ACTA NEUROBIOL. EXP. 1980, 40: 403-432

Warsaw Colloquium on Instrumental Conditioning and Brain Research
Poster presentation
May 1979

AVOIDANCE RESPONDING IN DOGS TRAINED IN SYMMETRICAL OR ASYMMETRICAL GO, NO–GO DIFFERENTIATION

Danuta M. KOWALSKA and Kazimierz ZIELIŃSKI

Department of Neurophysiology, Nencki Institute of Experimental Biology
Warsaw, Poland

Abstract. The acquisition and the consolidation processes of avoidance responding in go, no–go differentiation with asymmetrical and symmetrical reinforcement procedures were studied in 49 male mongrel dogs. Differentiation training procedures with asymmetrical and symmetrical reinforcement were contrasted by the occurrence of painful shock on negative trials. The quality of conditioned stimuli and their relative saliency exerted strong effects on the rapidity of learning and the number of commision errors when the "asymmetrical" procedure was used, whereas these effects were strongly attenuated under "symmetrical" procedure of reinforcement. Dogs trained in "symmetrical" go, no–go differentiation showed characteristic responses executed with shorter latencies and larger percentages of errors on negative trials and numerous extra-and intertrial responding in early stages of differentiation learning. Retention tests showed a greater stability of acquired differential responding trained under "symmetrical" than under "asymmetrical" procedure of reinforcement. The data indicate that the strength of the secondary punishing effect of CS prolongation is directly related to the saliency of the stimulus. The relations between the primary and secondary punishing effects in the two types of differentiation task, and problem of signalling and arousing properties of stimuli used in training, were discussed.

INTRODUCTION

Go, no-go differentiation is a commonly used behavioral test for studying discriminative abilities and/or capacities for internal inhibition. In initial experiments employing instrumental reflexes go, no-go differentiation procedures were used in which only the positive conditioned stimulus (CS^+) signalled the possibility of reinforcement given immediately after the performance of an instrumental response. On other trials independent of instrumental responses, the unconditioned stimulus (US) was never paired with the negative conditioned stimulus (CS^-).

In several studies from the early 1960's, Gross and Weiskrantz employed another kind of go, no-go differentiation test. They reinforced correct responding with food presentation on both positive and negative trials, so that food was given not only after instrumental response to the CS^+ but also after inhibition of such response to the CS^-. They described this type of test as differentiation with symmetrical reinforcement, as distinct from the earlier go, no-go differentiation procedures which they called differentiation with asymmetrical reinforcement (15, 16). They considered the difference between the two tasks in terms of the presentation of unconditional reinforcement on positive and negative trials, but they did not examine the mechanisms responsible for their acquisition and performance.

Both differentiation tasks have been used in experiments designed to study prefrontal cortical functions. The greatest disturbance in retention of asymmetrically reinforced go, no-go differentiation occurred after the removal of the orbital part of the prefrontal cortex in monkeys (7, 28) and the medial part of the prefrontal cortex in dogs (4–6). In contrast, retention of symmetrically reinforced go, no-go differentiation was most heavily impaired after the removal of the dorso-lateral part of the prefrontal cortex in monkeys (15, 16) and in dogs (9, 10, 12).

On the basis of results obtained from studies of alimentary reflexes, different physiological mechanisms involved in performance under each type of differentiation procedure were postulated. According to Dąbrowska (10), there are excitatory connections from the cortical CS^+ center through the drive center to the center of the instrumental response. There is also a direct connection between the CS^+ center and the instrumental response center (40). In go, no-go differentiation with asymmetrical reinforcement the inhibition of responses to CS^- is due to the development of inhibitory connections between the CS^- center and the drive center. The correct performance to CS^- depends on the excitatory level of the drive center. The performance on symmetrically reinforced differentiation task reflects somewhat alternate processes. As Dąbrowska suggested, this type of differentiation is based on two opposite responses: flection and extension of the leg. The drive center is activated not only by the CS+ but also by the CS−. Only direct connections between centers of the stimuli and centers of the instrumental responses, reciprocally, define which movement should be performed to a given conditioned stimulus. Such a mechanisms has been proposed previously by Wyrwicka (41) for the left-leg, right-leg differentiation task. Similarly, Konorski (22, 23) postulated that during "asymmetrical" go, no-go differentiation, the CS+ excites the drive center, and CS− excites the anti-drive center having an inhibitory influence on the drive center. He considered go, no-go differentiation with symmetrical reinforcement as the differentiation of the two nondirectional motor acts.

Another aspect of the differences between the two go, no-go differentiation tests has been analyzed by Zieliński (47, 48). Based on Konorski's classification of conditioned reflexes (20, 24). Zieliński considered the differences between the two tests from the perspective of the influence of the subject's behavior on the appearance of unconditioned reinforcement. According to such an approach, the so called "asymmetrical" test is in fact a differentiation between instrumental responses on positive trials and classical responses on negative trials. In the "symmetrical" test the animal differentiates two instrumental responses, because not only on positive but also on negative trials performance of a specific motor response determines the likelihood of unconditional reinforcement presentation. In the case of defensive reflexes, Zieliński postulated that if the instrumental response is ineffective to terminate the CS− action, the response is punished due to the secondary negative reinforcement properties of the CS− (47, 48). A similar position was held by Dąbrowska, who considered defensive go, no-go differentiation tasks as "symmetrical" differentiation of the two motor acts independent of US appearance on negative trials (11).

However, the strength of secondary reinforcement based on fear-evoking properties of conditioned stimuli should depended on the extent of generalization between the CS+ and the CS−, related to both similarities between conditioned stimuli and their relative saliency. The effects of these variables on the two go, no-go differentiation tasks has not been previously investigated experimentally. We have published data from part of the dogs used in the present study, which suggest the importance of these variables for the learning of the two tasks (25, 26), however, no direct comparison of the two procedures was presented.

Thus, so far the physiological mechanisms responsible for learning and performance of the two differentiation tests were established on the basis of research containing a limited number of independent variables.

The aim of this study was to examine the course of the acquisition and consolidation processes of avoidance response differentiation with symmetrical and asymmetrical reinforcement. Pairs of conditioned stimuli having presumably different generalization gradients were employed. Some dogs were trained with a CS+ of greater saliency than CS–, while others were trained with the opposite salient relations between CS+ and CS–. To more clearly observe the stability of the acquired conditioned reflexes, a control pause of ten days was incorporated into the experimental procedure.

MATERIAL AND METHODS

In a set of 4 experiments 49 male naive mongrel dogs with weights ranging from 5 to 14 kg were used. A 2×2×2 experimental design was employed with the type of differentiation task, the acoustical CS quality, and the arrangement of stimuli pairs as independent variables (Table I).

TABLE I

Outline of experiments

Quality of stimuli	Differentiation task	Stimulus arrangement	
		Group 1	Group 2
Click vs. Tone	Asymmetrical (Exp. I)	CS+: Click CS–: Tone	CS+: Tone CS–: Click
	Symmetrical (Exp. II)	CS+: Click CS–: Tone	CS+: Tone CS–: Click
White noise intensity	Asymmetrical (Exp. III)	CS+: 70 dB CS–: 50 dB	CS+: 50 dB CS–: 70 dB
	Symmetrical (Exp. IV)	CS+: 70 dB CS–: 50 dB	CS+: 50 dB CS–: 70 dB

Training was conducted in an acoustically shielded chamber. The animals from Experiment I were trained in a cage measuring 55×55××40 cm and containing a bar, located 10 cm above the gridfloor in the middle of the oblong wall opposite to the entrance door of the cage. To facilitate shaping of bar-pressing, a 25×12 cm platform was used as an extension of the bar during initial training. The platform dimensions were subsequently changed to 12×7 cm and then to 11×3 cm, before the final use of the 10×2 cm bar. The sources of the CSi, located near the center of the cage ceiling were a loudspeaker, through which a 1,000 Hz, 65 dB tone was presented, and an electromagnetic relay, which produced a rhythmic 5/s click. Alternating current of 50 Hz and 25 V to 100 V from a transformer was used as the US. The optimal voltage for each dog was chosen at the beginning of training and remained constant throughout experimental sessions.

In Experiments II, III, and IV the dogs were placed on a platform measuring 68 cm wide and 177 cm long. Their limbs were secured with straps suspended from above the platform and they were secured in a harness. The sources of CSi were located facing the dog. A loudspeaker presented a 1,000 Hz 65 dB tone or white noise of 50 dB or 70 dB (*re* 0.0002 dyne/cm^2) intensity, and an electromagnetic relay produced a 5/s click. The instrumental response consisted of pressing a bar measuring 20 cm long × 15 cm wide located on the right side of the stand in front of the right foreleg. A current from a condenser, one pulse per second administered through electrodes placed on the left hindleg, was used as the US.

The experiments contained the following stages:

1. Acquisition of the avoidance response. During this stage there were 10 trials in each daily session. A trial started with CS$^+$ onset and terminated with the bar press. A bar-press executed within 5 s after CS$^+$ onset terminated the CS$^+$, prevented the US presentation, and was scored as an avoidance response. If an avoidance response did not occur 5 s after CS$^+$ onset the electric shock was given, the occurence of the bar press coterminated both the CS$^+$ and US, and the response was labelled as an escape. The intertrial intervals were randomly ordered periods of 40, 60 and 80 s. Training was continued until each dog reached a criterion of 100 per cent avoidance responses on two consecutive days in Experiment I, and 90% avoidance responses in ten consecutive sessions for Experiments II, III and IV.

