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Escape from shock *versus* escape from shock accompanied by a visual stimulus in rats

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Abstract. Two groups of 15 rats each were trained in a shuttle box to escape foot-shock either unsignalled or presented in compound with a visual cue: darkness. The visual cue presented in shock compartment amplifies the behavioral tendency actually prevailing in the response repertory of the rat. During the 1st session the compound enhanced the species-specific flight resulting in shortening of the rat's escape latency. Thereafter, during subsequent sessions, darkness exaggerated resistance to enter the other compartment; thus escape latencies were longer under compounded than under unsignalled procedure. The darkness cue reduces the intertrial response rate relative to the unsignalled group. This latter finding supports the discrimination model of the effect, since the compound helps the animals to discriminate the illuminated "safe" period between trials from the aversive shock period. Our data seem to suggest that the darkness presented synchronously with escapable grid-shock acquires aversive properties.

Key words: two-way escape, visual cue, intertrial responses, anticipation, rat

INTRODUCTION

Under escape procedure the animal is exposed to aversive stimulation, usually painful, which is not preceded by any warning signal and so is by no means avoidable. Pain can be only terminated by the animal's instrumental response. A typical escape response differs from the motor unconditioned nociceptive reflexes. Thus, in the course of escape training the hierarchy of defensive responses is changed: inborn responses are eliminated or weakened, whereas the instrumental response is strengthened. Such factors as biological characteristics of the subject, physical parameters of painful stimulation, pattern of the required response, experimental situation setting - all of these influence the course of training.

The aim of the present study was to find out how a rather weak neutral stimulus, darkness, presented synchronously with shock, would affect escape performance. Any change of the experimental situation may act as an unconditioned arousing stimulus. Moreover, a darkness presented in shock compartment may facilitate flight to the other compartment in which illumination was not changed. A new stimulus given in a compound with shock may help to discriminate the actual shock and non-shock times and/or places, thereby exerting a favorable influence on escape performance.

Studies with Pavlovian conditioning showed that any cue presented simultaneously with shock, does not acquire signalling properties and is not able to elicit the expectation of the shock (Pakovich 1956, Bierbaum 1958, Bitterman 1964, 1965, Smith et al. 1969). Neither the warning signal from avoidance training nor the conditioned stimulus from defensive classical conditioning presented without pain are able to evoke and control the escape response (Ehrman and Overmier 1976). However, associative aspects of a neutral stimulus can not be entirely excluded, since a stimulus consistently paired with shock onset and the contrasting stimulus presented after shock termination may acquire fear-evoking properties.

In the avoidance procedure darkness employed as the warning signal resulted in slower avoidance acquisition and much higher intertrial response (ITR) rate than observed with an auditory warning signal (Zieliński et al. 1991, 1995). Both these effects reflect a low saliency of a darkness stimulus. If a darkness cue accompanying shock helped discriminate the actual shock and other compartment and alter the ITR rate, the discriminative hypothesis postulated above will receive a strong experimental support.

We recently demonstrated that rats given two-way avoidance learning display a kind of anticipatory behavior preceding each next trial. In the first portion of each intertrial interval (ITI), immediately after the avoidance response and termination of the warning signal, the excitation of the animal abruptly subsides and only few, if any, ITR's are emitted. But in the second portion the ITR rate rises gradually up to maximum, as the next signal is expected to occur (Zieliński and Nikolaev 1997). Therefore, in the present study we examined whether a similar temporal discrimination within ITI's will also develop in rats trained to escape electric foot-shock.

Basing on the difference of latencies of escape (shock terminating) responses performed by each rat in the first and the second half of the initial training session, we were able to distinguish between good and poor learners (Savonenko et al. 1999a). The difference between subgroups was preserved in subsequent escape training. We expected that a similar distinction could be made with respect to rats given a compounded escape stimulus, although different dynamics of escape responses might then develop across sessions.

Two groups of rats were trained in a two-way shuttle box. In the unsignalled escape procedure the foot-shock was neither preceded nor accompanied by any discrete stimulus. The other group of rats trained in the compounded escape procedure received darkness stimulus which started and terminated together with the shock. Comparison of learning parameters of the two experimental groups, each trained according to a different procedure, may reveal possible modulatory role of the compound on behaviors elicited by the shock itself.

METHOD

Subjects

In this experiment, the rules established by the Ethical Committee on Animals Research of the Nencki Institute and based on the disposition of the President of Polish Republic were strictly followed.

