DO AMYGDALOID NUCLEUS CENTRALIS AND NUCLEUS LATERALIS SERVE SIMILAR FUNCTIONS IN DEFENSIVE RESPONDING IN CATS?

Kazimierz ZIELIŃSKI, Tomasz WERKA and Temuraz NANEISHVILI

Department of Neurophysiology, Nencki Institute of Experimental Biology, Pasteura 3, 02-093 Warsaw, Poland

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Abstract. Bar pressing escape response has been trained, extinguished, retrained and then transformed into avoidance response in cats subjected to electrocoagulation of either the dorsolateral part of the central nucleus (Group CE) or the lateral nucleus (Group L) of amygdala. In comparison with normal cats Group L was deficient in acquisition of the short latency escape responses and Group CE was handicapped in reacquisition of the escape response after the extinction procedure. Both lesioned groups were unable to acquire avoidance responding. Group CE was marked by gradual decrease of the sensitivity to shock in the course of learning, whereas Group L was less sensitive to changes in experimental procedures than the other two groups. However, most of the observed group differences were related to a decrease of sensitivity to shock and to a lowered general emotionality produced by lesions in both amygdaloid nuclei.

INTRODUCTION

We have recently shown (18) that small lesions restricted to the lateral part of the amygdaloid nucleus centralis resulted in retarded acquisition of the bar pressing avoidance response in cats. Postoperative retention test conducted on another group of cats discovered impairment after similar lesions. In both cases the performance of short latency avoidance responses was significantly reduced. Cats with amygdaloid
nucleus centralis lesions were severely deteriorated in acquisition of short latency escape responses as well (16). This last effect could not be related to changes in sensitivity to shock as estimated by the threshold values of unconditioned and instrumental reactions. However, lesioned cats responded to low intensities of the grid-floor shock with much longer latencies than normal control cats (16). It was postulated that the impairment of instrumental defensive responding in lesioned cats was related to the decrement in the animal's ability to evaluate biological value of external pain evoking stimuli.

Similar hypotheses concerning the nature of deficits observed in cats after amygdalar lesions were raised earlier. In experiments by Kling and others (10) rather massive lesions were done with basolateral nuclei of the amygdala completely removed, whereas varying parts of the corticomedial group of nuclei were left intact. Authors related the resulting retardation of the avoidance acquisition in cats trained in two-way shuttle box to the difficulties in learning the significance of the conditioned stimulus and not of the instrumental response. In the experiment conducted by Horvath (8) on cats lesions were restricted to the basolateral group of nuclei and again, acquisition of the two-way avoidance response was markedly impaired. Acquisition of the one-way avoidance was only slightly poorer and behavior in the feeding inhibition test (commonly labeled as "passive avoidance") was the same as in normal control cats. A comparison of results in three tests forced Horvath to conclude that "the general deficit of the lesioned cats can be described as an inability to integrate their motivational state and the experimental cues with the anticipatory response which was most efficient for solving the problem of avoiding the painful shock" (8, p. 388).

There were many differences between the mentioned experiments. Among them, one concerns the localization and extent of lesions. In our experiments lesions were restricted to nucleus centralis of the amygdala. This nucleus was spared in most of the cats investigated both by Kling et al. (10) and by Horvath (8).

However, nucleus centralis is crossed by a number of fibers from the basolateral part of the amygdala and some fibers coming from the lateral and basal nuclei terminate in the nucleus centralis (12). Moreover, it is reasonable to assume that "the behavioral changes produced by amygdala lesions may not depend on the nuclear damage but rather on interruption of one or several of the many fiber systems passing through this complex" (17, p. 672).

In spite of the fact that in our experiments lesions were small and precise, there is an open question whether observed changes of instrumental defensive responding were related to the specific involvement of
the nucleus centralis or to the more general functions common for different nuclei of the amygdalar complex. Thus, it was decided to compare behavioral effects of the lesions placed in nucleus centralis and nucleus lateralis, each belonging to the opposite amygdalar systems. Basing on our experience with instrumental defensive responding in cats (21), a battery of tests was employed. If the effects observed earlier were specific for the nucleus centralis, a double dissociation of the lesion effects will be observed. On the other hand, similarities in the effects produced by lesions in the nucleus centralis and in the nucleus lateralis would suggest similar functions of both nuclei in the mediation of defensive responding.

MATERIAL AND METHODS

Experiments were carried out on 15 adult male cats. The apparatus was a rectangular cage (55 cm long, 55 cm wide and 40 cm high) with a bar measuring $10 \times 2$ cm located in the center of the wall opposite to the entrance to the cage, 8 cm above the floor. The source of the conditioned stimulus (CS) was a loud-speaker located near the centre of the ceiling of the box, through which 70 dB (re 0.0002 dyn/cm²) white noise was delivered. The unconditioned stimulus (US) was a scrambled electric shock delivered through the grid-floor to the paws of the animal.

