may be expected. However, in two cats out of four the amount of bar-pressing responses executed during the "difficult" inhibitory compound increased slightly after post-operative relearning of the avoidance reflex. This may suggest that the "dis-

inhibition syndrome" similar to that observed in experiments with alimentary reflexes (Brutkowski 1957, 1959, 1964, 1967, Brutkowski et al. 1956, Ławicka 1957, Sołtysik and Jaworska 1967) or in experiments with classically conditioned defensive reflexes (Auleytner and Brutkowski 1960) did in fact appear, but was masked by the weakening of the avoidance reflex due to the prefrontal lesion.

To examine this possibility the distributions of latencies of bar-pressing responses occurred to the inhibitory compound during the last pre-operative 100-trials block and during the first block of 100 trials after the post-operative reintroduction of inhibitory trials were compared. As seen from Fig. 13 the two cumulative distribution curves ful-

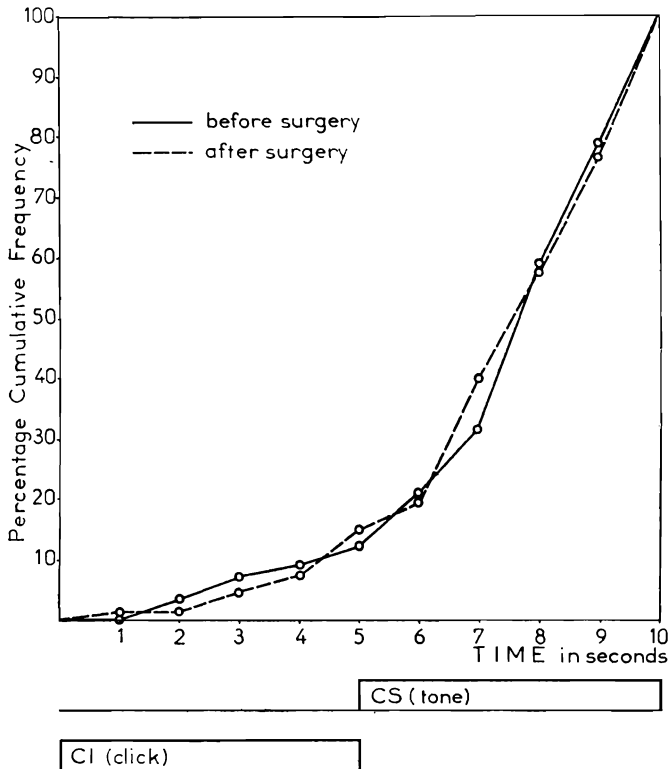


Fig. 13. Cumulative frequency distributions of the latencies of bar-pressing responses to the inhibitory compound before and after prefrontal lobectomy.

ly overlap, which indicates that after prefrontal lesions the click exerts the same inhibitory effect on the responding to the CS as before. So, typical "disinhibition syndrome" has not been observed in the avoidance situation.

*Interaction of classical and instrumental components
in the avoidance reflex*

Data concerning changes of the latency distributions of classically conditioned defensive responses are not available. However, some studies on dogs suggest that after prefrontal lesions latent periods of responses were shortened (Auleytner and Brutkowski 1960, Sołtysik and Jaworska 1967). Experiments now performed in our Laboratory indicate that not only in cats but also in dogs shortening of the avoidance response latencies after prefrontal lesions is not observed. Thus, the problem arises: why prefrontal lesions have different effect on response latencies in these two types of defensive conditioned reflexes?

This problem is of great importance, because most theories of avoidance conditioning assume that the classically conditioned fear response is an intervening variable indispensable for the elicitation of the instrumental avoidance response (Konorski and Miller 1933, Miller and Dollard 1953, Mowrer and Lamoreaux 1942, Mowrer 1947, Schoenfeld 1950, Solomon and Wynne 1953, Sołtysik and Kowalska 1960, and others). Thus, it may be expected that lesions in the frontal cortex would have a parallel effect both on the classically conditioned defensive reflexes and on the instrumental avoidance reflex. As experimental data did not support this expectation, the "drive disinhibition hypothesis" attempted to explain the impairment of the avoidance reflex after frontal lesion as a result of an increase in defensive-aggressive emotional responses, which interfere with the avoidance response (Brutkowski and Wojtczak-Jaroszowa 1963, Brutkowski 1965, 1966, Balińska et al. 1966). However, it is not clear how the "drive disinhibition hypothesis" may explain perfect retention of escape reflexes, i.e. instrumental movements terminating application of noxious stimuli which ought to evoke more intense defensive-aggressive emotional responses than conditioned stimuli signalling avoidable noxious stimulation. When marked decrease of the threshold of the emotional defensive reactions after dorsal amygdala lesions were observed, not only avoidance responses (Fonberg 1966), but also the conditioned escape responses were severely impaired (E. Fonberg, personal communication).