The experiment was conducted on 30 adult male outbred Möll-Wistar rats bred in the Nencki Institute, experimentally naive, and weighing 320-360 g. Subjects were kept five to a home-cage (43 cm long, 25 cm wide, 18.5 cm high) having food and water available *ad libitum*. A few days before experiments rats were transferred to a room lighted through a large window. A natural light-dark cycle from external illumination was maintained. Rats were trained in the morning or early afternoon in the same order and about the same time each day. Experiments were completed within 50 days of May and June.

Apparatus

The shuttle box apparatus was 62 cm long, 18 cm wide, and 29 cm high with walls of opaque white acrylic. The box was divided in half by a wall with a rectangular (7 cm wide, 10 cm high) opening situated at the grid-floor level which permitted the animal's passage from one side of the shuttle-box to the other. Each compartment was covered with a movable transparent acrylic ceiling and illuminated with a 5 W lamp mounted centrally just below the ceiling. The animal's crossing through the opening was recorded by photocells mounted 4 cm to either side of the central partition, 5 cm above the floor level. The floor of each compartment was made of 16 0.4 cm dia stainless steel bars, distributed 1.5 cm apart parallel to the central partition. The shuttle-box apparatus was placed in a sound-proof dimly lighted room. The subjects' behavior was observed on a TV monitor in an adjoining room, where equipment for automatic programming of the experiment and recording of data was located.

Procedure and groups treatment

Before the experiment, the rats were assigned randomly to two experimental groups (i.e. procedures) of 15 subjects each. One group was trained to escape from shock given without any other change in the experimental situation (Group Esc). The other group was trained to escape from shock accompanied by darkness presented in shock compartment (Group Esc_D). The shock was terminated as soon as the animal moved to the other compartment, or was switched automatically if the rat failed to escape within 30 s.

Each rat was habituated to the situational cues of the apparatus for 10 min on each of two consecutive days. Training started the day after the 2nd habituation session. At the beginning of each session, the rat was placed in the left compartment of the shuttle-box, close to and facing the end wall. The first trial started 20 s later. Each of the five training sessions consisted of 50 trials. The intertrial intervals lasted 14, 20, or 26 s (mean = 20 s) and varied in a mixed order. A 20 s period preceding the first trial of each session was also taken as an intertrial interval. During intertrial intervals subjects were permitted to move in any direction, so they could cross away from or back into the compartment in which they had been previously. The next trial always started in the compartment where the subject was present at the end of the ITI.

The visual stimulus, darkness (D), was provided by switching off the ceiling light. The light was switched on again as soon as the rat left the shock compartment. During intertrial intervals both compartments were illuminated. The unconditioned stimulus (US) for all rats was a nominal 1.6 mA scrambled, pulsed DC shock (10 ms pulse duration, 50 Hz pulse rate) delivered through the grid-floor. If the rat failed to escape within 30 s, the shock was terminated automatically.

Measures

Beginning of each trial, duration of intertrial intervals, termination of a session and latency of each crossing response either terminating a trial or emitted during the intertrial interval were measured with an electronic timer, accurate to 0.01 s.

The measures of behavior were the latency of escape response and the latency of ITR's performed after termination of the trial. Indices of escape performance (mean and median latency) were calculated for each rat, group and session, and cumulative frequency distributions of escape responses were constructed. The Kolmogorov--Smirnov two-sample test was used to compare the cumulative distributions of escape response latencies. The maximum vertical distance (D_{max}) between two cumulative distributions is the statistic allowing an inference about agreement or disagreement of two sets of sample values (Siegel 1956).

Cumulative distributions of escape response latencies for the two groups (i.e. procedures) were compared for each session independently (the sample sizes: $n_1=n_2=750$). Additionally, cumulative distributions of escape response latencies were constructed for the first and the second halves of the 1st session of each subject independently (the sample sizes: $n_1=n_2=25$). The cumulative frequency distribution of escapes for the trials 1-25 will be denoted as S_1 and for trials 26-50 as S_2. The S_1 minus S_2 difference was calculated for each subject. A positive value of the S_1-S_2 difference indicates shortening of escape latency (improvement of escape performance) whereas the negative value denotes lengthening of escape latency (impairment of performance) within a session. The value of the D_{max} between two cumulative within-subject distributions of the 1st session was used to divide rats subjected to a given procedure arbitrarily into subgroup of good learners (these with $D_{max} \geq 10$, $P<0.05$), and subgroup of poor learners (those with $D_{max}<10$, $P>0.05$).