Before experiments the cats were divided into three groups. Six cats were subjected to bilateral lesions of the dorsal part of the nucleus centralis of the amygdala (Group CE), five cats received bilateral lesions of the nucleus lateralis of the amygdala (Group L), and four cats were left intact (Group N). Lesions were done electrolytically in a stereotaxic apparatus under aseptic conditions with Nembutal anesthesia (40 mg/kg). The tungsten lesioning electrodes (0.5 mm in diam.) were insulted up to 0.5 mm of the tip. A cathodal current of 1.5 mA DC for 1 min (Group CE) or 1.5 min (Group L) was used. The coordinates were AP: 13.0, H: -6.5, L: 9.2 (Group CE) and AP: 11.5, H: -5.0, L: 11.5 (Group L), according to the atlas by Jasper and Ajmone-Marsan (9), corrected by the method of Kucinski (11). Prior to the training, ten days postoperative recovery period was given for lesioned cats. All cats were subjected to the same training and testing procedures, which consisted of the following stages:

1. Acquisition of escape response. An escape bar press response automatically and immediately terminated the electric shock from the grid-floor. A trial started with the activation of the grid-floor which had to be terminated with the bar press response. Shock intensity was individually adjusted for each cat during the first, shaping session
according to subject's responsiveness to shock. To make the acquisition of instrumental response easier during the first 10–20 trials of escape training a series of platforms of decreasing size were used to shape the bar press response (19). Then followed 35 training sessions, of 10 trials each. The intertrial intervals (ITI) were of 40-, 60-, and 80-s duration given in predetermined order. Tonic pressing of the bar during ITI did not preclude the start of the next trial. In this case, the cat was required to take its paw away from the bar and press it again to terminate the trial.

The training sessions were split into Blocks I–VII containing 5 sessions each. After Block II and after each consecutive block there were given single testing sessions. The testing sessions differed from the training sessions in three aspects: (i) each session had 14 trials, (ii) a testing trial was terminated by a bar press reaction, or after 60 s, (iii) shocks of increasing intensities were used. In consecutive trials root-mean-square values of electric shock (R. M. S. current) were estimated and presented in Table II. After the first test session a definite shock intensity was choosen for a given cat and it was kept constant through the remaining training.

2. Extinction of escape response. During this stage of experiment the trial consisted in the activation of the grid-floor for a constant 5 s period independently of the cat's behavior. If there was no bar press response during the trial, the following ITI was of 60 s duration. This stage consisted of 10 extinction sessions, 10 trials each, split into two blocks (Blocks E1 and E2). After the last extinction session a single testing session was given.

3. Retraining of escape response. The regular procedure of escape training (grid-shock terminated by bar press response) was resumed. This stage consisted of 15 training sessions split into three blocks (Blocks VIII–X). After each block a single testing session was given, similarly as during Stage 1 of the experiments.

4. Training of avoidance response. In this stage of experiments a CS consisting of 70 dB white noise was introduced. A 5 s CS–US interval was used. The bar press response performed within 5 s after the CS onset immediately terminated the CS and precluded the activation of the grid-floor. The bar press response performed with a latency longer than 5 s after the CS onset terminated both the CS and the grid-shock. This stage consisted of 15 avoidance training sessions split into three blocks (Blocks XI–XIII). After the last block of avoidance training sessions a single testing session was given.
After completing the avoidance acquisition stage, the lesioned cats were sacrificed with an overdose of Nembutal and their brains were subjected to histological analysis using Klüver's and Nissl's techniques.

RESULTS

Acquisition of escape response

The best measure of the effectiveness of escape training is mean shock duration during each trial. This index estimated for each group and consecutive 50-trials blocks throughout the experiments is presented in Fig. 1. An analysis of variance of the data for the escape response acquisition stage (Blocks I–VII) revealed a highly significant effect of blocks ($F_{6/72} = 46.67, P < 0.001$) a lack of group effect and a significant interaction ($F_{12/72} = 3.03, P < 0.005$). In the course of training a monotonic decrease of shock duration was observed. The Duncan test discovered significant differences between Block I and all consecutive blocks of sessions ($P's < 0.001$), Block II and Block III ($P < 0.05$) and the next blocks ($P < 0.001$), and also between Block III and Blocks VI and VII ($P < 0.01$). The differences in mean shock durations between Block I and Block VII, which were the largest in Group N and the smallest in Group L, were responsible for the significant interaction of the main effects. This was verified by the Duncan test which discovered that in Block I shock duration was longer in Group N than in both lesioned groups ($P's < 0.05$), whereas in Block VII differences between groups were not significant.

Analysis of median latencies of escape responses estimated for each subject and block of training sessions independently yielded analogous results as the mean shock duration. Distribution of latencies of escape responses during consecutive blocks of training sessions are presented in Fig. 2. During the first two blocks of sessions both lesioned groups of cats emitted more short-latency responses than cats from Group N. However, starting with Block III, relations between control and lesioned cats changed. As seen from Table I, the Smirnov test discovered that not only the direction of difference between normal and lesioned cats, but also the point of the maximal difference changed drastically after Block II. It must be stressed that both the better performance of lesioned cats at the very beginning of training and their slower responding later on were more pronounced in cats with lesions of the nucleus lateralis than with lesions of the nucleus centralis of the amygdala. In effect, in Block II response latencies were significantly shorter in Group L than in Group CE, and in Blocks III–VII latencies were significantly longer in Group L than in Group CE.
Fig. 1. Mean shock duration for each trial and experimental groups (circles — Group N, triangles — Group CE, squares — Group L) during consecutive blocks of escape training, extinction, escape response retraining and avoidance training stages.

Comparisons of cumulative distributions of response latencies estimated for consecutive blocks of escape acquisition stage. For each between group comparison and block of sessions direction of difference, value of the maximum vertical distance ($D_{\text{max}}$), and point of $D_{\text{max}}$ in s are given. $N < CE$ denotes that Group N emitted smaller proportion of responses with latencies shorter than point of $D_{\text{max}}$ than Group CE.

**TABLE I**

Comparisons of cumulative distributions of response latencies estimated for consecutive blocks of escape acquisition stage. For each between group comparison and block of sessions direction of difference, value of the maximum vertical distance ($D_{\text{max}}$), and point of $D_{\text{max}}$ in s are given. $N < CE$ denotes that Group N emitted smaller proportion of responses with latencies shorter than point of $D_{\text{max}}$ than Group CE.

