IMPAIRMENT OF SOCIAL BEHAVIOR IN AMYGDALAR CATS

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Abstract. Social dominance in predatory animals was tested before and after amygdala lesions. Cats after damage of dorsal part of amygdala did not show predatory behavior in group and lost their social rank in hierarchy, but in the same animals predatory attack remained unchanged in nonsocial situations. In the cat with medial amygdala lesions total abolishment of mouse-killing behavior was observed in both social and nonsocial situations. It has been concluded that amygdala plays an essential role in emotional-motivational mechanisms of predatory competitions as one of the forms of social behavior.

INTRODUCTION

The role of the amygdaloid complex in the social behavior of animals has been investigated by many authors in various aspects. The changes of the level of fear and aggression in agonistic as well as in affiliational relations were studied by several authors, but their results were not uniform. Some authors reported docility, reduction of fear and aggressiveness in different species (1, 13, 21, 30). In other papers an increase of aggressiveness was described (2, 15). The investigations in which selective lesions, restricted only to definite nuclei or parts of amygdala were applied, are more clear and throw more light on the subject. Fonberg (8) observed in dogs that a lesion of the dorso-medial part of the amygdala caused an increase of aggressiveness. On the other hand damage of the medial part of the amygdala produced an increase of
docility leading even to apathy. Wood (29) also observed increased aggressiveness in cats after lesions of dorso-medial as well as basal amygdalar nuclei. The same symptom was reported by Lewińska (22) after lesions of nucleus basalis of the amygdala.

Particularly interesting are investigations of gregarious animals. It is obvious that all changes in fear and aggression level after amygdala lesions lead to changes of relations in a social group. Such experiments were performed on monkeys living under laboratory conditions (19, 24, 25), as well as in the natural environment (7, 20). These studies showed that after operation, previously dominant monkeys became placid, tame, fearful and finally they lost their social status and their rank in the animal hierarchy. Lately, the iguanid lizard — a species with a very well organized social structure — was also a subject of investigations which found a marked decrease of aggressiveness and dominance, as well as increased timidity in that animal (26). Similarly, in the experiment of Fuller et al. (12) the decrease of social dominance in pairs was described in dogs. Bunnel (4) showed that bilateral amygdalectomy in the hooded rats can produce marked changes in intraspecific interactions, characterized by a reduction of aggressiveness and a drop in social rank. On the other hand, Bunnel et al. (5) reported that preoperatively dominant and submissive golden hamsters retained their social status after amygdalectomy.

Cats belong to a particularly unsocial species. There exists a generally accepted conjecture that social hierarchy does not appear in Felidae. Formation of rank order in domestic cats is a very rare phenomenon indeed, but it exists in natural conditions (23). It occurs in the time of parental care, when some kittens get first to the richest teat owing to their strength and weight and thus achieve a better position than their litter mates. During a normal and undisturbed development of the litter the “top” animal retains its privileged position until the family disbands after 6–8 months. It seems that some leadership tendencies from the first experiences remain in this cat for the whole of its life. It may be expected that when such cat has to stay on the same limited territory with other individuals of his species, it will display a dominance tendency. Leyhausen (23) described an experiment in which twelve cats were kept in one compartment and a definite dominance order between the animals was observed. In addition, Leyhausen observed that the intensity of expressing emotions depends largely on social position. For showing the same degree of emotion a pariah needs to growl, hiss, fight etc. whereas the top animal lays its ears back and this is enough to get the attention of other animals.

Data concerning the effect of amygdala lesions on social behavior in
cats are very scarce. Some observations of interspecies interactions were performed by Glendenning (14), who found the absence of any postoperative differences in dominance during food competition between operated and control group. The aim of our experiment was to investigate social interactions in a predatory situation i.e., in a competition for a mouse after partial destruction of the amygdaloid complex. As we know from our preliminary studies (9), a predatory competition is an adequate situation for observing social behavior in cats.

METHOD

The experiment was performed on six adult, male cats (1.5–3 years old) weighing 3.5–6.0 kg. Five of them were selected earlier as good predators, one cat learned to catch and kill prey in the course of our experiment.

Predatory behavior in nonsocial situation. Each cat after 24 h food deprivation was placed in a test compartment (180×180 cm). After 5 min a freely moving, white mouse was introduced through a special window. In order to describe the particular pattern of the predatory act and to evaluate the components of aggression which eventually occurs in this type of reaction, the following aspects of the cat’s behavior were observed during 20 min: the manner and speed of moving; the tail, head, ear and back position; the pattern of attack; the latency of attack; the time between killing and the start of eating the prey; the time of consuming the mouse. The piloerection, pupillary dilatation or constriction, sniffing, defecation, urination, vocalization, playing with the mouse and duration of this play were also noted. The mean latency of attack was established on the base of 3 to 5 experimental sessions.