The latency of each ITR performed during the intertrial interval was measured from the moment of termination of the preceding trial. ITRs were collected and analyzed separately for intertrial intervals of 14, 20, and 26 s ITI duration, each divided into consecutive 2 s epochs. The number of ITRs emitted within a given epoch was divided by total duration of the epoch for a group of rats ($n = 15$), days of training ($n = 5$) and number of corresponding ITIs within a session ($n = 17$). This measure was labeled ITR rate (number of crosses per min of the particular ITI duration).

A rejection criterion of $P<0.05$ was used for all statistical analyses. Statistical calculations were made using the package STATISTICA 5.0 for Windows.

RESULTS

Effects of procedure on escape latency

Mean and median escape latencies for each session are presented in Fig. 1 for Group Esc (left panel) and for Group Esc_D (right panel). Median latencies were shorter than the means for all groups and sessions indicating positively skewed distributions of response latencies due to a low rate of long escape latencies. Rats from the Group Esc started training with long escape latencies which shortened across sessions. In contrast, escape latencies in the Group Esc_D were shorter initially and did not change markedly over the course of training. A 2 (procedures) x 5 (sessions) ANOVA for repeated measures of median escape latency showed no effect of procedure, $F_{4,28} = 0.39$, $P=0.53$; effect of session, $F_{4,112} = 10.19$, $P<0.001$; and no significant interaction, $F_{4,112} = 1.92$, $P=0.11$. Post-hoc Newman-Keuls tests revealed that in Group Esc the median latency of the 1st session differed from the median latency of each successive session ($P<0.001$), whereas in the Group Esc_D no differences between sessions were noted.

To determine whether the differences between the two procedures were limited to the short-, the long-latency, or to both classes of escape responses, the cumulative distributions of escape response latencies for the two groups were compared for each session independently. As seen from Fig. 2, during the 1st session the escape responses were stochastically shorter in Group Esc_D than those emitted by rats in Group Esc ($P<0.001$, Kolmogorov-Smirnov two sample test). The distributions differ after 1 s shock action with the $D_{max}=-0.13$ located at the 2.0 s point. The stability of the localization of the D_{max} during the 1st session was additionally tested for the 1-25 and 26-50 trial blocks and was found at the 2.0 s and at 2.5 s points, respectively (P's<0.02).

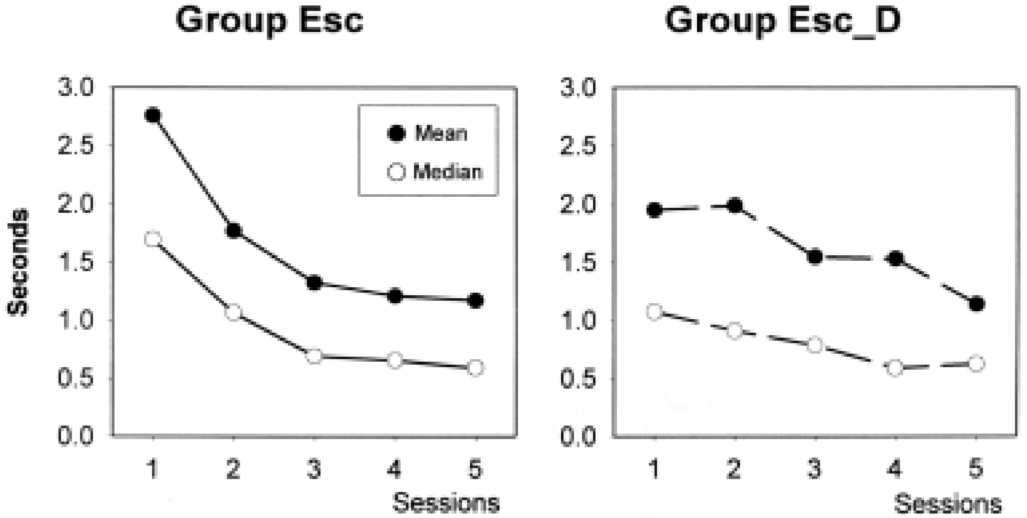

Fig. 1. Mean and median escape latency for Group Esc (left panel) and Group Esc_D (right panel) in consecutive training sessions.