<table>
<thead>
<tr>
<th>Block</th>
<th>N vs. CE</th>
<th>Difference</th>
<th>$D_{\text{max}}$</th>
<th>s</th>
<th>N vs. L</th>
<th>Difference</th>
<th>$D_{\text{max}}$</th>
<th>s</th>
<th>CE vs. L</th>
<th>Difference</th>
<th>$D_{\text{max}}$</th>
<th>s</th>
</tr>
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<tbody>
<tr>
<td>I</td>
<td>N &lt; CE</td>
<td>0.20***</td>
<td>3.65</td>
<td></td>
<td>N &lt; L</td>
<td>0.18**</td>
<td>2.85</td>
<td></td>
<td>CE &lt; L</td>
<td>0.04</td>
<td>3.05</td>
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<tr>
<td>II</td>
<td>N &lt; CE</td>
<td>0.26***</td>
<td>5.55</td>
<td></td>
<td>N &lt; L</td>
<td>0.29***</td>
<td>3.45</td>
<td></td>
<td>CE &lt; L</td>
<td>0.17***</td>
<td>1.35</td>
<td></td>
</tr>
<tr>
<td>III</td>
<td>N &gt; CE</td>
<td>0.32***</td>
<td>0.55</td>
<td></td>
<td>N &gt; L</td>
<td>0.31***</td>
<td>0.75</td>
<td></td>
<td>CE &gt; L</td>
<td>0.15**</td>
<td>3.45</td>
<td></td>
</tr>
<tr>
<td>IV</td>
<td>N &gt; CE</td>
<td>0.28***</td>
<td>0.55</td>
<td></td>
<td>N &gt; L</td>
<td>0.41***</td>
<td>0.75</td>
<td></td>
<td>CE &gt; L</td>
<td>0.24***</td>
<td>0.95</td>
<td></td>
</tr>
<tr>
<td>V</td>
<td>N &gt; CE</td>
<td>0.11</td>
<td>0.35</td>
<td></td>
<td>N &gt; L</td>
<td>0.32***</td>
<td>0.75</td>
<td></td>
<td>CE &gt; L</td>
<td>0.26***</td>
<td>0.75</td>
<td></td>
</tr>
<tr>
<td>VI</td>
<td>N &gt; CE</td>
<td>0.15**</td>
<td>0.35</td>
<td></td>
<td>N &gt; L</td>
<td>0.38***</td>
<td>0.65</td>
<td></td>
<td>CE &gt; L</td>
<td>0.31***</td>
<td>0.65</td>
<td></td>
</tr>
<tr>
<td>VII</td>
<td>N &gt; CE</td>
<td>0.27***</td>
<td>0.35</td>
<td></td>
<td>N &gt; L</td>
<td>0.43***</td>
<td>0.55</td>
<td></td>
<td>CE &gt; L</td>
<td>0.24***</td>
<td>0.75</td>
<td></td>
</tr>
</tbody>
</table>

* $P < 0.01$; ** $P < 0.05$, *** $P < 0.001$.

Within-group comparisons of the response latency distribution showed that in all groups latencies were shorter during Block II than
Fig. 2. Frequency histograms showing distributions of latencies of escape responses during consecutive blocks of escape acquisition sessions.
during Block I and a similar change occurred in Group N and Group CE between Blocks II and III (all $P's < 0.001$). In Group L, however, other significant change occurred only between Blocks IV and V ($P < 0.01$). All other within-group differences of latency distribution in the consecutive blocks of sessions in the escape acquisition stage were statistically not significant.

Cats performed bar presses not only in response to shock onset, but also during ITIs. Analysis of variance of the frequency of intertrial responses (ITR) showed a significant effect of consecutive blocks of training sessions ($F_{6/72} = 3.29$, $P < 0.01$), whereas group effect and interaction were not significant. Frequency of ITR increased monotonically in the course of training. The Duncan test discovered differences between Block I and Block IV ($P < 0.05$), Block VI ($P < 0.01$) and Block VII ($P < 0.01$). As seen from Fig. 3A, the frequency of ITR during the first 5 s after shock termination was several times higher than in the later parts of ITI, however, decay of the ITR frequency in Group N was less regular than shown before for avoidance response training (22).

The groups did not differ in shock intensity used in training sessions. For three cats 1.82 mA, for eight 2.24 mA and for five 2.80 mA shocks were used. These intensities were about 1.5 mA higher than those which regularly evoked bar press responses during test sessions. As seen