2. Go, no–go differentiation training. The day after the avoidance acquisition criteria were met under the both training procedures, differentiation training was introduced. At this stage of the experiment each daily session consisted of 10 positive and 10 negative trials. The order of positive and negative trials was changed each day according to a Gellerman series (14). A positive trial started with CS$^+$ onset and terminated with the avoidance or the escape response. A negative trial consisted of the 5 s CS$^-$ presentation independent of instrumental bar-pressing responses. Differentiation training procedures with symmetrical and asymmetrical reinforcement were contrasted by the occurence of an electric shock on negative trials. No shock was given on negative

trials in the asymmetrical procedure of reinforcement, whereas in the symmetrical procedure of reinforcement each bar-press during the CS$^-$ action was punished by shock. Differentiation training was continued until the criterion of 95% correct responses to CS$^+$ and to CS$^-$ during ten consecutive sessions was reached in Experiment I and 90 per cent correct responses on positive and on negative trials in ten consecutive sessions was reached in Experiments II, III and IV.

3. Control rest period. After attaining differentiation criteria, a 10-day rest from the experimental procedures followed, in which the dogs remained in their home-cages.

4. Retention of go, no-go differentiation. After the control pause, retention of go, no-go differentiation was tested using the same procedures and criteria measures for each experimental group as used in Stage 2.

The main indices of behavior were: (i) the number of avoidance responses executed to CS$^+$; (ii) the number of disinhibited negative trials; (iii) latencies of the avoidance and escape responses, and of the first bar-press response emited to CS$^-$ in disinhibited negative trials, all measured to the nearest 0.2 s; and (iv) the number of extra responses to CS$^-$ and intertrial responses (E + ITR). During all stages of the experiments the dogs' behavior was observed through a one-way window from the room adjacent to the training chamber.

It should be noted that the major differences between Experiment I and Experiment II–IV were the type of apparatus used for training and testing, and the criteria measures employed for acquisition and differentiation training. For statistical analysis an attempt was made to equate all experiments. That is, that portion of acquisition performance in Experiments II–IV, which occurred to the criteria level used in Experiment I, was used in the statistical comparison. Conversely, differentiation performance in Experiment I was restricted to the 90 per cent correct response level to CS$^+$ and to CS$^-$; i.e., the criterion of Experiments II–IV. Thus, although the first experiment was distinquished from the others, for statistical purposes all were treated together according to the three-factorial design.

RESULTS

AVOIDANCE ACQUISITION

During avoidance acquisition identical procedures were used in Experiments III and IV, and the results obtained at this stage were analysed together. Within the combined results of Experiments III and IV as well as the other procedures (Experiment I and Experiment II) Group 1 and Group 2 were separately analyzed. The comparison between experimental groups was done with a uniform criterion of acquisition, the same as used for Experiment I — 100% avoidance responses in the two consecutive experimental sessions. An analysis of variance (27) showed no significant differences between groups in the speed of avoidance acquisition and in the number of escape responses (errors) to criterion. Moreover these data showed no influence from the two experimental apparatuses (cage or platform) on the acquisition of conditioned reflexes.

The quality and intensity of CSi influenced the latency of instrumental responses (Fig. 1). There were shorter avoidance response laten-

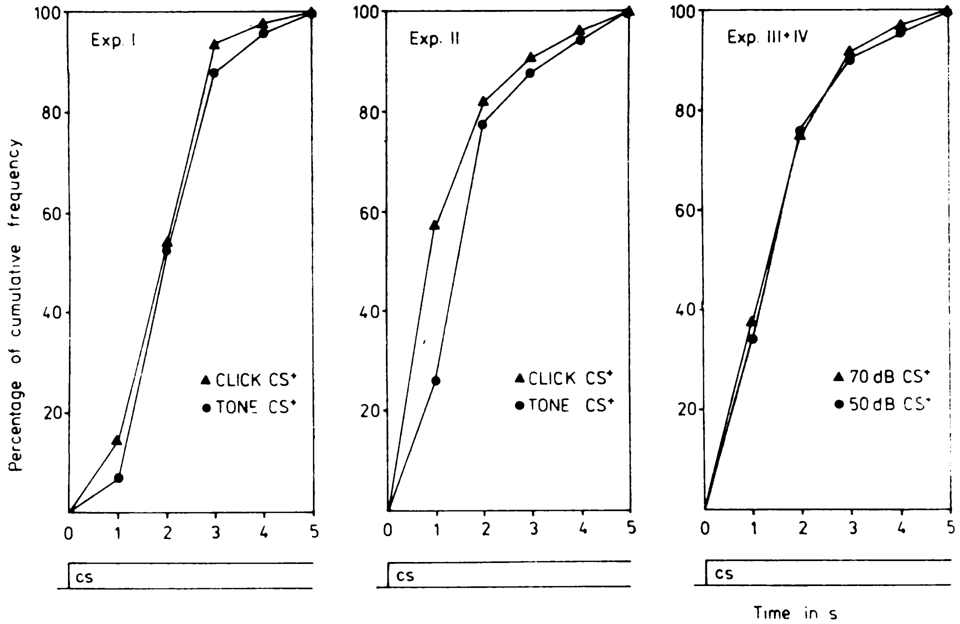

Fig. 1. Cumulative frequency distributions of the latencies of bar-pressing responses in the criterion sessions of acquisition of the avoidance reflex.

cies in Groups 1 than in Groups 2 of each experiment (see Table II). In Experiment I a low level of instrumental response performance during the first second of CS action was connected with the approaching movement of the dogs to the pedal. Table II shows the comparisons between cumulative frequency distributions of response latencies to the CSi used in each experiment (8). As is evident, the largest diffe-

TABLE II

Between group comparisons of changes in the distribution of response latencies on CS^+ trials in criterion sessions of the avoidance acquisition stage. S Click > S Tone denotes that in dogs trained with the click CS^+ a greater proportion of responses was emitted with latencies shorter than the point of D_{max} than in dogs trained with the tone CS^+; n_1 denotes number of trials in Group 1, and n_2 denotes number of trials in Group 2

	Size of samples	Difference	D_{max}	Point of D_{max} in s
Exp. I	$n_1 = n_2 = 160$	$S_{Click} > S_{Tone}$	0.131	1.3
Exp. II	$n_1 = n_2 = 140$	$S_{Click} > S_{Tone}$	0.321*	0.9
Exp. III+IV	$n_1 = 200$ $n_2 = 180$	$S_{70dB} > S_{50dB}$	0.060	1.1

* $P < 0.001$ (Smirnov Test)

rences between compared distributions, the D_{max}, were localized at the beginning of the CS–US interval (Smirnov two-tailed test). It is interesting that among the dogs that were trained in the same experimental situation (Exp. II and Exp. III+IV) an especially high level of short-latency responses occurred to the CS^+ click.

On the first CS^+ presentations during initial avoidance acquisition, clear orienting responses were observed. The conditioned fear response to the CS^+ occurred on the second or third trial, at which time strong emotional and motility symptoms in the dogs developed and involved vocal responses (barking, whining and squeaking) and autonomic responses (pupil dilatation, gasping, salivation, and occassionally urination and defecation). The dogs tried escape from the cage or from the harness. They sometimes bit the cage walls, the pedal, the grid floor or the harness. Then, in some dogs strong emotional responses changed to freezing responses. These forms of fear reactions disappeared together with acquisition of the effective instrumental response. Some dogs trained in the cage revealed stereotype behavior such as walking around, running and whirling, wheeling just before pressing the bar. After the instrumental response was acquired, each dog performed the bar-pressing response by using one, and always the same, foreleg.

DIFFERENTIATION TRAINING

During this stage a common criterion for Experiment I and Experiments II–IV was also employed. For this purpose the performance of each animal from Experiment I was limited to the number of trials and errors committed to criterion from subjects in the remaining experiments: 90% correct responses on CS$^+$ and CS$^-$ in ten consecutive experimental sessions.