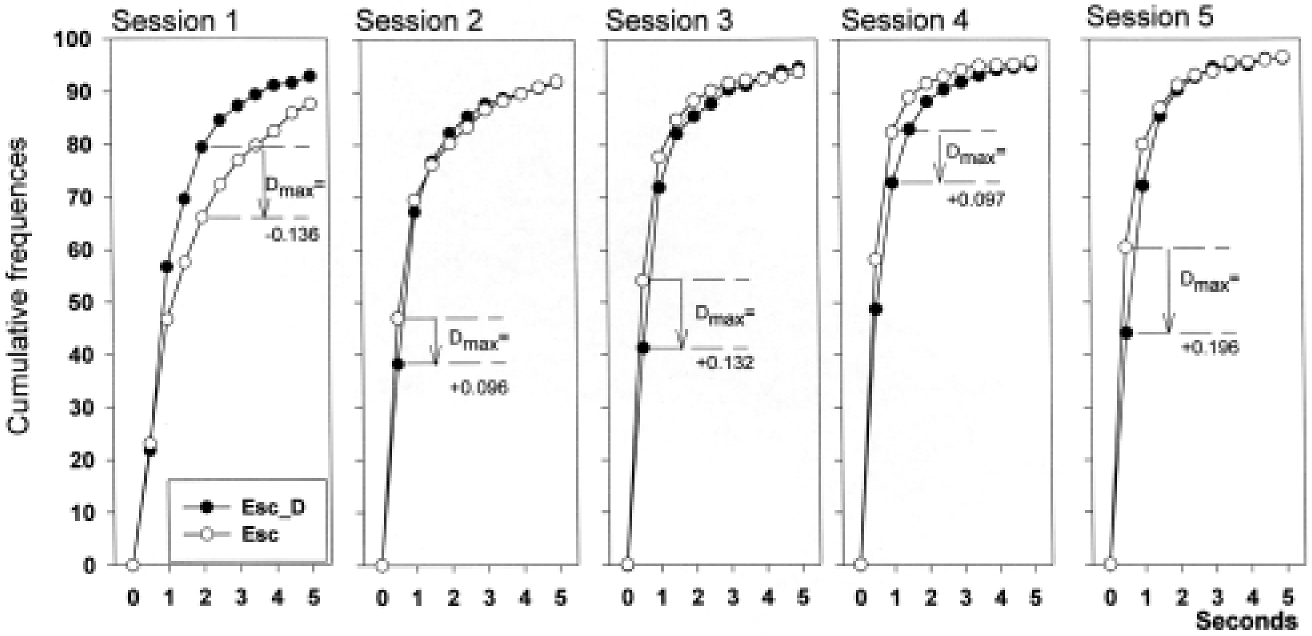

Fig. 2. The cumulative distributions of escape latencies emitted by Group Esc and Group Esc_D in consecutive sessions of training.