Table II

<table>
<thead>
<tr>
<th>No. of trial</th>
<th>R. M. S. values of electric shock</th>
<th>Percentage of responses*</th>
<th>Median latencies of responses in s</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Group N</td>
<td>Group CE</td>
</tr>
<tr>
<td>1</td>
<td>0.05 ± 0.01</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>2</td>
<td>0.12 ± 0.01</td>
<td>5</td>
<td>0</td>
</tr>
<tr>
<td>3</td>
<td>0.21 ± 0.01</td>
<td>10</td>
<td>0</td>
</tr>
<tr>
<td>4</td>
<td>0.29 ± 0.01</td>
<td>30</td>
<td>10</td>
</tr>
<tr>
<td>5</td>
<td>0.42 ± 0.01</td>
<td>35</td>
<td>20</td>
</tr>
<tr>
<td>6</td>
<td>0.49 ± 0.01</td>
<td>55</td>
<td>37</td>
</tr>
<tr>
<td>7</td>
<td>0.56 ± 0.02</td>
<td>75</td>
<td>80</td>
</tr>
<tr>
<td>8</td>
<td>0.77 ± 0.02</td>
<td>90</td>
<td>90</td>
</tr>
<tr>
<td>9</td>
<td>1.01 ± 0.02</td>
<td>100</td>
<td>100</td>
</tr>
<tr>
<td>10</td>
<td>1.24 ± 0.03</td>
<td>100</td>
<td>100</td>
</tr>
<tr>
<td>11</td>
<td>1.52 ± 0.03</td>
<td>100</td>
<td>100</td>
</tr>
<tr>
<td>12</td>
<td>1.95 ± 0.04</td>
<td>100</td>
<td>100</td>
</tr>
<tr>
<td>13</td>
<td>2.55 ± 0.05</td>
<td>100</td>
<td>100</td>
</tr>
<tr>
<td>14</td>
<td>3.10 ± 0.07</td>
<td>100</td>
<td>100</td>
</tr>
</tbody>
</table>
Fig. 3. Frequencies of intertrial responses per s in consecutive 5 s periods of the intertrial intervals for the escape response acquisition (A), escape response extinction (B), escape response retraining (C) and avoidance training (D) stages. For the escape response extinction stage frequencies of extra responses per s are also presented (black bars).
from Table II, there was some tendency in control cats (Group N) to perform bar presses at lower shock intensities than in the lesioned cats. However, groups did not differ statistically in any of the two measures of responding during test sessions.

Summing up, only small differences between the two lesioned groups were observed during the escape response acquisition stage. Comparisons between groups indicate that at the beginning of training Group L responded with the shortest and toward the end with the longest latencies. In effect, in all blocks of training the differences in performance level between Group L and Group N were larger than the differences between Group CE and Group N.

Extinction of escape response

The extinction procedure consisted in the presentation of grid shock of fixed 5 s duration which could not be terminated by a bar pressing response. As seen in Fig. 4 these changes resulted in a decrease of instrumental responding in all groups of cats. A comparison of the number of escape responses performed within the first 5 s of US action in Block VII with the number of trials in which at least one bar press was recorded in the presence of shock during Block E1 showed that in 13 out of 15 cats the level of performance was lowered due to extinction procedure. In the remaining two cats no difference was noted. This decrease of instrumental responding seems to be more pronounced in Group L, however, analyses of variance have not discovered group effect on the level of performance. Specifically, the number of trials in which instrumental responses were executed within 5 s of the US onset in

![Fig. 4. Cumulative frequency distributions of bar press response latencies at the end of escape response training (Block VII), and at the beginning (Block E1) and the end (Block E2) of escape extinction.](image-url)
Blocks VI and VII (pre-extinction period), in Blocks E1 and E2 (extinction), and in Blocks VIII and IX (post-extinction period) revealed significant differences between “periods” ($F_{2/24} = 14.77, P < 0.001$) and joint effect of “periods” and blocks ($F_{2/24} = 5.41, P < 0.025$) only, whereas group effect was negligible ($F < 1$).

A shock of fixed duration may have different effects, depending on the latency of previously acquired escape responding. If a cat tends to respond with long latency, a shock of fixed duration in many cases terminate before the execution of response. If short latency responding is acquired, a shock will terminate with some delay after the instrumental response. The longer the delay of shock termination, the stronger will be the punishing effect of shock on the bar pressing response.

In both situations the probability of instrumental response decreases, however, in the second case symptoms of increased emotionality resulting in performance of extra responses before shock termination and of numerous ITRs will be observed.

These considerations were supported by the Spearman rank correlation method with all groups pooled. The shorter the median latencies of escape responses in Block VII, before the introduction of extinction procedure, the higher were the levels of performance in Blocks E1 and E2 ($r_s = -0.513$ and $r_s = -0.573$ respectively, $P's < 0.05$). These values were only slightly higher than estimated for Block VII when median latency and number of escape responses performed during the first 5 s of shock action were correlated ($r_s = -0.690, P < 0.01$). The influence of the median latencies of escape responses in Block VII on performance levels in Blocks E1 and E2 was further supported by the Kendal partial rank correlation method.

As mentioned before, the groups did not differ statistically in the level of performance during the extinction sessions due to a great individual variability of this index. Nevertheless, the above analyses provide an explanation of a somewhat more rapid extinction of escape responding in Group L, which was marked by the longest latencies of escape responses before the introduction of extinction procedure (compare Table I).

The introduction of extinction procedure resulted in a shortlasting increase of ITR frequency in all groups. ITR rate during Blocks VI, VII (pre-extinction period), E1 and E2 was analyzed. The effects of the main factors (group, period and block) were not significant. A significant interaction of periods and blocks ($F_{1/22} = 12.42, P < 0.005$) was related to a lower ITR rate in Block VI than in Block VII and a higher ITR rate in Block E1 than in Block E2. Differences between consecutive blocks were in Group L very small and in opposite direction than in
other groups, resulting in a significant triple interaction \(F_{2/12} = 13.93, P < 0.001\).

As seen from Fig. 3B, the pattern of ITR rate during the ITI was similar to that observed during the escape acquisition stage. The rate of extra responses performed before US termination was in all groups lower than the ITR rate during the first 5 s after US termination.

Comparisons of the two test sessions, one conducted before and the other — after the extinction sessions, revealed that only one cat from Group L had not changed its reactivity to shock. In all other lesioned cats and in two cats from Group N a higher shock intensity was necessary after extinction to evoke bar response. In the other two cats from Group N the threshold value for bar press was lowered.