The length of learning to criterion and number of errors. Comparisons of the number of trials to the differentiation training criterion for "asymmetrical" and "symmetrical" tasks in the same stimulus arrangement groups are shown in Fig. 2. The length of acquisition of the discrimination for dogs trained with the "asymmetrical" procedure depended on the quality and the arrangement of CSi. The most rapid differentiation learning was found in dogs trained with the easily discriminable stimuli when the CS$^+$ was more salient than the CS$^-$ (click CS$^+$ vs. tone CS$^-$). The most prolonged training to the criterion occurred in dogs differentiated two intensities of the white noise and when the CS$^+$ was less salient than the CS$^-$ (50 dB CS$^+$ vs. 70 dB CS$^-$). In comparison with "asymmetrical" differentiation training, the analogous groups of dogs in "symmetrical" test did not show such clear differences. Rather the most important factor for the rapidity of learning at this stage was the quality of CSi (Factor B, Table III). This factor also influenced the percent of trials with errors on CS$^+$ and on CS$^-$. The dogs trained with the click and the tone reached criterion faster and committed smaller numbers of errors on positive and on negative trials than the dogs trained with the intensities of white noise. Moreover, the frequency of trials with errors on CS$^-$ was higher in "symmetrical" than in "asymmetrical" differentiation (Factor A, Table III). The significance of the AB interaction indicates that when easily discriminable stimuli (click and tone) were used, the dogs trained with symmetrical reinforcement committed more errors to the CS$^-$ and reached the criterion more slowly than the dogs trained with asymmetrical reinforce-

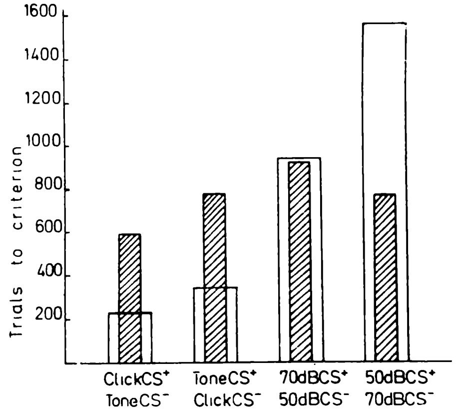

Fig. 2. Mean number of trials to 90% criterion of correct performance for each group of dogs trained in go, no-go differentiation with asymmetrical (wide open bars) and symmetrical (narrow, crossed bars) reinforcement.

ment. But when less discriminable conditioned stimuli were used (50 dB and 70 dB white noise) "symmetrical" training was faster, and dogs committed smaller numbers of errors to the CS$^-$ than dogs trained in "asymmetrical" differentiation.

The course of differentiation training. For each dog the number of trials to criterion was vincentized into five blocks (39), and the mean numbers of avoidance responses to CS$^+$ and trials with errors to CS$^-$ were calculated for each block and group. Figure 3 shows a comparison of the course of differentiation learning between the experimental groups trained with the same arrangement between CS$^+$ and CS$^-$ under asymmetrical and symmetrical differentiation procedures. At the beginning of training in each group many disinhibited responses to CS$^-$ occurred. Dogs trained with symmetrical reinforcement committed a higher per cent of errors on CS$^-$ trials than in the asymmetrical reinforcement procedures. Moreover, at the beginning of differentia-

TABLE III

Mean values of performance indices during differentiation training; *n*, number of dogs in a group

Differentiation task	Number of trials to criterion		Percentage of CS$^+$ trials with errors		Percentage of CS$^-$ trials with errors	
	CS$^+$: Click	CS$^+$: Tone	Click	Tone	Tone	Click
Asymmetrical (Exp. I)	$n = 8$ 230.0	$n = 8$ 340.0	2.4	2.8	3.9	6.1
Symmetrical (Exp. II)	$n = 7$ 591.4	$n = 7$ 774.3	2.6	5.9	16.4	20.3
	CS$^+$: 70 dB	CS$^+$: 50 dB	70 dB	50 dB	50 dB	70 dB
Asymmetrical (Exp. III)	$n = 5$ 940.0	$n = 5$ 1560.0	5.1	7.4	16.8	20.5
Symmetrical (Exp. IV)	$n = 5$ 920.0	$n = 4$ 765.0	4.1	3.3	21.2	29.4

Source of variation	*df*	Values of *F* statistics		
Differentiation task (A)	1;41	< 1	< 1	29.655***
Quality of stimuli (B)	1;41	29.601***	5.375*	26.547***
Stimulus arrangement (C)	1;41	2.911	1.193	2.518
AB	1;41	13.368***	3.155	4.795*
AC	1;41	1.612	< 1	< 1
BC	1;41	< 1	< 1	< 1
ABC	1;41	3.218	1.582	< 1

* $P < 0.05$; *** $P < 0.001$

tion training, more disinhibited responses were found in dogs trained with two white noise intensities than with the click and tone stimuli. The dogs trained in differentiation of easily discriminated stimuli committed more errors to the CS$^-$ click than to the CS$^-$ tone, and, similarly, the dogs trained with white noise intensities performed more errors to the 70 dB CS$^-$ than to the 50 dB CS$^-$. The data were submitted to an arc sin transformation for analysis of variance. In this

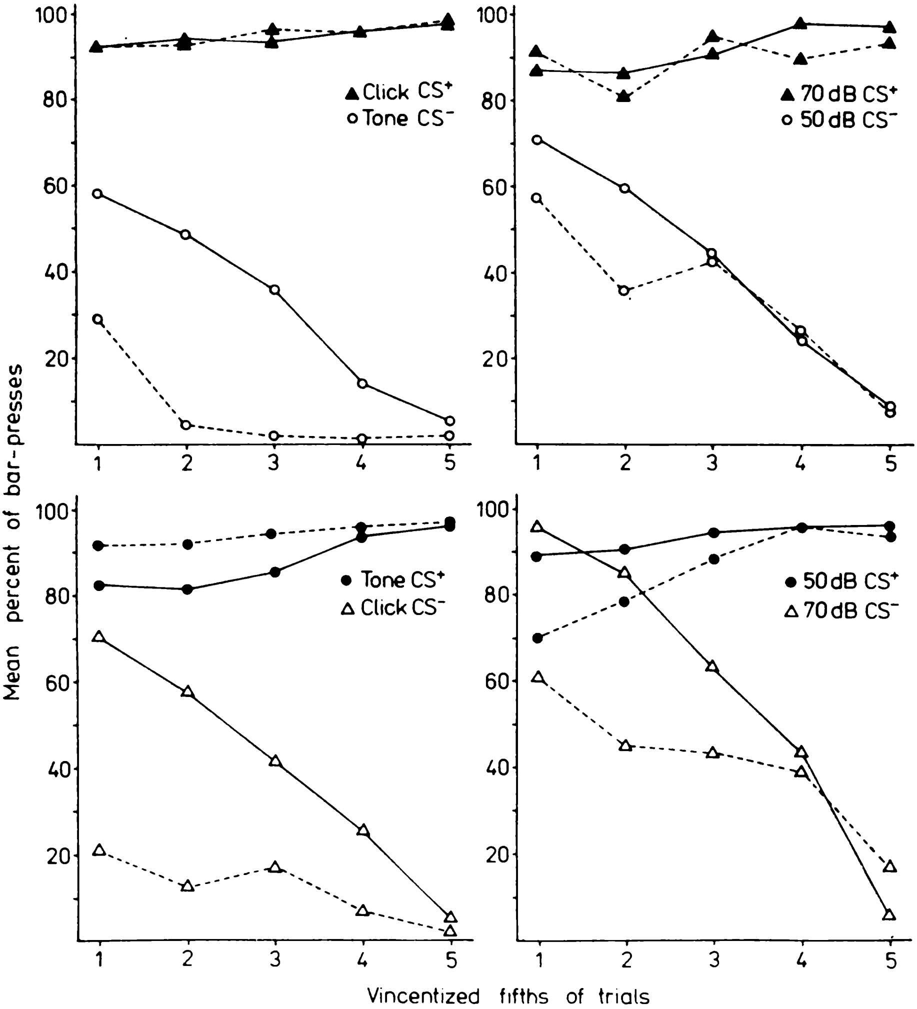

Fig. 3. Changes of performance in the course of differentiation training. The solid lines refer to groups trained in go, no-go differentiation with the symmetrical reinforcement, and the dotted lines show groups trained with the asymmetrical procedure of reinforcement.

analysis the data were collapsed across the variable of stimuli arrangement which had not significantly influenced the number of errors to CS^+ and to CS^- (compare Table III). The correlated factor, Vincentized fifths of the differentiation training, was indicated by "K". The influences of the uncorrelated factors (denoted as in Table III) were similar to that indicated in Table III. The per cent of errors to CSi diminished with progressive Vincentized fifths of trials ($CS^+ : F_{4;180} =$ $= 12{,}83$, $P < 0.001$; $CS^- : F_{4;180} = 63{,}37$, $P < 0.001$). The dogs that differentiated the intensities of white noise committed more errors at the beginning of training to CS^- than did the dogs that differentiated the tone and click (KB interaction: $F_{4;180} = 2.42$, $P < 0.05$). During differentiation learning the per cent of errors to CS^- diminished more rapidly in the symmetrically than in the asymmetrically reinforced procedure (KA interaction: $F_{4;180} = 12.53$, $P < 0.001$). In the course of differentiation training the number of intertrial responses and extra responses (bar-presses subsequent to the first) emitted to the CS^- (E + ITR index) also diminished (factor K : $F_{4;164} = 10.39$, $P < 0.001$). The two procedures of reinforcement also influenced the E + ITR index which was higher in "symmetrical" than in "asymmetrical" differentiation test (factor A: $F_{1;41} = 11.75$, $P < 0.001$). Similar to the extinction of responses to negative stimuli in successive blocks of training, the E + ITR index diminished faster in differentiation with symmetrical reinforcement (KA interaction: $F_{4;164} = 5.93$, $P < 0.001$). However, in each Vincentized fifth, the E + ITR index was higher in the "symmetrical" than in "asymmetrical" procedure. Moreover, when the dogs differentiated the tone and click, the index of E + ITR was higher under "symmetrical" training, but during white noise intensity differentiation this index was higher in "asymmetrical" training (AB interaction: $F_{1;41} = 5.14$, $P < 0.05$).