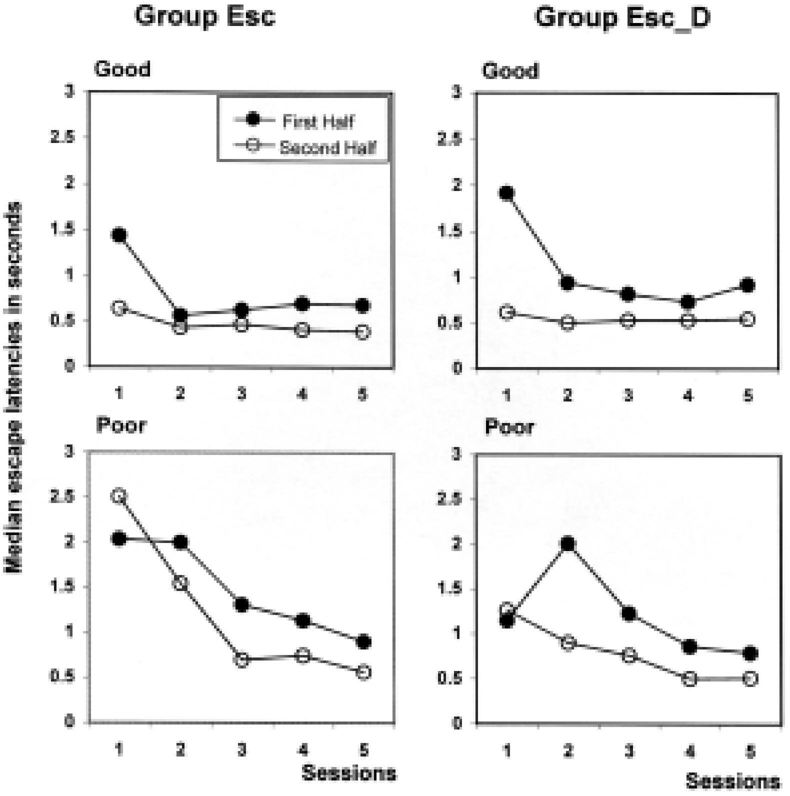

Fig. 3. Mean median escape latency for blocks of 1-25 and of 26-50 trials in consecutive training session for subgroups of good (top), and poor (bottom) learners in Group Esc (left panels) and in Group Esc_D (right panels).

In contrast, during the subsequent sessions escape response latencies were shorter in Group Esc than in Group Esc_D ($P<0.01$ for the 2nd, and $P's<0.001$ for each subsequent session). During the 2nd-5th sessions the D_{max} was located just after shock onset, at the 0.5 s point (during the 4th session at 1 s), thus not only the sign but also the position of the D_{max} changed after the 1st session.

Escape latency changes within subgroups of rats

The segregation of animals into subgroups of good and poor learners, based on the comparison of escape latency distributions between the 1st and 2nd halves of the 1st session, showed similar between-subjects variability within each procedure. For each group (i.g. procedure), either Esc or Esc_D, 7 rats were distinguished as good and 8 rats as poor learners. An analysis of changes in escape latency, performed for each subgroup separately, revealed that marked between-procedures differences were observed for poor learners only (Fig. 3). For Group Esc a 2 (subgroups) x 5 (sessions) x 2 (blocks of trials) ANOVA of median escape latency yielded main effects of session $F_{4,52} = 6.08$, $P<0.0005$; block $F_{1,13} = 21.19$, $P<0.0005$; and interaction of the three factors $F_{4,52} = 2.61$, $P<0.05$. Post hoc Newman Keuls tests revealed significant differences between the 1st and each other session. The median latency in poor learners gradually decreased during training for both the first half (difference between the 1st and the last two sessions) and the second half of the sessions (difference between the 1st and each other session).

For Group Esc_D the 3-way ANOVA yielded similar results (significant effects of session $F_{4,52} = 3.06$, $P<0.05$; block $F_{1,13} = 16.78$, $P<0.002$; and interaction of the three factors $F_{4,52} = 3.02$, $P<0.05$). In contrast to Group Esc, Post hoc Newman Keuls tests revealed that the escape latency in Group Esc_D was significantly decreased only from the 1st to the 4th session. In good learners the difference between median escape latency in the 1st half of the 1st session and each other session and half were revealed. The poor learners decreased their escape latency only during the 2nd session (1-25 and 26-50 blocks difference, $P<0.05$). The between-session differences in this group of rats were revealed only for the 1st block of trials between sessions 2 and 4-5 *(P*<0.05).

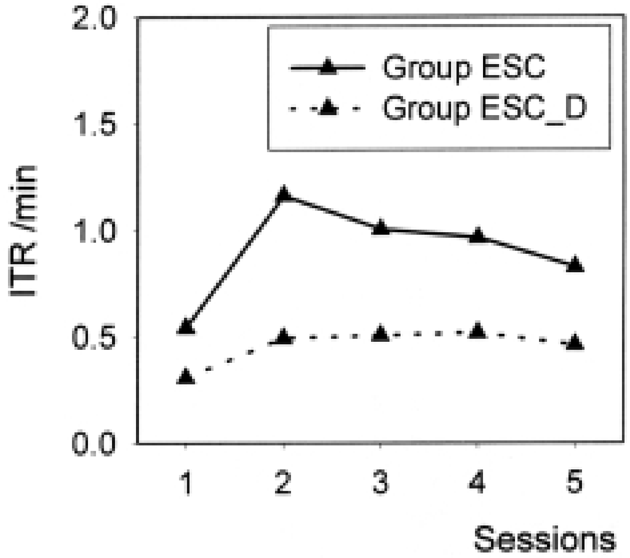

Fig. 4. Mean ITR rate (number of crosses per min) for each session and group of rats.