Summing up, statistical tests have not discovered any significant group differences in this stage of experiments except smaller susceptibility of ITR rate in Group L to changes in experimental procedure.

Retraining of escape response

The immediate effect of extinction procedure on the escape performance may be estimated by a comparison between the performance during Block VII and Block VIII. As seen from Table III, the extinction procedure resulted in a prolongation of escape response latencies in all groups; however, this effect was weakest in Group L. Individual comparisons supported this conclusion. In Group N and Group CE the extinction procedure had a pronounced effect on responses executed with short latencies, whereas in Group L the largest vertical distance between cumulative frequency distributions was observed among long latency responses. The number of trials in which response latencies were longer than 10.05 s increased in all groups, most dramatically in Group CE (12 times in Group CE, 6 times in Group L and 3 times in Group N). As a result of these changes mean shock duration was longer after extinction stage (compare Fig. 1). A comparison of this score for Blocks V, VI, VII (pre-extinction period) and Blocks VIII, IX, X (retraining period) showed a significant effect of period \(F_{1/12} = 17.65, P < 0.005\) and block \(F_{2/24} = 8.20, P < 0.005\). The lack of interaction of these two main variables \((F < 1)\) indicated that the shortening of mean shock duration with training had a similar course both before and after the extinction stage. The effect of group was also negligible \((F < 1)\). Similar results were obtained when median latencies of escape responses for the same periods were analysed (effect of period \(F_{1/12} = 5.30, P < 0.05\), effect of block \(F_{2/24} = 4.32, P < 0.025\), all other factors and interactions being not significant).

It is worthwhile to mention that differences between Group N and both lesioned groups in the distribution of response latencies observed
in the last blocks of acquisition stage (compare Table I) were preserved also during each block of reacquisition stage (all \( P < 0.005 \) or better). However, as a result of a more pronounced effect of extinction procedure on response latencies executed by cats with lesions of the nucleus centralis of the amygdala, the differences between Group CE and Group L disappeared.

**Table III**

Within group and individual comparisons of changes in the distribution of response latencies emitted during Block VII (the last five sessions before extinction) and during Block VIII (the first five sessions after extinction). \( S_{VII} > S_{VIII} \) denotes that prior to extinction a greater proportion of responses was emitted with latencies shorter than point of \( D_{max} \) than after extinction.

<table>
<thead>
<tr>
<th>Subjects</th>
<th>Change</th>
<th>( D_{max} )</th>
<th>( s )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Group N</td>
<td>( S_{VII} &gt; S_{VIII} )</td>
<td>0.26***</td>
<td>0.55</td>
</tr>
<tr>
<td>N - 62</td>
<td>( S_{VII} &gt; S_{VIII} )</td>
<td>0.42***</td>
<td>0.35</td>
</tr>
<tr>
<td>N - 63</td>
<td>( S_{VII} &gt; S_{VIII} )</td>
<td>0.54***</td>
<td>0.35</td>
</tr>
<tr>
<td>N - 64</td>
<td>( S_{VII} &gt; S_{VIII} )</td>
<td>0.56***</td>
<td>2.55</td>
</tr>
<tr>
<td>N - 71</td>
<td>( S_{VII} &lt; S_{VIII} )</td>
<td>0.14</td>
<td>0.65</td>
</tr>
<tr>
<td>Group CE</td>
<td>( S_{VII} &gt; S_{VIII} )</td>
<td>0.24***</td>
<td>1.45</td>
</tr>
<tr>
<td>CE - 66</td>
<td>( S_{VII} &gt; S_{VIII} )</td>
<td>0.36**</td>
<td>2.15</td>
</tr>
<tr>
<td>CE - 67</td>
<td>( S_{VII} &gt; S_{VIII} )</td>
<td>0.22</td>
<td>0.45</td>
</tr>
<tr>
<td>CE - 68</td>
<td>( S_{VII} &gt; S_{VIII} )</td>
<td>0.42***</td>
<td>1.45</td>
</tr>
<tr>
<td>CE - 69</td>
<td>( S_{VII} &gt; S_{VIII} )</td>
<td>0.36**</td>
<td>2.45</td>
</tr>
<tr>
<td>CE - 72</td>
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<td>0.28*</td>
<td>0.45</td>
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<tr>
<td>CE - 73</td>
<td>( S_{VII} &gt; S_{VIII} )</td>
<td>0.60***</td>
<td>0.55</td>
</tr>
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<td>Group L</td>
<td>( S_{VII} &gt; S_{VIII} )</td>
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<td>5.25</td>
</tr>
<tr>
<td>L - 65</td>
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<td>0.12</td>
<td>2.35</td>
</tr>
<tr>
<td>L - 70</td>
<td>( S_{VII} &gt; S_{VIII} )</td>
<td>0.10</td>
<td>1.05</td>
</tr>
<tr>
<td>L - 74</td>
<td>( S_{VII} &lt; S_{VIII} )</td>
<td>0.26</td>
<td>0.75</td>
</tr>
<tr>
<td>L - 75</td>
<td>( S_{VII} &gt; S_{VIII} )</td>
<td>0.16</td>
<td>3.55</td>
</tr>
<tr>
<td>L - 76</td>
<td>( S_{VII} &gt; S_{VIII} )</td>
<td>0.48***</td>
<td>1.55</td>
</tr>
</tbody>
</table>

* \( P < 0.05 \), ** \( P < 0.005 \) *** \( P < 0.001 \)

A comparison of ITR rate for the last three blocks of escape acquisition and three blocks of escape reacquisition stages showed that not a simple factor or interaction of factors reached significance. However, the effect of group was close to acceptance level (\( F_{2/12} = 3.82 \), with \( F_{2/12} = 3.88 \) necessary for \( P < 0.05 \)). This was due to a further increase of ITR frequency in Group N as compared with the absence of change in both lesioned groups (compare Fig. 3, A and C).