Response latencies to CS^+ and CS^-. Differences between "asymmetrical" and "symmetrical" training were also seen in the latencies of responses to CSi. An analysis of variance showed that the mean median latencies of responses during the 5 s of CS^+ and of CS^- actions were shorter in symmetrically than in asymmetrically reinforced differentiation (CS^+: $F_{1;41} = 26.20$, $P < 0.001$; CS^-: $F_{1;41} = 13.26$, $P < 0.001$). Interestingly, these differences occurred from the very beginning of training. An additional four-factor analysis of variance showed that in the first consecutive five sessions after CS^- trials were introduced, the latencies to CS^+ lenghtened ($F_{4;164} = 6.69$, $P < 0.001$), but in each session the mean median latencies of responses made by dogs trained with symmetrical reinforcement were shorter than in asymmetrically reinforced differentiation ($F_{1;41} = 13.26$, $P < 0.001$). Moreover, the same analysis showed that the response latencies to CS+ in Groups 2 (CS+ less salient than CS−) were longer than in Groups 1 (CS+ more salient than CS−). These differences were small for tone and click differentiation and very large in the white noise intensity differentiation (BC interaction, $F_{1;41} = 4.27$, $P < 0.05$). These relations were also influenced by the type of differentiation test (Fig. 4.) resulting in a significant triple ABC interaction ($F_{1;41} = 5.67$, $P < 0.025$). In fact, the click vs tone differentiation resulted in slightly longer latencies in Groups 2 than in Groups 1, both in the "symmetrical" and the "asymmetrical" procedure. On the other hand, the dogs differentiating intensities of the white noise in the "asymmetrical" test showed much longer latencies in Group 2 than in Group 1, whereas in the "symmetrical" test latencies were shorter in Group 2 than in Group 1.

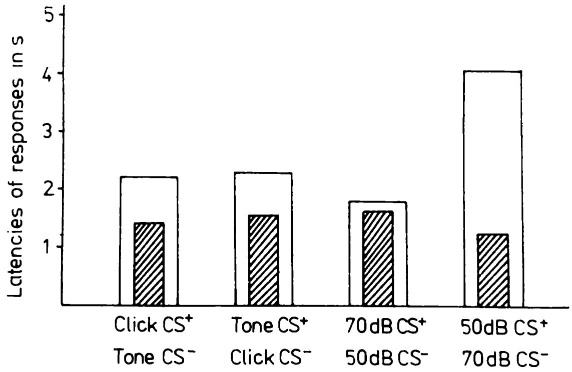

Fig. 4. Interaction among differentiation training, the quality of CSi and the stimulus arrangement, for response latencies to CS+ during the first five consecutive differentiation sessions. Denotations as in Fig. 2.

A relationship between responses latency and the physical strength of CSi was also found. Figure 5 shows the cumulative distributions of response latencies on CS+ trials during criterion sessions of differentiation training separately for each group and experiment. Dogs from Experiments III and IV emitted a larger proportion of short-latency responses to the 70 dB CS+ than to the 50 dB CS+. Similarly, in Experiment II more responses of short latencies occurred to the click CS+ than to the tone CS+. Only in Experiment I, during criterion sessions of the differentiation training, were more short latency responses observed to the tone CS+ than to the click CS+. Two-way Smirnov tests revealed highly significant between-group differences in each

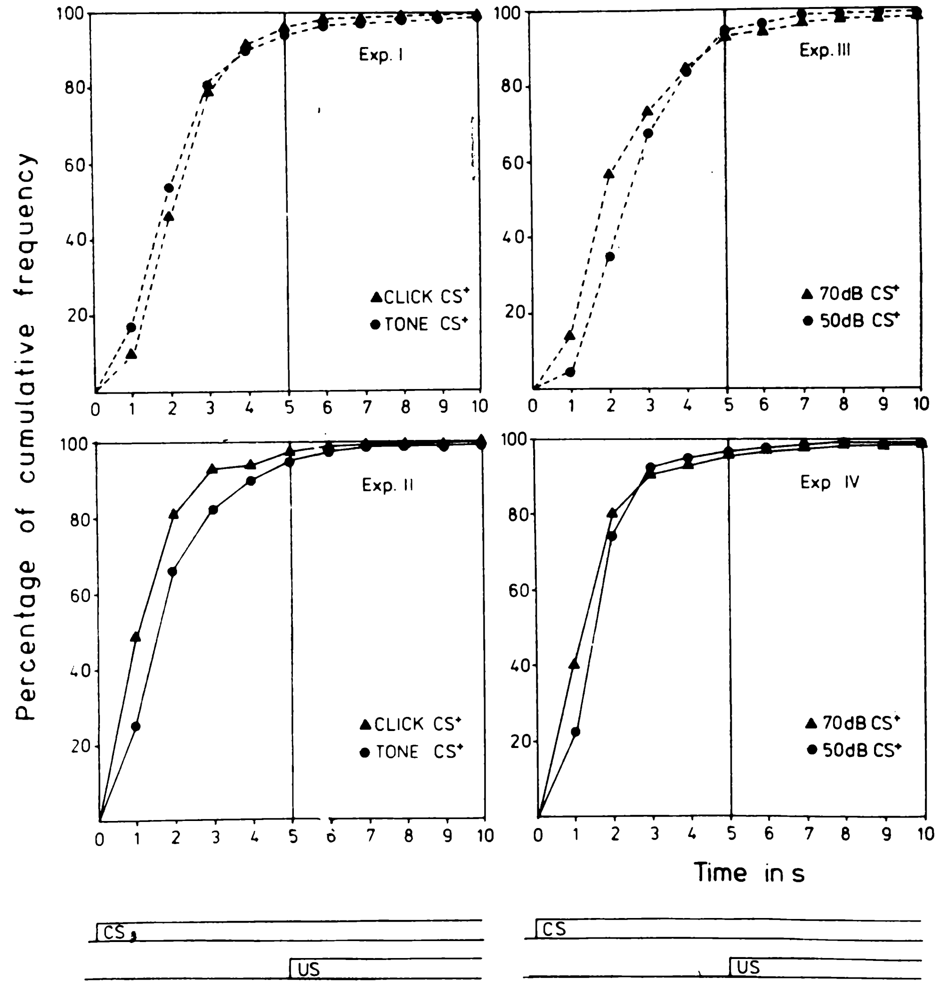

Fig. 5. Cumulative frequency distributions of response latencies to CS+ during criterion sessions of differentiation training. The solid lines refer to the symmetrically reinforced procedure, and the dotted lines indicate the asymmetrically reinforced procedure.

experiment (Table IV). Data from both Fig. 5 and Table IV support the finding that the dogs trained under the "symmetrical" procedure emitted more short latency responses than dogs trained with asymmetrical reinforcement. Due to this result, the points of maximal differences between distributions of responses latencies to different stimuli were located among shorter latencies for "symmetrical" than for "asymmetrical" differentiation.

TABLE IV

Between group comparisons of the distributions of response latencies on CS$^+$ trials during criterion sessions of differentiation training. Denotations as in Table II.

	Size of samples	Difference	$D_{\max}$	Point of $D_{\max}$ in s
Exp. I Asymmetrical	$n_1 = n_2 = 800$	$S_{\text{Click}} < S_{\text{Tone}}$	0.140***	1.3
Exp. II Symmetrical	$n_1 = n_2 = 700$	$S_{\text{Click}} > S_{\text{Tone}}$	0.236***	1.1
Exp. III Asymmetrical	$n_1 = n_2 = 500$	$S_{70\text{dB}} > S_{50\text{dB}}$	0.238***	1.5
Exp. IV Symmetrical	$n_1 = 500$, $n_2 = 400$	$S_{70\text{dB}} > S_{50\text{dB}}$	0.192***	1.1

*** $P < 0.001$ (Smirnov Test)

The dependence of the speed of responses on the physical strength of stimuli was even more evident for disinhibited responses on CS$^-$ trials. Figure 6 shows cumulative latency distributions of bar-presses emitted to negative CSi for the entire course of differentiation training. The diagonal straight lines in the four panels of the Fig. 6 represent the hypothetical distributions for the case when the probability of response was the same for each portion of the CS$^-$ action. Expansion of all empirically derived curves above this theoretical line indicates that CS$^-$ onset increased the probability of instrumental responses. Similarly to responding on positive trials, responses to CSi$^-$ were performed with shorter latencies under the "symmetrical" than under the "asymmetrical" procedure. Independent of the differentiation test, a greater proportion of responses in the first seconds was performed to the click CS$^-$ than to the tone CS$^-$, and to the 70 dB CS$^-$ than to the 50 dB CS$^-$. The differences between each empirical distribution and theoretical distribution (Kolmogorov Goodness of Fit test, two-tailed) and between the two empirical distributions within each experiment (Smirnov two-tailed test) were statistically significant (Table V).