Predatory behavior in social situation. A social group consisted of six cats with previously established characteristics and latency of predatory attack. Cats deprived of food for 24 h were introduced to the experimental compartment (Fig. 1A), in which two boxes and one small ladder were put in different places. When all six cats were collected there, a mouse was thrown in through a special small window placed 143 cm above the floor (see Fig. 1A) and the observations started. The following were noted: (i) which cat first attacked and consumed the mouse, (ii) latency of this first attack, (iii) latency and duration of mouse consumption, (iv) all social interactions within the group, i.e., between the members of the group. Absolute priority in the catching, killing and consuming the mouse was recognized as indicator of dominance. Each experimental session lasted 20 min, during which three
or more mice were offered to the cats. The sessions were repeated once a week to establish a definite hierarchy.

![Image of predatory competition](image)

**Fig. 1.** Changes in predatory competition. A, cat *Bialas* as dominant before operation; B, *Bialas* after dorsal amygdala lesion in nonsocial situation. Notice that there are no changes in predatory attack when cat is alone. C, *Bialas* after dorsal amygdala lesion in social situation. Mouse is denoted by arrow.

In order to establish not only the dominance of the top cat, but also the hierarchy rank within the whole group, the dominant cat was removed and the experimenter observed which cat would take the top position. That cat was subsequently removed and the dominance of the next cat was established. Such procedure was repeated till the dominance of one from the two last members of the group was established. The position of particular members of the group was tested in ten experimental sessions. Each cat, with the exception of the last animal, was successively operated, beginning from the top member of the hierarchy rank. In order to avoid having more than one operated cat in a social group, each lesioned cat was withdrawn from the group after three experimen-
tal sessions. For the observation of postoperative restitution process, the lesioned cats were tested within the group in separate sessions.

**Competition for food.** The competition for food was studied in the same group of six cats. These tests were performed after 24 h of food deprivation in the same experimental compartment three times before the operation, independently from predatory tests (on different days). When all members of the social group were collected in the experimental compartment, a plastic bowl containing 500 g of raw minced horse meat was offered through the door which was thereafter immediately closed. Observations were made through a special window (see Fig. 1A). It was noted which cat first started to eat and what was the behavior of the other cats at that moment. Observations were performed until the bowl was emptied.

**Surgery.** The operation was performed under Nembutal anaesthesia (40 mg/kg). Wolfram electrodes (diam 0.5 mm) insulated with enamel except for 0.3 mm tip, were placed according to the coordinates in the atlas of Jasper and Ajmone-Marsan (16). Electrolytic lesions were made by DC anodal current (2.5 mA) applied for 2 min.

In four cats (named Duży, Łowny, Biały and Maskotka) the lesion was aimed at the dorsal part of the amygdala. In one cat (Czarny) it was aimed at the ventro-medial region of the amygdala.

**Histology.** After the experiments had been accomplished, the animals were anaesthetized with an overdose of Nembutal, perfused with saline and a 10% solution of formalin. The brains were preserved in formalin. Frozen sections 50 μm thick were made, and each 10th section was stained by the Klüver method. Anatomical verification of the localization and dimensions of lesions was made.

**RESULTS**

**I. Before operation**

*Predatory behavior in nonsocial situation.* Usually our cats crouched as soon as they saw a mouse some distance away and in this posture ran very fast towards it. The tail was stretched behind the body and its tip twitched with increasing speed. The ears were erected and turned towards. Evident piloerection on the tail and on the head was observed in most cases. Already within one second of the presentation of the white mouse the cat would catch it immediately by the head
in a killing grip. After killing the prey the cat began to eat it, although occasionally it would first play with the dead mouse. Sometimes the cats displayed another kind of predatory attack which is described as typical (23). In such case the whole body lay flat on the ground, the forelegs were drawn back and the paws directly below the shoulder joints, supporting the body. The body itself was slightly hunched, the sole of each paw lay flat on the ground and the tail was either stretched behind, or curved around the body, its tip twitching gently. The head was stretched forward, the ears erected and turned forward. Sometimes mild piloerection was observed. In this position the animal would watch the prey for a moment and subsequently would catch and consume it.