Test sessions conducted during the stage of escape response retraining suggest a tendency in all groups to lower shock intensity necessary to evoke bar presses.
Data collected during the escape response reacquisition stage indicate that the extinction procedure exerted a pronounced influence on the escape response performance. Group CE suffered most and Group L least. As a consequence, the differences between Group CE and Group L in response latency distributions, evident before the introduction of extinction procedure, disappeared during the escape response reacquisition stage.

**Training of avoidance response**

The distribution of response latencies in the consecutive blocks of avoidance training sessions are presented in Fig. 5. Dotted lines in each panel denote distribution of escape response latencies during Block X, prior to CS introduction. If no transfer of escape to avoidance responding occurs, the cumulative frequency distribution of response latencies during avoidance training sessions will coincide with reference function starting at the US onset. If a full transfer of escape to avoidance responding is observed, distribution during avoidance training sessions will be close to the reference function starting at the CS onset.

As seen from the Fig. 5, only a small proportion of trials was terminated by an avoidance response during the first 50-trial block of avoidance training sessions. Two cats from Group CE and one from Group L did not show any avoidance response during Block XI. In the next blocks an increase of avoidance responding was observed in Group N and to some extent also in Group L. Analysis of variance based on the

![Fig. 5. Cumulative frequency distributions of bar press response latencies during consecutive blocks of avoidance training sessions. The reference functions (broken lines) denote cumulative frequency distributions of bar press responses during the end of the escape retraining stage (Block X).](image)
number of avoidances performed in Blocks XI–XIII discovered a significant effect of group \((F_{2/12} = 4.90, \ P < 0.05)\), block \((F_{2/24} = 18.96, \ P < 0.001)\) and interaction \((F_{4/24} = 4.86, \ P < 0.01)\). The Duncan test showed that Group N differed from Group CE \((P < 0.01)\) and Group L \((P < 0.05)\), whereas both lesioned groups were alike. Significant interaction of the two main factors was related to the fact that the most regular increase in the number of avoidance responses was in Group L whereas in Group CE changes were not monotonic.

When median latencies of instrumental responses (measured from the CS onset) were analysed in a similar way, the group \((F_{2/12} = 5.69, \ P < 0.025)\), block \((F_{2/24} = 4.45, \ P < 0.025)\) and interaction \((F_{4/24} = 6.12, \ P < 0.01)\) effects proved to be significant. The Duncan test discovered that Group N differed from Group CE \((P < 0.01)\) and Group L \((P < 0.05)\). Overall mean median latencies were shorter during Block XIII than during Block XI \((P < 0.01)\). This improvement in instrumental responding was due to Group N, for which mean median latencies in Block XIII differed from those in Block XI and in Block XII \((P's < 0.001)\). In both lesioned groups differences between blocks were not significant.

In Table IV there is additional information concerning changes in instrumental response latencies obtained with the more powerful Smirnov test. Comparisons of the cumulative frequency distributions indicate that in Group N a significant shortening of response latencies in consecutive blocks was observed. These changes were due to an increase of avoidance responding, as shown by the localization of the \(D_{\text{max}}\). In Group CE frequency distributions also differed statistically; however, the maximum vertical distances were located shortly after the US onset. More important, Group CE performed during Block XII a smaller pro-

<table>
<thead>
<tr>
<th>Group</th>
<th>Change</th>
<th>(D_{\text{max}})</th>
<th>(S)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Group N</td>
<td>(S_{\text{XI}} &lt; S_{\text{XII}})</td>
<td>0.30***</td>
<td>3.25</td>
</tr>
<tr>
<td></td>
<td>(S_{\text{XII}} &lt; S_{\text{XIII}})</td>
<td>0.34***</td>
<td>1.35</td>
</tr>
<tr>
<td></td>
<td>(S_{\text{XI}} &gt; S_{\text{XII}})</td>
<td>0.13*</td>
<td>5.55</td>
</tr>
<tr>
<td></td>
<td>(S_{\text{XII}} &lt; S_{\text{XIII}})</td>
<td>0.13**</td>
<td>5.25</td>
</tr>
<tr>
<td>Group CE</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>(S_{\text{XI}} &gt; S_{\text{XII}})</td>
<td>0.13*</td>
<td>5.55</td>
</tr>
<tr>
<td></td>
<td>(S_{\text{XII}} &lt; S_{\text{XIII}})</td>
<td>0.14*</td>
<td>4.95</td>
</tr>
</tbody>
</table>

* \(P < 0.05\), ** \(P < 0.01\), *** \(P < 0.001\)
portion of avoidance and short latency escape responses than during Block XI. Although not significant, the same picture was observed in Group L. As seen in Fig. 5, in both lesioned groups the cumulative distribution functions for consecutive blocks of sessions were inter-crossed, indicating a low efficiency of avoidance training. Careful examination of the course of distribution functions for Block XI and XII discovered important differences between Group CE and Group L. Group CE performed during Block XII a smaller proportion of avoidance and short latency escape responses, whereas starting from 6.05 s the responding was elevated, resulting in a decrease of long latency escape responses in comparison with Block XI. On the other hand, Group L performed during Block XII more avoidance and short latency escape responses (up to 5.55 s), whereas the ability to terminate long lasting shock was deteriorated. It seems that in Group L, contrary to other groups, the introduction of avoidance contingency had a disruptive effect on escape responses terminating the painful shock. Nevertheless, the final level of instrumental responding was better in Group L than in Group CE, as shown by a comparison of distribution functions during Block XIII (CE < L, $D_{\text{max}} = 0.18$, $P < 0.001$, point of $D_{\text{max}} = 3.45$ s).