In a number of psychological and neurophysiological studies the lack of parallelism between the classically conditioned defensive reflexes and the instrumental avoidance reflexes has been observed. There are reasons to consider the scheme of the avoidance reflex based on the CS center — Fear Drive center — Instrumental Movement center (CS—Fear Drive—CR_{II}) connections as too simple, not adequate to experimental data. Although the main aim of Mowrer's papers was to substantiate the two-factor theory in avoidance reflex activity, Mowrer himself mentioned that

his analysis may not be valid for those conditioning experiments, in which the avoidance responses are executed with very short latency (Mowrer and Lamoreaux 1946). Similarly Solomon and his co-workers nearly twenty years ago noted (Solomon et al. 1953, Solomon and Wynne 1954) that avoidance responses are frequently performed with latencies shorter than required for the emotional reaction to take place in the presence of the CS. A substantial proportion of the well trained avoidance responses had latencies shorter than the sum of the latency of conditioned fear reaction plus the latency of the instrumental motor response itself. Thus, the simplest scheme of the avoidance reflex besides that of the CS-Fear Drive-CR_{II} connections has also to include direct connections between the conditioned stimulus center and the instrumental movement center.

The analysis of extensive experimental data has shown the importance of the direct CS-CR_{II} connections both in alimentary (Wyrwicka 1952, 1960) and in defensive (Wyrwicka 1958) instrumental conditioned reflexes for response differentiation. The lack of transfer of the well trained avoidance reaction to unsignalled unconditioned noxious stimuli indicate that the excitation of the defensive center manifested by the fear reaction is not sufficient for elicitation of the instrumental movement (Fonberg 1958a, 1962). Only when an animal became restless and showed general motor excitement the avoidance response differentiation was abolished (Fonberg 1961) and transfer of the instrumental avoidance response to the unsignalled noxious stimuli was observed (Fonberg 1958b). It is important to note that the instrumental defensive response either occurred at the onset of the unsignalled noxious stimulus or was not performed at all in spite of prolongation of noxious stimulation (Fonberg 1962.). This indicates that the raise of the excitation of the defensive center in the course of the noxious stimulation inhibits rather than facilitates the previously established defensive instrumental response. A similar statement was raised before in the paper concerning the avoidance reflex activity in sympathectomized dogs (Wynne and Solomon 1955).

It must be pointed out that there are controversies as to the importance of the fear component in elicitation of the well trained avoidance response. Nevertheless authors in whose concepts the fear state is a necessary condition for elicitation of the well trained avoidance response, have no objections to the statement that avoidance response may be performed before the fear reaction reaches its full strength.

Short-latency avoidance responses are very effective. One may say that in performing a response with very short latency a subject is avoiding not only the painful stimulus but also the fear state or, at least, the development of fear is drastically cut off, whereas performing a res-

ponse with longer latency a subject is escaping the fear state and only pain is avoided. Obviously, in the case of short-latency avoidance responses the conditioned fear reaction component has to be weaker than in the case of long-latency avoidance responses, because the fear response has not enough time to develop fully. Thus, the short-latency avoidance responses are based more on the direct CS-CR_{II} connections than on the indirect CS-Fear Drive-CR_{II} connections.

The marked post-operative decrease of the short-latency avoidance responses and lack of such changes in avoidance responses executed with longer latencies suggest that the removal of the proreus and orbitalis gyri in cats affects the direct CS-CR_{II} connections and does not impair the fear-eliciting properties of the CS acquired at the first stages of avoidance training, before the animals learned to avoid the electric shock. Because we did not observe full recovery of the pre-operative level of short-latency avoidance responses during post-operative training, we may infer that the weakening of the CS-CR_{II} connections cannot be compensated for in lesioned animals.