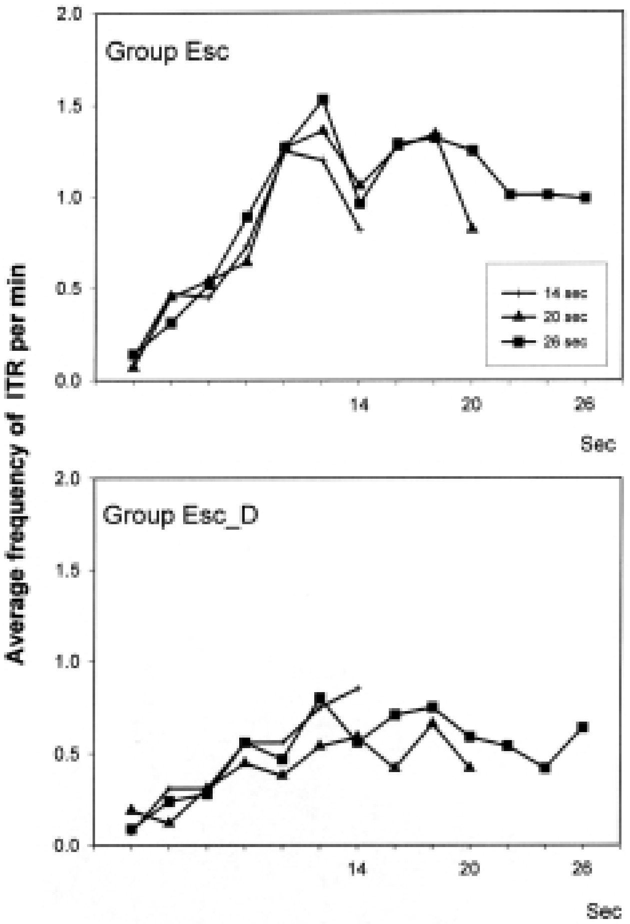

Fig. 5. The mean ITR rate for consecutive 2 s fragments of the 14 s, 20 s, and 26 s intertrial intervals over 5 sessions for each group of rats independently.

Changes of the ITR rate

Rats of Group Esc performed more intertrial responses than rats of Group Esc_D and as seen in Fig. 4 this difference was noted during each training session. This was confirmed by a 2 (procedures) x 5 (sessions) repeated measures ANOVA for the number of ITRs which yielded significant effects of procedure, $F_{1,28} = 5.68$, $P<0.03$, session, $F_{4,112} = 4.17$, $P<0.001$ and no significant interaction, $F_{4,112} = 1.11$, $P=0.35$. Comparison within the Group Esc showed that the ITR rate for the 1st and the 2nd sessions differed at $P<0.001$, and between the 1st, the 3rd and the 4th sessions - at $P<0.02$ each, whereas no difference in ITR rate was noted between the 1st and the 5th sessions. This analysis indicate that the changes in the ITR rate in Group Esc were curvilinear, whereas no change was observed across training in Group Esc_D.

Changes of the ITR rate during the intertrial intervals of different durations are presented in Fig. 5 for Group Esc (upper panel) and for Group Esc_D (bottom panel). As seen, immediately after termination of a trial very few ITRs were performed. Rats increased their ITR rate during the following seconds reaching a maximum toward the end of the shortest, 14 s, ITI. Some nonsystematic fluctuations of the ITR rate were noted in the remaining parts of the longer ITIs intervals.

DISCUSSION

The present results show that the darkness stimulus given in compound with foot-shock exerts definite effects on escape latencies and ITR rate. During the 1st session escape response latencies were shorter in the compounded than in the unsignalled escape procedure and during subsequent sessions the opposite relation occurred. Whereas the compound escape procedure facilitates escape responding only at the initial session, reduction of intertrial responding has permanent character. Moreover, the median escape latency analysis revealed that the switching took place at the beginning of the second session and was restricted to the subgroup of poor learners.

The opposite effects of the darkness stimulus during the 1st and subsequent sessions are compatible with a hypothesis that the darkness given in compound with shock, exerts an arousing influence on the behavioral tendency actually prevailing in the response repertory of the rat in such a stressful situation. At the beginning of training in a shuttle box the rat, perceiving pain, immediately leaves the shock compartment and crosses to the opposite compartment. Such an initial flight of a rat has been considered to be a species-specific response (Bolles 1970, 1971). Our observations indicate that this short-latency fleeing has neither been preceded nor accompanied by freezing (Savonenko and Zieliński 1998a, Savonenko et al. 1999a). During the first shock presentation the darkness stimulus enhances the species-specific fleeing response only in compounded escape but not in a signalled avoidance procedure (Savonenko and Zieliński 1998b). The short-latency crossing responses performed at the beginning of the 1st session attenuate the development of the resistance to enter the opposite, previously shocked compartment and, therefore, caused more effective escape responding under the compounded than under the unsignalled procedure. During the 1st session the mean and median escape latencies of the Group Esc_D were shorter by about one s than those of the Group Esc and this difference was statistically reliable.