The behavior of the dogs. At the beginning of differentiation training, CS$^-$ onset evoked orienting responses that eventually habituated. The inability to terminate the CS$^-$ action resulted in the reappearance of the anxiety syndrome in all subjects. Some of dogs trained in asymmetrically reinforced differentiation (Exp. I and III) increased the frequency of bar-press responses at the very beginning of differentiation training. In two dogs from Experiment I a violent increase of emotional responses (whining, squeaking and running) was observed, which

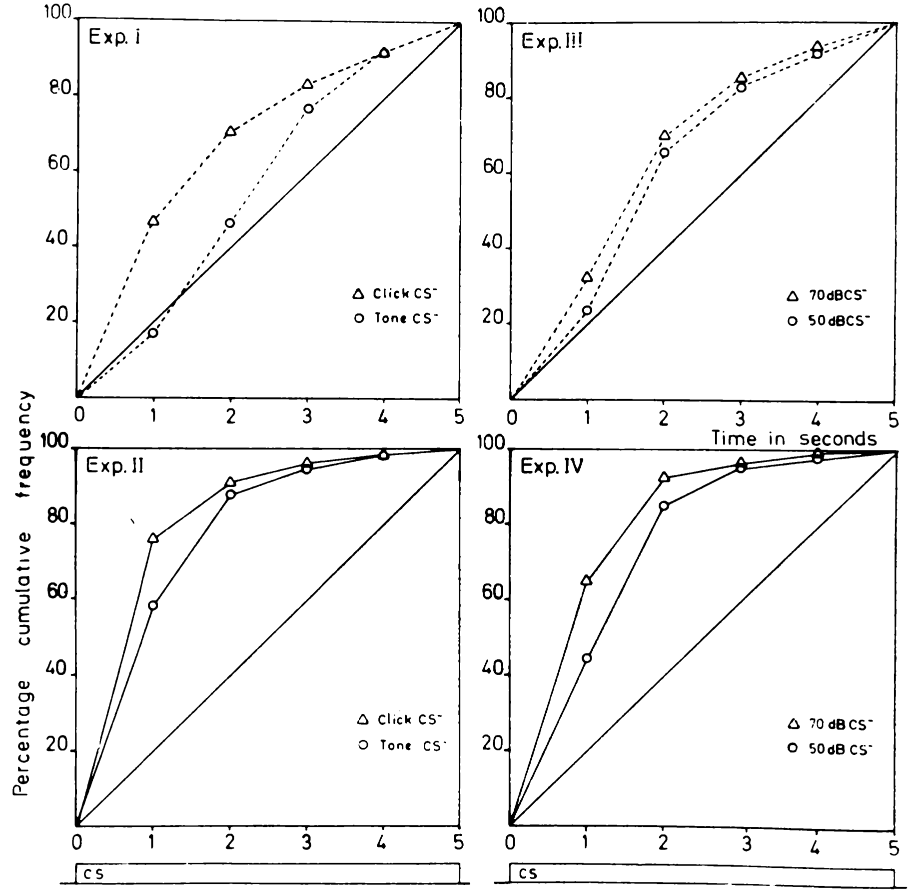

Fig. 6. Cumulative frequency distributions of the latencies of bar-pressing response to CS— during the entire differentiation training. Denotations as in Fig. 5.

extinquished after several presentation of CS$^-$. Gradually, the dogs calmed and stayed quietly in the harness or sat near the pedal. Errors to CS$^-$ as a rule consisted of emission of a single bar-press response. The emotional excitability of dogs trained with symmetrical reinforcement was even stronger. Punishment of instrumental responses to the CS$^-$ resulted in enhancement of defensive responses, similar to the behavior observed at the very begining of avoidance conditioning. The increased frequency of instrumental responses was noted not only to CS$^+$ and CS$^-$, but also during intertrial intervals. On the other hand, shock punishment of each bar-press response to CS$^-$ caused the withholding of instrumental responses even during the CS$^+$ action. Accordingly, at the beginning of differentiation training performance

TABLE V

Between group comparisons of the cumulative frequency distributions of response latencies on CS$^-$ trials in differentiation training. Denotations as in Table II

	Size of samples	Difference	$D_{\max}$	Point of $D_{\max}$ in s
Exp. I Asymmetrical	$n_1 = 78$ $n_2 = 219$	$S_{Tone} > S_{Theoret.}$	0.169*	2.9
		$S_{Click} > S_{Theoret.}$	0.307**	1.7
		$S_{Click} > S_{Tone}$	0.299***	0.9
Exp. II Symmetrical	$n_1 = 703$ $n_2 = 989$	$S_{Tone} > S_{Theoret.}$	0.502**	1.5
		$S_{Click} > S_{Theoret.}$	0.573**	1.1
		$S_{Click} > S_{Tone}$	0.259***	0.5
Exp. III Asymmetrical	$n_1 = 853$ $n_2 = 1608$	$S_{50dB} > S_{Theoret.}$	0.260**	1.7
		$S_{70dB} > S_{Theoret.}$	0.297**	2.1
		$S_{70dB} > S_{50dB}$	0.084***	0.9
Exp. IV Symmetrical	$n_1 = 1102$ $n_2 = 938$	$S_{50dB} > S_{Theoret.}$	0.454***	1.7
		$S_{70dB} > S_{Theoret.}$	0.554***	1.5
		$S_{70dB} > S_{50dB}$	0.300***	0.5

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$ (Kolmogorov or Smirnov Tests)

fluctuated from responding to both CSi to complete inhibition of responding. Abortive responses to both CSi were also observed. By the end of training there were no important differences in the behavior observed from dogs trained with asymmetrical or symmetrical reinforcement.

CONSOLIDATION OF DIFFERENTIATION

An analysis of variance (Table VI) showed that the crucial factors affecting the speed of reaching the retention criterion were the type of differentiation test and the quality of stimuli. During retention testing the dogs trained with symmetrical reinforcement reached the criterion more rapidly than did the dogs trained with asymmetrical reinforcement, whereas during original differentiation training the effect of the type of differentiation task on the speed of learning was not significant (see Table III). Table VI also shows that dogs trained with the two intensities of white noise required more trials to the retention criterion and committed a higher percentage of errors on negative trials than did dogs that discriminated between click and tone stimuli. The number of trials to criterion and the percentage of errors to CS$^-$ were also influenced by the joint action of the type of differentiation test and the quality of CSi. Among the dogs trained with symmetrical reinforcement, only small differences between groups were

TABLE VI

Mean values of performance indices during testing of the differentiation retention

Differentiation task	Number of trials to criterion		Percentage of CS+ trials with errors		Percentage of CS− trials with errors	
	CS+:Click	CS+:Tone	Click	Tone	Tone	Click
Asymmetrical (Exp. I)	310	200	3.4	1.5	8.6	2.2
Symmetrical (Exp. II)	212	202	1.7	5.4	5.6	2.7
	CS+:70 dB	CS+:50 dB	70 dB	50 dB	50 dB	70 dB
Asymmetrical (Exp. III)	352	548	3.9	2.6	13.9	21.5
Symmetrical (Exp. IV)	200	224	1.2	3.2	5.8	5.4

Source of variation	*df*	Values of F statistics		
Differentiation task (A)	1;41	7.253*	< 1	2.368
Quality of stimuli (B)	1;41	5.099*	< 1	14.816***
Stimulus arrangement (C)	1;41	< 1	< 1	< 1
AB	1;41	4.356*	3.215	6.059*
AC	1;41	< 1	5.623*	< 1
BC	1;41	4.309*	< 1	3.214
ABC	1;41	1.572	< 1	< 1

* $P < 0.05$; *** $P < 0.001$

observed, whereas the dogs trained with asymmetrical reinforcement required more trials to criterion and committed more errors on CS− trials, especially in the case of white noise intensity differentiation.

It is worthwhile to note that at this stage of the experiments, in addition to the main effect of the quality of stimuli on the number of trials to criterion, an interaction between the quality and the arrangement of stimuli was also observed. In Groups 1 the mean number of trials to retention criterion was the same for both qualities of stimuli. Dogs differentiating intensities of white noise had more prolonged training in Groups 2 than in Groups 1, quite opposite to the dogs differentiating tone and click. Accordingly, the criterion was reached most rapidly by dogs that differentiated tone CS+ and click CS− as a result of the fewer number of errors to the CS−, but this kind of interaction for the percentage of CS− trials with errors did not reached statistical significance. For the percentage of errors made on CS+ trials, the significance of the interaction between the quality of stimuli and the type of differentiation task indicates that during "asymmetrical" training more errors were observed in Groups 1, whereas during "symmetrical" differentiation more errors to CS^+ appeared in Groups 2.

The joint effect of the quality of stimuli and the differentiation task also influenced the E + ITR index. Similar to the previous stage of experiment for those dogs differentiating between the tone and the click, this index was higher under "symmetrical" training, whereas for dogs differentiating white noise intensities, the higher values of this index were observed in "asymmetrical" training (AB interaction: $F_{1;41} = 8.55$, $P < 0.001$).

Similar to original differentiation training on the criterion reacquisition trials, the latencies of instrumental responses to CS^+ were shorter in symmetrically than in asymmetrically reinforced training ($F_{1;41} = 5.31$, $P < 0.05$).