The above analysis indicates that the acquisition of avoidance and the ability to terminate shock are not necessarily directly related. This was confirmed by the analysis of variance, in which mean shock duration for each cat and block of sessions (Blocks XI–XIII) were the raw data. Only interaction between group and block was significant ($F_{4/24} = 4.34$, $P < 0.01$). This was due to marked changes in Group N, in which the longest mean shock duration was observed in Block XI and the shortest in Block XIII ($P < 0.05$, Duncan tests). All other within-group differences were not significant.

The pattern of ITR rate was, during the avoidance acquisition stage, similar to that observed previously. However, in Group N a further increase of ITR rate was observed, which was not evident in the other groups. Analysis of variance of the ITR score for Blocks XI–XIII yielded a significant effect of group ($F_{2/12} = 9.56$, $P < 0.005$) with a negligible block effect and interaction. The Duncan test showed that Group N differed in the ITR rate from Group CE ($P < 0.001$) and from Group L ($P < 0.01$).

This last information is very important for a proper evaluation of group differences in the acquisition of avoidance response. It has been shown previously that in the early stages of avoidance training the probability of the occurrence of avoidance response is similar to the ITR rate (20). In the present experiments the frequency of avoidance responses in each group during Block XI was about two times higher
than the probability of ITRs occurrence during the 5 s CS-US interval. However, a significant correlation was observed between the ITR rate and the frequency of avoidance responses. With all group pooled, the Spearman rank correlation coefficients were: $r_s = 0.770$ ($P < 0.01$) for Block XI, $r_s = 0.604$ ($P < 0.05$) for Block XII, and $r_s = 0.609$ ($P < 0.05$) for Block XIII.

Test sessions gave us information about the reactivity to different shock intensities. For each group the results obtained before and after the extinction sessions were compared and are presented in Fig. 6. As seen from the graphs, the probability of termination of low shock intensities by bar pressing increased in Group N and Group L in the course of experiments. On the other hand, in Group CE responding during the test sessions decreased after the extinction stage. This decrease of responding in Group CE was statistically significant ($P < 0.01$, Smirnov test), whereas changes in the other groups were far from the acceptance level. As mentioned before (compare Table II), during the escape response acquisition stage the groups did not differ in reactivity to shock. In the second part of experiments a significant difference between Group CE and Group N appeared ($P < 0.01$, the same test).

Summing up, results obtained during this stage of experiments indicate that differences between groups in the acquisition of avoidance response were correlated with differences observed in the reactivity to shock and in the general emotionality of the animals.

![Graph showing responding to different shock intensities](image)

Fig. 6. Responding to different shock intensities during test sessions conducted before extinction of escape response (solid lines) and after extinction of escape response sessions (dotted lines).

**Anatomical verification of lesions**

All operated cats had acceptable symmetrical and bilateral lesions (Fig. 7). The injuries of adjoining structures were very small and mainly unilateral.
In the central group (Group CE) the dorso-lateral fragment of the central nucleus was destroyed. Moreover, in all subjects there was some small bilateral invasion of the putamen region adjacent to the central nucleus. In two cats a unilateral electrode tract cut also some capsula extrema fibers. A small, unilateral lesion in the dorso-medial part of the lateral nucleus was found as well. No stria terminalis, and most likely no longitudinal association fibers were damaged.

In the lateral group (Group L) lesions were comparatively larger than in the previous group, and they mainly affected the basolateral part of the nucleus lateralis, extending dorsally in two cats. In at least three subjects there was some unilateral, and in one cat — bilateral invasion of capsula extrema fibers. In the last case the claustrum area that is immediately lateral to the lateral nucleus of the amygdala was slightly affected. Unilateral electrode tract was seen in the central nucleus region in one subject. There was no damage to the adjacent pyriform cortex.
DISCUSSION

Results obtained in earlier studies determined the detailed procedure of the present experiments. It has been shown that cats subjected to nucleus centralis lesions showed deteriorated performance of short latency escape responses (16). Moreover, when shocks of low intensities were used in test sessions, the lesioned animals performed bar presses after very long latencies. This difference between lesioned and intact cats disappeared in the 1.01–1.95 mA range of shock intensities (16). On the basis of these data it was decided to use in the course of training shock intensities 1.5 mA higher than the threshold values. In consequence, the difference between normal cats and those subjected to nucleus centralis lesions became markedly attenuated in the present experiment. Under these conditions, the short latency escape responding was erratic only in cats with nucleus lateralis lesions.

The high intensity of shock used in the present experiment resulted in responding much more effective in terms of response latency duration than in the previous experiment. Although such comparisons ought to be done with caution, even Group L in the present study performed more short latency escape responses that the normal cats in the previous experiment. This indicates that neither lesions in the amygdalar nucleus centralis nor those in the nucleus lateralis cause the inability to perform short-latency responses. The differences between groups are not sharp and the ability to acquire short-latency responding changes depending on shock intensity used in training.