Lack of impairment in long-latency avoidance responses suggests that the indirect CS-Fear Drive-CR_{II} connections are preserved after the removal of the proreus and orbitalis gyri in cats. Perfect retention of the classical defensive reflexes and escape reflexes after the same lesions give additional support to this hypothesis.

Fear is an innate response to pain (Miller 1951) and the noxious stimulation evokes strong excitation of the fear drive center. On the other hand, onset of shock in avoidance and/or escape situation is a signal that painful stimulus and fear state will persist until the performance of the instrumental response. Both innate and signalling properties of pain involve only the Fear Drive and CR_{II} connections and the escape responses are performed after removal of proreus and orbitalis gyri in cats as easily as in normal animals. Thus, there is no change in the threshold value of shock necessary to elicit the escape response. Neither is there a difference between normal and prefrontal cats in latencies of escape responses to shock intensities higher than those used in regular training sessions (Zieliński 1970). So, neither "drive disinhibition", nor exaggeration of unconditioned responses to shock were observed to occur following prefrontal lesions in cats in which the instrumental escape reflex was pre-operatively established.

The classical conditioned defensive reflex is based on the CS and Fear Drive center connections and excitation of the drive center affects different autonomic responses and the motor system activity level (Kornorski 1967). Recovery of the avoidance performance after prefrontal lesions in cats due to the increase of the proportion of long-latency

avoidance responses indicates that the strength of the CS-Fear Drive connections may increase during the post-operative training, when due to some impairment of the avoidance reflex performance level, the CS-US pairings (the shock applications) occur more often than before.

Comparison in the groups of cats trained with different CS intensities and the CS-US intervals of various durations show that the smaller the proportion of short-latency responses were observed before lesions, the larger was (in seconds) the flattened portion of the frequency distribution curve after prefrontal lesions. It is related to the fact that conditioning and consolidation of the classical defensive reflex is more difficult, when the CS-US interval is long and the CS is of small intensity. When the reactivity of animals to the CS is decreased after prefrontal lesions, in the case of weak classical defensive reflex the fear reaction needs more time to reach the level necessary to initiate the avoidance response than if the strong classical defensive reflex had been established during previous training.

Retention of the classically conditioned defensive reflex after frontal lesions (Auleytner and Brutkowski 1960, Maher and McIntire 1960, Sołtysik and Jaworska 1967, Sołtysik et al., this symposium) as well as retention of the emotional fear reaction to the onset of the CS in spite of post-operative impairment of the avoidance reflex (Brady et al. 1954, Thompson 1963, 1964) supported the notion that frontal lesions do not affect the CS-Fear Drive center connections.

It has to be stressed once again that the two defensive situations — classical and avoidance — differ in many aspects. First of all in the classical defensive conditioning reflex the painful stimulus is applied independently of how the animal behaved, whereas in the avoidance reflex painful stimulus is under the subject's control. Thus, in the course of the avoidance reflex acquisition the "danger" of the situation decreases, whereas, in the classical conditioning situation it remains without change. It was shown that in the course of the avoidance training the fear-evoking properties of the CS decrease but no such changes were observed during the classical defensive conditioning (Kamin et al. 1963).

The notion that well trained avoidance reflexes are based on mechanism in which the emotional state plays a little role has further support in studies on the involvement of the amygdaloid complex in defensive behavior. The total removal of the amygdaloid complex in dogs abolished the classically conditioned defensive reactions but no changes in performance of the well trained avoidance reflex have been observed (Fonberg et al. 1962). Similarly, stimulation of the baso-lateral portion of the amygdaloid complex exerts an inhibitory effect on the general fear reactions, but the avoidance performance to the CSi

remained unchanged both in cats (Fonberg and Delgado 1961), and in dogs (Fonberg 1963, 1967).

Thus, both behavioral and neurophysiological data call for careful examination of the classically conditioned and instrumental components participation in different varieties of defensive reflexes in order to understand their changes after prefrontal lesions.

This investigation was partially supported by Foreign Research Agreement No. 05-275-2 of the U.S. Department of Health, Education and Welfare under PL 480. One of the reported experiments has been aided by a grant from the Foundations' Fund for Research in Psychiatry. I am greatly indebted to Drs. F. R. Brush, E. Fonberg and T. Górska for valuable suggestions during preparation of this paper, and to Mrs. J. Kilijanek and A. Radziwonka for technical assistance in conducting experiments.

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Received 11 October 1971

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