Significant changes in behavior were not observed after the control pause. The dogs continued their earlier acquired sterotypes of responding. Only one dog from Experiment I (Group 1) showed the typical syndrome of the experimental neurosis state (13). It was restless, resisted entering the chamber, trembled and defecated. These manifestation were accompanied by enhance responding on negative trials. After 29 retraining sessions it was decided to discontinue training of this dog for ten days. Normal behavior of this dog in the homecage soon recovered, and when training was renewed, it reached the criterion after an additional 18 sessions.

DISCUSSION

Although data reported in this paper were derived from four separate experiments, identical experimental designs and the possibility of recalculation of the data using the same criteria allowed joint examination of the results. We believe that such multifactorial analyses may throw some light on the mechanisms of acquisition, consolidation and extinction of defensive conditioned reflexes. Our first concern was the effects of the reinforcement procedures on the course of go, no-go differentiation tasks. However, these effects interacted both with the quality of stimuli and the relative saliency of CS^+ and CS^-. Moreover, these interactions changed in the course of training.

Generalization between CS^+ and CS^-

Inspection of the tables presented in this paper indicate that at all stages of differentiation training a large portion of variance in most measures was controlled by the quality of stimuli variable. This factor had no influence on the rapidity of original acquisition of the avoidance response, indicating that all stimuli used in the experiments were equally discriminable from the background. The dogs differentiating the intensities of white noise required longer training and committed more errors to CS^+ and to CS^- than the dogs differentiating the click and the tone. These differences were related to the amount of generalization between CS^+ and CS^-. This conclusion is supported by many experimental results showing more difficult discriminations when physically similar CSi have been used (1, 17, 29, 31, 32). However, all of these studies employed go, no–go differentiation tasks with asymmetrical reinforcement. Our data clearly indicate that the influence of CSi quality on the rapidity of differentiation learning and numbers of errors to CS^- was strongly attenuated in the case of the go, no–go differentiation with symmetrical reinforcement. This effect was documented by significant interactions between the type of differentiation task and the quality of stimuli on number of trials to criterion and the percentage of CS^- trials with errors. Group means for most of the measures influenced by this interaction showed that the punishment of errors on CS^- trials increased the number of trials to criterion, the number of errors and the $E + ITR$ index only when easily discriminable stimuli (click vs. tone) were used, conversely punishment of errors to CS^- shortened the length of training when difficult discriminable stimuli (50 dB vs. 70 dB white noise) were employed.

Before attempt to explain this effect of reinforcement procedure, some important information must be recalled. At the beginning of differentiation training a much larger proportion of the errors to CS^- was committed by dogs trained in "symmetrical" than in "asymmetrical" differentiation independent of the quality of CSi and the relations between their relative saliency. In effect the percentage of CS^- trials with errors was significantly higher in dogs trained in the "symmetrical" task even if the number of trials to acquisition criterion was lower than in dogs trained with the same stimuli under the "asymmetrical" procedure. The reinforcement procedure also exerted a main effect on the latencies of responses. Both on CS^+ and on CS^- trials responses were performed with shorter latencies when differentiation with symmetrical reinforcement was employed. Moreover, the level of intertrial responding was higher in the "symmetrical" than in the "asymmetrical" differentiation task. All of these data indicate that the introduction of shock punishment of bar-pressing responses emitted in the presence of CS^- leads to a strong increase of the fear level in animals.

The following mechanism of acquisition and consolidation of instrumental defensive responses may be proposed. At the beginning of training, when only CS$^+$ trials were employed, the dogs learned that the CS$^+$ signals painful shock which has to be either avoided or terminated by the escape response. Thus, the CS$^+$ acquires fear-evoking properties according to the rules of classical conditioning. Termination of the CS$^+$ action has a positive secondary reinforcing effect on the instrumental response. For this reason the dogs emitted the majority of instrumental responses during the two initial seconds of the CS–US interval. At the beginning of the differentiation training the CS$^-$ introduced to the experimental situation acquired aversive features due to generalization from the CS$^+$. In effect instrumental responses on negative trials appeared. However, inability to terminate the CS$^-$ by the instrumental response is in fact a punishment of this reaction (2, 3, 37, 38, 48), and increases the fear drive conditioned both to the whole experimental situation, evidenced by more numerous ITRs, and to the CSi resulting in an enhancement of generalization from CS$^+$ to CS$^-$. Similar symptoms have also been observed in dogs trained in type of partial reinforcement procedure, in which only one CS was used not terminated by the instrumental escape or avoidance response on some proportion of trials (49).

These processes were even more intense in the case of go, no–go differentiation with symmetrical reinforcement. In addition to the introduction of a CS$^-$ of fixed duration, under this reinforcement procedure each bar press executed during the CS$^-$ action was punished by the application of shock. The appearance of the aversive US (which had occurred previously only on positive trials) in contiguity with the responses emitted during the action of CS$^-$ resulted in greatly increased defensive behavior. Besides observations of dogs behavior this effect was evidenced by even stronger shortening of response latencies to CS$^+$ and CS$^-$ in the "symmetrical" than in "asymmetrical" differentiation task. In effect, generalization between positive and negative trials is also more intense, and at the beginning of "symmetrical" differentiation many instrumental responses on negative trials appeared. They occurred in series and sometimes one of them coincided with the end of CS$^-$ action, providing an incidental positive reinforcing effect, which made the extinction of instrumental responses on negative trials more difficult.

The above stated considerations provide explanations of the main effects of the type of go, no–go differentiation task on the latencies of instrumental responses, the percentage of disinhibited CS$^-$ trials and the frequency of ITRs. Although influencing all of differentiation learning, these differences between "symmetrical" and "asymmetrical" procedures were especially visible at early stages of training.

Both secondary (i.e., prolongation of the CS$^-$ action after bar-pressing response) and primary (i.e., application of shock when the instrumental response to the CS$^-$ is executed) punishments are responsible for the withholding of instrumental responses on CS$^-$ and acquisition by this stimulus of inhibitory properties. At early stages of training this inhibition in some cases generalized on positive trials and resulted in the temporary disappearance of avoidance responses. Therefore the punishment of responses to CS$^-$ occurring at the beginning of differentiation learning quite often made discrimination between positive and negative trials even more difficult.

To solve the task the dogs had to discriminate two CSi, differentiate contingencies related to the CS$^+$ and CS$^-$, and adjust their behavior on positive and negative trials. At the stage when the dogs began to discriminate CSi and relate the contingencies with them, both secondary and primary punishments of responding to CS$^-$ had quite opposite effects than previously. The application of shock on CS$^-$ trials in the symmetrically reinforced procedure, initially resulting in an enhancement of generalization between CS$^+$ and CS$^-$, then helped in breaking out the pattern of responding to CS$^-$, and accelerate process of extinction of bar-pressing in presence of the CS$^-$. These two opposite effects on differentiation learning canceled each other and only measures reflecting the emotional state of the dogs (i.e., the latencies of responses, the E + ITR index, percent of errors on negative trials) showed significant main effects of the type of differentiation task.

The main effects of the quality of CSi on the percentages of errors to CS$^+$ and CS$^-$ and on rapidity of differentiation training are readily explained by the fact that the discrimination of the two intensities of white noise is more difficult than between click and tone.

Primary and secondary negative reinforcement

The amount of secondary punishment is related to characteristics of the CS$^-$, and depends on the quality of stimuli used in experiments. It should be recalled that on the stage of avoidance response acquisition, the quality of CS$^+$ influenced the latencies of instrumental responses. Taking into account dogs trained in the same experimental situation the shortest latencies were observed to the click and the longest to the 50 dB white noise. A similar dependency has been shown previously in cats trained with either click or tone (50) or with different intensities of white noise (19, 43–46, 48). It has to be noted that differences in quality of CSi are confounded by differences in their physical intensity. During differentiation learning the reflexogenic strength of a stimulus depends not only on its physical features but also on the relative saliency of the CS^+ and CS^-, labelled in this paper as the stimulus arrangement. In many studies it has been shown that differentiation learning is easier when the CS^+ is more salient than the CS^-, and conversely, is more difficult when the stimulus arrangement is in reversed order (18, 25, 29, 30, 33–36, 42, 50, 51). And again all of these studies employed go, no–go differentiation tasks with asymmetrical reinforcement. Our data indicate that in the case of go, no–go differentiation with symmetrical reinforcement the length of training was not influenced by the relative saliency of CSi of different quality (26) or intensity (Experiment IV of the present study).

Our explanation of the significant interaction between the quality of stimuli and the type of differentiation task is based on the assumption that the fear-evoking properties of the CS^- are directly related to the saliency of the CS^-. The saliency of CS^-, or more exactly the reflexogenic strength of the CS^- used in differentiation training, depends not only on its physical intensity but also on the amount of generalization to the CS^- from the CS^+. This last reason is the main confounding factor between the quality of stimuli and their physical intensity in any go, no–go differentiation situation. Thus, the similarity between CS^+ and CS^-, and in addition, the higher CS^- intensity than that of the CS^+, increases the reflexogenic strength of CS^- evoking a larger increase of the fear state resulting in the execution of a greater number of bar-presses to the CS^-, compared to the situation in which CS^+ and CS^- are easily discriminable and the CS^- is less intense than the CS^+. The fear-evoking properties of the CS^-, which action is not controlled by animals' behavior, is in the "asymmetrical" task the only factor increasing the level of fear. This factor explains why the similarity between CS^+ and CS^- has a great importance in the case of go, no–go differentiation with asymmetrical reinforcement. Such an effect, although evident, is strongly attenuated in the case of go, no–go differentiation with symmetrical reinforcement, in which punishment of errors to CS^- with application of the shock US plays a dominant role. Thus, significant interactions between the type of differentiation and the quality of stimuli on such measures as the E + ITR index, the percentage of errors on CS^- trials, and the rapidity of differentiation learning may be easily explained when we took into account the roles played by primary and secondary punishments for extinction of the instrumental responses emitted to the CS$^-$ in the "symmetrical" and in the "asymmetrical" tasks.