Another variable influencing the manifestation of deficiency of the amygdalar cats is the stage of training. No differences in bar pressing response latencies between normal cats and those subjected to nucleus centralis lesions were observed in the early stages of the previous experiment (16). It is well known that at the beginning of training the shock evoked various inborn defensive reactions. In our situation the dominant form was an attempt to escape from the experimental cage. These inborn defensive reactions interfere with the performance of the learned instrumental bar pressing response. In the early stages of the present study both lesioned groups performed more bar pressing responses with short latencies than the normal cats, which indicated a weakening of the interfering inborn defensive reactions after amygdalar lesions. This may be interpreted as evidence of a lowered emotionality after nucleus centralis and nucleus lateralis amygdalar lesions in cats. Specifically, it has been shown that electrical stimulation of the rostral part of the nucleus lateralis and the region of nucleus
centralis both elicited flight responses in cats (15). Lesions localized in the rostral part of nucleus lateralis were the most effective for the reduction of flight behavior (14).

The frequency of intertrial responses is considered as a more general index of emotionality. In the course of training the ITR rate gradually increased in all groups. Then, beginning with the escape response reacquisition stage, gradual decrease of the ITR rate was observed in both lesioned groups, resulting in significant group differences at the late stage of the experiment, with the lowest ITR rate in cats with nucleus lateralis lesions and the highest in normal cats.

Test sessions in which different shock intensities were used for the evocation of bar pressing response, gave us information about sensitivity of cats to painful shock. In all stages of the experiments the probability of response to low shock intensities was higher in normal than in lesioned cats. In cats subjected to nucleus centralis lesions the sensitivity to low intensities of shock gradually decreased in the course of experiments, resulting in significant differences between Group CE and normal cats. In the previous experiment cats with nucleus centralis lesions were characterized by a lowered reactivity manifested by very long latencies of responses to shocks of low intensities (16). This difference in the expression of impairment between the two experiments may be due to large differences in shock intensities used in the training sessions.

The results obtained in the present study suggest that cats with nucleus lateralis lesions were more resistant than the other groups with respect to the change of behavior according to contingencies used in different stages of the experiments. The level of performance during the escape extinction sessions was strongly correlated with median escape latency attained before the change in the procedure. Since these latencies were longest in cats with nucleus lateralis lesions, the lowest level of bar press responses during the escape extinction was expected in this group of cats. However, no statistically significant group differences in the level of performance were observed during the extinction sessions. This was probably related to the peculiar pattern of escape response extinction in cats with nucleus lateralis lesions: rapid decrease of bar presses at the beginning of extinction training with no further changes in the level of responding later on. The extinction procedure resulted in a prolongation of response latencies in all groups of cats. This effect was weakest in cats with nucleus lateralis lesions and differences in response latencies between cats with nucleus centralis and with nucleus lateralis lesions existing prior to the extinction disappeared during the escape response reacquisition stage. The third example of
this specificity of cats with nucleus lateralis lesions was provided by
the avoidance training procedure. It has been shown that the ITR rate
and the performance of newly acquired avoidance responses are
correlated. In spite of the fact that cats with nucleus lateralis lesions
performed significantly more ITRs than cats with nucleus centralis
lesions, the differences between these groups in the number of avoidance
responses were not significant.

It should be tested in specially designed experiments whereas cats
subjected to nucleus lateralis lesions are, or not are, less sensitive to
changes in experimental procedures than the other groups. There is
very little information concerning this problem in previous studies.
In some respect our suggestion may be supported by Werka at al. (17)
results, who found in rats subjected to basolateral amygdalar lesions
only a moderate impairment in the acquisition and retention of one-way
avoidance and a marked deterioration in the following forced extinction
of the task. Some initial slowness of rats with precise nucleus lateralis
lesions in the acquisition of two-way avoidance and a rapid acquisition
of alimentary instrumental reflexes reported by Kiev’s workers (1)
may suggest that the difficulty in recognition and utilization of experimental
contingencies by animals with amygdalar nucleus lateralis lesions may
be restricted only to defensive conditioning. It is not necessarily the
case, since in an old study by Schwartzbaum et al. (13) it has been
shown that amygdalectomized rats were strongly deteriorated in the
reacquisition of frequency discrimination after each generalization test
conducted under extinction procedure. In spite of a bilateral involvement
of putamen in their lesions, the authors concluded that damage to the
amygdala “seems to decrease the plasticity of behavior as seen in the
persistence of response tendencies that are no longer adaptive or, in
other words, in the failure of nonreinforced events to exert adequate
control over the behavior” (13, p. 265).

Generally, the results of the present study are in disagreement
with predictions based on results of experiments in which rather large
lesions of either dorsomedial or basolateral groups of amygdalar nuclei
or electric stimulation of these areas were employed. Fonberg considered
the dorsomedial group of nuclei as involved in emotional behavior and
having excitatory functions, whereas the basolateral group of amygdalar
nuclei — as a part of a system exerting inhibitory influence not only
on alimentary, but also on fear and aggressive reactions (2-4,7). An
increased interest in the environment shown by cats and dogs subjected
to lesions in basolateral amygdala was contrasted with negativism
exhibited by subjects after dorsomedial lesions (5, 6).

The nucleus centralis belongs to the dorsomedial group and the
nucleus lateralis — to the basolateral group of amygdalar nuclei. The results of the present experiment indicate that escape responding in cats with lesions restricted to each of these nuclei was similar, but clearly different than in intact cats. A marked similarity of changes produced by these lesions in the consecutive stages of the experiments is in contradiction to the existing descriptions of the functional heterogeneity of the amygdalar complex.

The results of the present experiment suggest that further investigations may give a positive answer to the question formulated in the title of this paper.

REFERENCES


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Temuraz NANEISHVILI, Beritashvili Institute of Physiology, Tbilisi, USSR.