In three cats the effective attack occurred immediately. That is, within 1 s of the presentation of the mouse the cat caught it with his paws in a characteristic killing grip and broke its neck. In two cats the mean latency of effective attack was longer (up to 5 s). One cat (Maskotka) initially did not make an effective predatory attack — he played with the mouse but did not kill it. Gradually, during experimental sessions he learned to catch and kill the prey, and before surgery was performed on this cat, his latency of muricide attack was 1 to 5 s.

*Predatory behavior in social situation.* A social group consisted of six cats named Duży, Łowny, Białas, Czarny, Tchórz and Maskotka. In the initial period of the experiment (the first three sessions) the cats were fighting with each other even before mouse presentation. In the very first experimental sessions Duży, who was the biggest of all cats, quick in reacting and a very good predator took a top position, but Łowny and Czarny and at first also Tchórz fought for this position as well. Tchórz, who was rather timid, after a few defeats, resigned from competition and most of the time was sitting under the roof of the cage suspended on the bar supporting the wall grill. Białas during the whole period of observations was passive and from the first day of social experiments occupied a safe place on a box in the corner of the cage. Maskotka initially did not kill the mouse, just played with it. None of the cats were ever aggressive towards Maskotka, who was smaller than the others. After 10 experimental sessions a definite linear hierarchy was established. The “top” dominance order was stable as well as the “bottom” position, while the “middle” of the rank order was fluctuating. The boss of the social group with absolute priority in catching, killing and consuming the mouse was Duży. The next place in hierarchy rank was taken by Łowny. Then, third, fourth and fifth positions belonged sometimes to Tchórz, sometimes to Maskotka or Czarny. Białas occupied always the last position in hierarchy order.
**Table I**

Latency of predatory attack in nonsocial situation

<table>
<thead>
<tr>
<th>Cat</th>
<th>Lesion</th>
<th>Before operation Mean latency in s</th>
<th>Experimental sessions after operation</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>1 2 3 4 5 6 7 8 9 10</td>
<td></td>
</tr>
<tr>
<td>Duży</td>
<td>DLA</td>
<td>1 25 20 15 1 1 1 1 1 1</td>
<td></td>
</tr>
<tr>
<td>Łowny</td>
<td>DLA</td>
<td>1 280 220 5 1 1 1 1 1 1</td>
<td></td>
</tr>
<tr>
<td>Białas</td>
<td>DLA</td>
<td>1 180 120 120 10 1 1 1 1 1</td>
<td></td>
</tr>
<tr>
<td>Maskotka</td>
<td>DLA</td>
<td>5 240 60 10 4 1 1 1 1 1</td>
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</tr>
<tr>
<td>Czarny</td>
<td>VMA</td>
<td>5 x x x x x x x x x</td>
<td></td>
</tr>
</tbody>
</table>

x — absence of predatory behavior

Fig. 2. Predatory behavior after VMA lesion. A, cat Czarny before operation; B, Czarny after operation in nonsocial situation; C, Czarny after operation in social situation. Notice postoperative lack of interest in the mouse under both (B and C) conditions. Mouse is denoted by arrow.


**TABLE II**

Dominance order in whole group

<table>
<thead>
<tr>
<th>Before operations</th>
<th>After operation of cat <strong>Duży</strong></th>
<th>After operation of cat <strong>Łowny</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Experimental sessions</strong></td>
<td><strong>Experimental sessions</strong></td>
<td><strong>Experimental sessions</strong></td>
</tr>
<tr>
<td>1</td>
<td>2</td>
<td>3</td>
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<tr>
<td><strong>Duży</strong></td>
<td><strong>Duży</strong></td>
<td><strong>Duży</strong></td>
</tr>
<tr>
<td><strong>Łowny</strong></td>
<td><strong>Łowny</strong></td>
<td><strong>Łowny</strong></td>
</tr>
<tr>
<td><strong>Tchórz</strong></td>
<td><strong>Tchórz</strong></td>
<td><strong>Tchórz</strong></td>
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<tr>
<td><strong>Czarny</strong></td>
<td><strong>Białas</strong></td>
<td><strong>Białas</strong></td>
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<tr>
<td><strong>Białas</strong></td>
<td><strong>Czarny</strong></td>
<td><strong>Białas</strong></td>
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<tr>
<td><strong>Maskotka</strong></td>
<td><strong>Maskotka</strong></td>
<td><strong>Maskotka</strong></td>
</tr>
</tbody>
</table>

**Competition for food.** Food intake from the bowl evoked no conflicts. When tested in a social group, sometimes the dominant cat was the first to start eating, but it was not a rule. Very often **Białas** for example — the most passive member of the group — came up first to the food bowl. Sometimes two or three cats simultaneously started to eat.