The above discussion raises an important problem concerning the meaning of symmetrical and asymmetrical reinforcement contingencies in the case of go, no–go differentiation of defensive instrumental reflexes. Previous analyses of the mechanisms underlying the two tests emphasized the contingency between the instrumental response and the application of the unconditioned stimulus on negative trials in the "symmetrical" task and the lack of such a contingency in the "asymmetrical" task (47, 48). From this point of view a full analogy exists between differentiation of alimentary and defensive instrumental reflexes. However, not only the USi and their innate reinforcing values, but also acquired secondary reinforcements play important roles in learned behavior. In the case of defensive reflexes the execution of an instrumental response has no effect on the termination of the fear-evoking CS$^-$ either in asymmetrical or in symmetrical go, no–go differentiation tasks. In this respect both procedures of go, no–go differentiation of instrumental reflexes do not differ from the go, no–go differentiation of classically conditioned defensive reflexes. In all of these tests prolongation of the action of the fear-evoking CS$^-$ denote secondary punishment of the response performed during the CS$^-$ action.

This very aspect was emphasized by Dąbrowska in her discussion of the mechanisms of instrumental defensive reflex differentiation (11). She preferred to consider both types of go, no–go differentiation of defensive instrumental reflexes as "symmetrically" reinforced tasks. Our data indicate that the strength of the secondary punishing effect of the CS$^-$ prolongation is dependent on the reflexogenic properties of the CS$^-$. Therefore, if responses emitted to the CS$^-$ are not punished by the painful US, the extent to which go, no–go differentiation of defensive reflexes may be considered as "symmetrical" depends on the secondary punishing effect of the prolongation of CS$^-$ action. Accordingly, such factors as the amount of generalization from CS$^+$ to CS$^-$, the saliency of the CS$^-$, and the latency of instrumental responses emitted to the CS$^-$ of fixed duration play a role for differentiation learning. Since all of these factors change in the course of extinction of the generalized fear response on negative trials, the "symmetry" of the task is not the same at the beginning and toward the end of the go, no–go differentiation of defensive instrumental reflexes.

The role of secondary reinforcing (punishing) effects in differentiation tests calls for more detailed examination. Before it will be done we prefer to base our classification of go, no–go differentiation tasks on the contingencies between the conditioned response and the occurrence of the US (47, 48).

The stability of differentiation

The behavior of the dogs after the control pause when differentiation retention was tested, provide additional arguments in favor of the above considerations. Nearly all of the dogs (20 out of 23) trained in "symmetrical" differentiation reached the retention criterion in a minimal number of trials, whereas such behavior was observed less frequently among dogs trained in "asymmetrical" differentiation (14 out of 26). Thus, independent of the length of original training, differential responding was more consolidated when "symmetrical" reinforcement was employed.

The retention of the differentiation is better when dissimilar stimuli have been employed. This was evidenced not only in the number of trials to the retention criterion but even more strongly in the percentage of disinhibited CS^- trials. Since the quality of stimuli effect was markedly attenuated when "symmetrical" reinforcement procedure was employed, one may infer that punishment of the bar-presses emitted to the CS^- helps to overcome generalization from CS^+ to CS^-. The smaller percentage of errors on CS^- trials committed after the control pause by dogs trained in go, no–go differentiation with symmetrical reinforcement reflects influences which were in action at the end of original differentiation training. While the main effect of the quality of stimuli was the same for acquisition and retention, the main effect of the type of differentiation task on the number of trials to criterion and the percentage of errors to CS^- was quite opposite at these two stages of the experiments. This finding provides the main reason for the introduction of the control pause into design of the present experiments, which was to attempt to reveal factors that influenced last phases of original differentiation training.

The effect of stimulus arrangement was observed only during retention testing, resulting in a significant interaction with the quality of the stimuli (on the number of trials to criterion measure) and with the type of differentiation task (on the percentage of CS^+ trials with errors). Among dogs differentiating intensities of the white noise, those in Groups 1 (CS^+ more intense than CS^-) regained the criterion more rapidly than those in Groups 2 (CS^+ less intense than CS^-), whereas in the case of tone and click differentiation Groups 1 required more training to reach reacquisition criterion than Groups 2. The dogs differentiating tone CS^+ and click CS^- reached the criterion in the minimal number of trials. This interaction is easily explained by the fact that similar relations, although not significant, were observed between the stimulus arrangement and the quality of stimuli on the percentage of errors on CS^- trials. The smallest percentage (and the absolute number) of errors to the click CS^- after the control pause, similar to the smallest number of trials to reacquisition criterion in dogs trained with the tone CS^+ and the click CS^-, might be due to the strongest secondary punishing effect of errors committed to this reflexogenic CS^- in original differentiation learning.

The percentage of errors of omission on positive trials observed during the retraining phase of the experiments was dependent on the inhibitory influences exerted by the CS^- on the CS^+. The significant interaction of the type of differentiation task and the stimulus arrangement on this measure should be expected.

The arousing and signalling properties of stimuli

At the end of this discussion it should be recalled that the complex interplay of signalling and arousing properties of stimuli, both conditioned and unconditioned, is the most characteristic feature of differentiation learning. The signalling properties of the CSi used in differentiation learning depend on many factors: their discriminability from the background, the physical differences between CSi, the contingencies between each CS and the US, the consequencies of the performance of learned responses on stimuli action, etc. Any difference between the physical properties of the CSi or between the effects elicited by them in the central nervous system possesses information value and may be used by a subject. Different levels of arousal evoked by more or less intense stimuli, otherwise identical, may be the basis for the animal's classification of stimuli. If the stimuli differ in many aspects, their discrimination is easier. However, the difficulty of differentiation learning is not a simple function of the discriminability of CSi depending on their physical properties. The contingencies between CSi and US, the relationships among CSi, US and the conditioned response imposed by the conditioned procedure, play an important role. The information about contingencies employed may be obtained only when a subject emitted different behaviors during consecutive presentations of the same stimulus. Analysis of "errors" distribution may give valuable data on the strategy by which a subject recognize contingences within a given task.

The present study showed that the difficulty of differentiation learning involving the same pair of CSi depends on the contingencies employed on CS^- trials. The comparison of the course of go, no-go differentiation learning with symmetrical and asymmetrical reinforcement procedures provides strong support for the necessity to distinguish between the two processes: the discrimination of stimuli and their differentiation. According to Konorski (21) differentiation is a process by which discriminated stimuli are utilized for differential responding of the organism.

The contingencies related to the CSi may have an effect on measures of the discriminability of stimuli. When more salient stimulus from a pair is used as the CS^+, the amount of generalization exerted on the CS^- is less and differentiation training is easier than with the opposite stimulus arrangement (18, 42, 51). Different efficacy of reinforcement, depending on the salienty relations between the two conditioned stimuli, bears on the problem labelled as constraints of conditioning. In light of the present discussion the effects of the stimulus arrangement and the stimulus quality factors illustrate how the signalling properties and arousing values of stimuli interact in the course of differentiation learning.

REFERENCES

1. BLACKWELL, M. R. and SCHOLSBERG, M. 1943. Octave generalization, pitch discrimination, and loudness thresholds in the white rat. J. Exp. Psychol. 33: 407–419.
2. BREGADZE, A. N. 1953. On the question of elaboration of conditioned defensive reflex in dogs (in Russian). Tr. Inst. Fiziol. I. S. Beritashvili. 9: 43.
3. BREGADZE, A. N. and AKHMETELI, M. N. 1953. Elaboration of defensive reflex in guinea pigs (in Russian). Tr. Inst. Fiziol. I. S. Beritashvili 9: 61.
4. BRUTKOWSKI, St. 1967. A cortico-subcortical system controlling differentiation ability. *In* E. A. Asratyan (ed.), Brain reflexes. Elsever Publ. Co., Amsterdam, 265–272. Prog. Brain Res. 22.
5. BRUTKOWSKI, St. and DĄBROWSKA, J. 1963. Disinhibition after prefrontal lesions as a function of duration of intertrial intervals. Science 139: 505–506.
6. BRUTKOWSKI, St. and DĄBROWSKA, J. 1966. Prefrontal cortex control of differentiation behavior in dogs. Acta Biol. Exp. 26: 425–439.
7. BRUTKOWSKI, St., MISHKIN, M. and ROSVOLD, M. E. 1963. Positive and inhibitory motor conditioned reflexes in monkeys after ablation of orbital or dorso-lateral surface of the frontal cortex. *In* L. Gutman, P. Hnik (ed.), Central and peripheral mechanism of motor functions. Proceedings of the Conference held at Liblice near Prague, May 15–21, 1961. Czechoslovak Academy of Sciences, Prague, 133–141.
8. CONOVER, W. J. 1971. Practical nonparametric statistics. John Willey and Sons, New York.