The advantage of compounded over unsignalled escape was lost in subsequent sessions. After the 24 h retention interval the memory of the instrumental response acquired during the 1st session dissipated and each subject was again required to cope with the conflict situation inherent in the two-way escape problem (Savonenko et al. 1998). Detailed examination of behavior of rats trained to escape unsignalled shock showed that staying responses, a marker of a conflict tendency in two-way shuttle, rises more rapidly at the beginning of the second than during the previous session (Savonenko et al. 1999a). Thus, freezing and resistance to enter the other compartment, another species-specific response, became predominant in the response repertory and escape performance became less efficient in the compounded than in the unsignalled escape procedure. Such an effect was especially evident within poor learners. It has been shown before that an increase of shock intensity results in slowing down acquisition a two-way avoidance response (Levine 1966, McAllister et al. 1971). It seems that the shock and darkness compound exerts effects similar to those elicited by more intense shock presented alone.

Segregation of rats based on D_{max} values yielded subgroups that differ in changes in escape latency over the course of training. Good learners reached the minimal level of escape response latency already by the end of the 1st session. In contrast, poor learners lengthened their escape response latencies during the 1st training session. This reflect an increase of freezing and other forms of competitive behaviors interfering with the shock-terminating response (Savonenko et al. 1999a). Longer response latencies within poor learners of Group Esc_D at the beginning of each subsequent session were mostly responsible for the inferiority of the compounded relative to the unsignalled escape procedure during the 2nd-5th sessions of training. However, more effective within-session learning in compounded than in unsignalled escape was due to better discrimination between the actual shock and the opposite safe compartment.

In the present study the ITR rate was lower in Group Esc_D than in Group Esc and this difference additionally supports the discriminative role of the darkness cue. Changes in the ITR rate reflect fluctuations of emotional tension classically conditioned to the apparatus cues. Frequency analysis of grooming and ITR, two opposite modes of emotional behavior, showed that grooming was restricted to the initial part of intertrial interval only, whereas ITR rate increased within intertrial interval duration. This temporal patterning develops rather quickly, already during the first training session (Savonenko et al. 1999b). Thus, a safe period lasts for only a few seconds after the crossing escape response. A steady increase of ITR rate until the end of the shortest ITI indicates that there is a consistent rise of emotional tension in anticipation of the next shock. No further increase of ITR rate was observed in the next period, or even during the 22-26 s immediately preceding shock after the longest ITI. This later period of the ITI reveals the steady state of fear in the rat before the inevitable shock and is reminiscent of the behavior observed in uncontrollable aversive situations (Seligman et al. 1971). Our data suggest that the early and late parts of the ITI differ in their affective value both in escape (present study) and in avoidance procedure (Zieliński and Nikolaev 1997).

Early trials of avoidance training consist in paired, sequential presentations of a neutral stimulus, for example darkness, and the painful US. In the course of such a procedure the CS acquires the capacity to arouse the memory of the US and the expectancy of its painful properties. Therefore, in subsequent trials the CS serves as a warning signal. In contrast, any cue presented simultaneously with shock US, does not acquire signalling properties and is not able to elicit the expectation of the shock (Pakovich 1956, Bierbaum 1958, Bitterman 1964, 1965, Smith et al. 1969).

Some researchers opposed contiguity learning and "fear learning" (Davis and Klinger 1994). They claim that association of the paired occurrence of the CS and US by the delayed procedure and association of the CS and painful effects of the US are mediated by different brain pathways or neurotransmitter systems. Our data seem to indicate that the visual cue, the darkness presented synchronously with escapable foot-shock, becomes part of the discriminative cue for the escape response. It is necessary to apply series of transfer tests to prove the usefulness of the compound escape procedure for shaping the association of the darkness with the painful effects of shock. Only after demonstration of acquired aversive properties of the darkness cue presented synchronously with escapable foot-shock in the non-aversive situation may our data be regarded as experimental support of Davis and Klinger's proposal.

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