**II. After operation**

**Predatory behavior in nonsocial situation.** In four cats (**Duży**, **Łowny**, **Białas** and **Maskotka**) effective predatory behavior was observed immediately after the operation. However, in the first postoperative days latency was longer than before the operation (Table I). All these cats were normally reactive, they were interested in the mouse, they approached the window through which mice were supplied, caught, killed and ate them (Fig. 1B). Only in one cat (**Czarny**) the absence of predatory behavior was observed. This cat was for a few postoperative days apathetic and indifferent (for example, he did not react to experimenter’s caresses), soon he started to respond to external stimuli, however, he was still indifferent to the mouse (Fig. 2B). The impairment of mouse-killing behavior was not permanent — gradually also this cat started to be interested in the mice and progressively caught, killed and ate them.

**Predatory behavior in social situation.** The “top” cat **Duży**, was operated first. After the dorsal amygdala damage, as was mentioned above, **Duży** attacked mice, killed and ate them. But it occurred only when he was alone in the experimental compartment. In a group, he did not dare to approach the mouse and consequently he lost his social status and fell from the top to the bottom position. Now **Łowny** became...
before and after operation

<table>
<thead>
<tr>
<th></th>
<th>After operation of cat <strong>Czarny</strong></th>
<th>After operation of cat <strong>Maskotka</strong></th>
<th>After operation of cat <strong>Białas</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Experimental sessions</strong></td>
<td>1  2  3</td>
<td>1  2  3</td>
<td>1  2  3</td>
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<tr>
<td>Maskotka</td>
<td>Białas</td>
<td>Białas</td>
<td>Tchorz  Białas</td>
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<td>Białas</td>
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<td>Czarny</td>
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Fig. 3. Postoperative restitution of dominance of first boss cat Duży (denoted by arrow). Six weeks after operation.
dominant. After the operation of Łowny his predatory behavior in a nonsocial situation remained without change, but he also lost his previous social status, because he allowed the other cats to catch the mouse. Next Czarny was operated. After lesions in the ventromedial part of the amygdala he lost his predatory behavior and then his social dominance (Fig. 2C). The “top” position in the hierarchy order was filled by Maskotka. After the operation he stopped catching and killing the mouse in the group, but his predatory behavior, as such, was preserved. In the last pair of normal cats — Białas and Tchórz — Białas had the superior position. After the surgery, Białas similarly as Duży, Łowny and Maskotka attacked mice in a nonsocial situation, but did not show predatory behavior in the presence of Tchórz as well as of other lesioned cats. Tchórz remained unoperated. Changes in dominance order after the lesions in particular members of the group are shown in Table II. All cats after some time (from two weeks — in the case of Duży to five weeks in the case of Białas) started to catch and kill mice also in a social situation. Duży recovered his dominance after six weeks, and as a result of several fights with Czarny came to the top of the group again (Fig. 3). The preoperative hierarchy order did not return entirely. Tchórz, who was unoperated, lost in the predatory competition only with Duży and at the end of the experiments he took the second place after Duży.

Competition for food. After the operation non-competitive behavior to the food bowl was not changed at all. As before the operation no dominance order was observed in the situation of food intake from the bowl.

Anatomical verification. In the cats Duży, Łowny and Białas, dorsal area of the amygdala was damaged bilaterally. In Białas the lesion unilaterally involved also a part of nucleus entopeduncularis. In cat Maskotka the lesion bypassed the optic tract slightly involving the dorsal part of the amygdala, and cut the fibers of stria terminalis. In the cat Czarny the lesion damaged the medial part of the amygdala (Fig. 4).

DISCUSSION

The results of our experiments demonstrated and confirmed the fact that hierarchical social structure can exist in cats. Under laboratory conditions we simulated a situation of natural competition and it appears that competition in predatory behavior can evoke a level of emotions conducive to mutual interactions and to the establishment of hierarchy. Dominance order in our experiment was much more evident than in
studies performed by Leyhausen (23), who did not use a predatory test when observing social behavior in cats. In his investigations the privileged position was connected with lair or food bowl only. In our experiments it was shown that food intake from the bowl is not an indicator of social relations. The reason of the absence of competitive alimentary behavior might be the fact that our cats, being laboratory animals, were never hungry, they never needed to fight for food. In contrast, predatory behavior plays an essential role in social dominance and it is a sensitive test of changes in this respect. In addition, our data confirmed earlier results of other authors (4, 5, 7, 9–12, 19, 20, 24–26) showing that the amygdala is involved in social behavior.