9. DĄBROWSKA, J. 1971. Dissociation of impairment after lateral and medial prefrontal lesions in dogs. Science 171: 1037–1038.
10. DĄBROWSKA, J. 1972. On the mechanism of go–no go symmetrically reinforced task in dogs. Acta Neurobiol. Exp. 32: 345–359.
11. DĄBROWSKA, J. 1975. Prefrontal lesions and avoidance reflex discrimination in dogs. Acta Neurobiol. Exp. 35: 1–15.
12. DĄBROWSKA, J. and SZAFRAŃSKA-KOSMAL, A. 1972. Partial prefrontal lesions and go–no go symmetrically reinforced differentiation test in dogs. Acta Neurobiol. Exp. 32: 817–834.
13. FONBERG, E. 1958. Transfer of instrumental avoidance reactions in dogs. Bull. Acad. Pol. Sci. Ser. Sci. Biol. 6: 353–356.
14. GELLERMAN, L. N. 1933. Chance orders of alternating stimuli in visual discrimination experiments. J. Gen. Psychol. 42: 206.
15. GROSS, C. G. and WEISKRANTZ, L. 1962. Evidence for dissociation between impairment of auditory discrimination and delayed response in frontal monkeys. Exp. Neurol. 5: 453–476.
16. GROSS, C. G. and WEISKRANTZ, L. 1964. Some changes in behavior produced by lateral frontal lesions in the macaque. *In* J. M. Warren, K. Akert (ed.), The frontal granular cortex and behavior. McGraw-Hill Book Co., New York, p. 74–101.
17. HANSON, H. M. 1959. Effects of discrimination training on stimulus generalization. J. Exp. Psychol. 58: 321–334.
18. JAKUBOWSKA, E. and ZIELIŃSKI, K. 1976. Differentiation learning as a function of stimulus intensity and previous experience with the CS$^+$. Acta Neurobiol. Exp. 36: 475–516.
19. JAKUBOWSKA, E. and ZIELIŃSKI, K. 1979. Avoidance acquisition in cats as a function of temporal and intensity factors. Acta Neurobiol. Exp. 39: 67–86.
20. KONORSKI, J. 1948. Conditioned reflexes and neuron organization. Univ. Cambridge Press, Cambridge, 267 p.
21. KONORSKI, J. 1967. The integrative activity of the brain. An interdisciplinary approach. Univ. Chicago Press, Chicago, 531 p.
22. KONORSKI, J. 1972. Some ideas concerning physiological mechanism of so-called internal inhibition. *In* R. A. Boakes M. S. Halliday (ed.), Inhibition and learning. Acad. Press, London, p. 341–357.
23. KONORSKI, J. 1972. Some hypotheses concerning the functional organization of prefrontal cortex. Acta Neurobiol. Exp. 32: 595–613.
24. KONORSKI, J. and MILLER, St. 1933. Podstawy fiziologicznej teorii ruchów nabytych. Ruchowe odruchy warunkowe. Książnica-Atlas TNSW, Warsaw, 168 p.
25. KOWALSKA, D., DĄBROWSKA, J. and ZIELIŃSKI, K. 1975. Effects of partial prefrontal lesions in dogs on go–no go avoidance reflex differentiation and reversal learning. Acta Neurobiol. Exp. 35: 549–580.
26. KOWALSKA, D., DĄBROWSKA, J. and ZIELIŃSKI, K. 1975. Retention of symmetrical go–no go avoidance differentiation after prefrontal lesions in dogs. Bull. Acad. Pol. Sci. Ser. Sci. Biol. 23: 487–494.
27. LINDQUIST, E. F. 1953. Design and analysis of experiments in psychology and education. Riverside Press, Cambridge.
28. ŁAWICKA, W., MISHKIN, M. and ROSVOLD, H. E. 1966. Dysocjacja zaburzeń

działalności odruchowo-warunkowej u małp (*Macaca mulatta*) po cząstkowych uszkodzeniach okolicy czołowej mózgu. X Zjazd P. T. Fiz. Lublin, (Abstract) 178–179.

29. MOORE, J. W. 1964. Differential eyelid conditioning as a function of the frequency and intensity of auditory CSs. J. Exp. Psychol. 68: 250–259.
30. PIERREL, R. and SHERMAN, I. G. 1960. Generalization of auditory intensity following discrimination training. J. Exp. Anal. Behav. 3: 313–322.
31. PIERREL, R. and SHERMAN, I. G. 1962. Generalization and discrimination as a function of S^D–S^{Δ} intensity diference. J. Exp. Analysis Behav. 5: 67–71.
32. PIERREL, R., SHERMAN, I. G., BLUE, S. and HEGGE, F. W. 1970. Auditory discrimination: a three-variable analysis of intensity effects. J. Exp. Anal. Behav. 13: 17–35.
33. ROSIC, N., FRONTALI, M. and BIGNAMI, G. 1969. Stimulus factors affecting go–no go avoidance discrimination learning by rats. Communications in Behavioral Biology. 4: 151–156. Abstract No. 12 690 061.
34. SADOWSKY, S. 1966. Discrimination learning as a function of stimulus location along an auditory intensity continuum. J. Exp. Anal. Behav. 9: 219–225.
35. SHEVELEV, I. A. 1961. Effects of physical strenght and signalling value of the visual conditioned stimulus on parameters of motor response in man (in Russian). Tr. Inst. Vyssh. Nervn. Deyat. 6: 12–23.
36. SHEVELEV, I. A. 1963. Differentiation of visual stimuli according to brightness with opposite change of their intensity and signalling value (in Russian). *In* Asratyan E. A. (ed.), Nervnye mechanizmy uslovnoreflektornoĭ deyatelnosti. Izdat. Akad. Nauk SSSR, Moscow, p. 41–48.
37. SOŁTYSIK, S. and ZIELIŃSKI, K. 1962. Conditioned inhibition of the avoidance reflex. Acta Biol. Exp. 22: 157–167.
38. SOŁTYSIK, S. and ZIELIŃSKI, K. 1963. The role of afferent feedback in conditioned avoidance reflex. *In* L. Gutman and P. Hnik (ed.), Central and peripheral mechanism of motor functions. Proceeding of the Conference held at Libice near Prague, May 15–21, 1961. Czechoslovak Academy of Sciences, Prague.
39. VINCENT, S. P. 1912. The function vibrissae in the behavior of the white rat. Behav. Monogr. 1: 81.
40. WYRWICKA, W. 1960. An experimental approach to the problem of mechanism of alimentary conditioned reflex, type II. Acta Biol. Exp. 20: 137–146.
41. WYRWICKA, W. 1966. The effect of flood reinforcement on the level of alimentary excitation. Acta Biol. Exp. 26: 183–191.
42. ZIELIŃSKI, K. 1965. The influence of stimulus intensity on the efficacy of reinforcement in differentiation training. Acta Biol. Exp. 25: 317–335.
43. ZIELIŃSKI, K. 1972. Effects of prefrontal lesions on avoidance and escape reflexes. Acta Neurobiol. Exp. 32: 393–415.
44. ZIELIŃSKI, K. 1972. Stimulus intensity and prefrontal lesion effects on latencies of the bar-pressing avoidance response in cats. Bull. Pol. Sci. Ser. Sci. Biol. 20: 821–826.
45. ZIELIŃSKI, K. 1973. Stimulus intensity dynamism in normal and prefrontal animals. Act. Nerv. Sup. 15: 15–16.
46. ZIELIŃSKI, K. 1974. Changes in avoidance response latencies after prefrontal

lesions in cats: group versus individual data. Acta Neurobiol. Exp. 34: 477–490.

47. ZIELIŃSKI, K. 1976. Konorski's classification of conditioned reflexes: implications for differentiation learning. Activ. Nerv. Super. 18: 6–14.
48. ZIELIŃSKI, K. 1979. Extinction, inhibition, and Differentiation learning. *In* A. Dickinson, R. A. Boakes (ed.), Mechanisms of learning and motivation. Lawrence Erlbaum Ass. Publ., Hillsdale, New Jersey, p. 269–293.
49. ZIELIŃSKI, K., BRENNAN, J. and KOWALSKA, D. 1979. Auditory frequency generalization in normal and prefrontal dogs trained in varietes of active avoidance reflexes. Acta Neurobiol. Exp. 39: 285–311.
50. ZIELIŃSKI, K. and CZARKOWSKA, J. 1973. Go–no go avoidance reflex differentiation and its retention after prefrontal lesions in cats. Acta Neurobiol. Exp. 33: 467–490.
51. ZIELIŃSKI, K. and JAKUBOWSKA, E. 1977. Auditory intensity generalization after CER differentiation training. Acta Neurobiol. Exp. 37: 191–205.

Danuta M. KOWALSKA and Kazimierz ZIELIŃSKI, Nencki Institute of Experimental Biology, Pasteura 3, 02-093 Warsaw, Poland.