![Brain images](image)

**Fig. 4. Reconstructions of lesion for each individual cat.**

Cats after lesions of the dorsal amygdala area did not lose their predatory behavior if they were alone when presented with a mouse. They attacked mice as well as ate them, so probably the rewarding values of both these factors were preserved. However, when tested in a pairs or a group, in the presence of other cats even lower in social hierarchy, they were completely inhibited from catching the mouse. Impairment of predatory behavior concerns only the social situation and predatory behavior is disturbed postoperatively only in this situation, as proved by the fact that food intake from the bowl remained as normal and noncompetitive in manner as before the operation. Any symptoms of fear described by many authors (6, 23, 27, 28), like enhanced piloerection, defecation, urination, tachycardy and others were not observed in operated cats. These cats in a group displayed complete
indifference to the mouse as well as to the other cats. The predatory attack was as effective and precise after the operation as before it if the cats were tested singly. In a previous study we have found (32) that sensory-motor functions in cats with ventromedial as well as dorsal amygdala lesions are not impaired. Initially the latency of effective attack was longer, but only for a few postoperative days. When the latency of attack reached the preoperative level, mouse-killing in a social situation was still inhibited. In the social competition aggressive motivation may play an important role. Predatory behavior as such is, according to ethological definition, connected with alimentary rather than agonistic behavior, but predatory competition undoubtedly included aggressive mechanisms. It was, in particular, clear in the early stage of the experiments, when the cats were doggedly fighting with each other. When a definite hierarchy was established, external signs of aggression were partly suppressed, however, often during the experiments it was observed that the next dominant cat in the group growled when the boss was consuming a mouse sometimes it also had a piloerection and pupillary dilatation. Therefore one of the explanations of disorders in predatory competition after dorsal amygdala lesions is that this part of amygdala might be related to aggression. Karli (17, 18) showed that damage of the dorsal part of amygdala, in particular, of nucleus centralis, abolished mouse-killing in rats. Mouse-killing in rats may be based on mechanisms different from the cat's predatory behavior, namely on territorial rivalry. This kind of reaction in rats is considered by most authors like Karli et al. (18), Van Hemel (31) and others as interspecies aggression. Therefore the data obtained by Karli (17) Karli et al. (18) confirmed our suggestion that dorsal amygdala is involved in aggressive mechanisms and our cats lost their social domination because of deterioration of specific aggressive mechanisms.

The impairment of social behavior after damage to dorsal amygdalar area may be explained by another supposition. It is probable that the amygdala is involved in evaluation of stimuli from the point of biological importance and rewarding value. After lesion in the dorsal part of the amygdala complex — the evaluation of social stimuli (i.e., a rival in a predatory competition) may be changed. It might be likewise supposed for instance, that after damage of the ventromedial part of the amygdala the cat lost his predatory behavior because he did not recognize the mouse as a prey and secondary to that he was not involved in a social competition. We have observed previously a similar effect in pairs of VMA lesioned cats (3, 11). However, initially we supposed that a situation of competition can provoke predatory motivation. It should be stressed that almost immediately after the recovery of predatory behavior, cats
with ventromedial amygdala lesions started to attack within pairs or group and soon regained their previous position. The interesting point for our studies are data about social behavior in cats with lesions in the ventro-posterior part of the hypothalamus. Experiments performed according to the same procedure showed that cats after this kind of lesion retained their social status in pairs during predatory competition (paper in preparation). This fact indicates at least that changes in social hierarchy are not caused by the traumatic effect of the surgery as such.

To recapitulate, we have shown that predatory competition is a good model for the investigation of social interactions in cats. Our experiments confirmed the facts that hierarchical structure can exist even in cats, which were considered as rather asocial animals.

The dorsal amygdala area is not concerned with predatory behavior as such, because in a nonsocial situation, i.e., when the cat was alone with the mouse, predatory behavior remained perfect and was unchanged by operation. Therefore it might be concluded that the dorsal part of the amygdala is specifically involved in social behavior. Cats investigated in a situation of predatory competition did not exhibit predatory attack after lesion and therefore lost their social status in the hierarchy rank. In contrast, the ventromedial amygdala lesioned cat lost his predatory behavior in a nonsocial as well as in a social situation. Therefore it might be supposed that in ventromedial cats the deterioration of social position was secondary and was probably produced by the impairment of predatory motivation as such. The role of the impairment of aggressive mechanisms in the deterioration of social dominance needs further elucidation.

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