

Stimulus control of predatory aggression*

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In contrast to enucleation or deafening, olfactory bulbectomy increases mouse-killing in rats. Mice coated with lavender oil are killed more frequently by intact rats. These and previous experiments indicate that olfactory bulbectomy releases an inhibition of mouse killing in the rat and suggest a specific mechanism for such inhibition.

The present investigation is one of a series of attempts to analyze the role of stimulus factors determining emotional and aggressive reactions in the albino rat. The present study is concerned with the effects of alterations of the perceived "prey" stimulus, on "predatory" aggression in the albino rat. Specifically, these experiments involve mouse killing in rats suffering a variety of sensory deficits, and killing of mice with altered olfactory characteristics.

EXPERIMENT I

Experiment I was a determination of the effects of specific sensory deficits on mouse killing in a rat strain in which nonkillers predominate. With the exception that a different rat strain was used, and that auditory deficits were also examined, this experiment was similar to that of Bugbee and Eichelman (1972).

Method

Subjects. The Ss were 38 male rats, 163 to 177 days of age, from the colony of Wistar-derived rats maintained by the Department of Psychology of the University of Hawaii. They were divided into five groups: deafened (D), enucleated (E), bulbectomized (B), operated control (OC), and unoperated control (UC). The first two groups consisted of seven Ss each, while the last three groups each had eight Ss. However, after the experiment was concluded, one member of the bulbectomized group was found to have frontal damage, and its data were omitted.

Surgical Procedures. All surgical procedures were carried out under 40 mg/kg sodium nembutal anesthesia. Each rat was allowed a 7-day recovery period before the test procedures were run.

Controls. The operated controls were anesthetized and placed in the stereotaxic instrument frame. No further surgical procedures were utilized.

Enucleation. To enucleate the animals, the E applied manual pressure around the orbit, resulting in the extrusion of the

eyeball. The eye muscle attachments and optic nerve were cut with surgical scissors.

Bulbectomy. With the rat's head in the stereotaxic frame, the frontal bones were drilled away until all of the olfactory bulb was visible. The bulbs were removed using a glass micropipet, attached to a vacuum hose. The olfactory capsule was packed with gelfoam and the wound closed with sutures.

Deafened. A 3-mm bent wire probe was inserted into the rat's middle ear and rotated, destroying the bones of the middle ear. In order to determine if the operation was successful, all deafened animals were tested for startle responses to a sudden 95-100 dB spl noise (pop gun). These tests were made one week after surgery and one or more days before each experimental procedure. Three animals in this group showed a startle response and were discarded.

Apparatus and Procedures. The rats were housed in individual 24 x 19 x 19 cm metal cages for 3 months prior to the experiment. Testing involved placing a male DBA mouse in the front of each rat's cage. The rat itself was not moved or handled. Checks were made at intervals of 15 min 30 min, 1 h, 1½ h, and 2 h after the mice had been introduced, to determine if the rats had killed. The experiment was terminated after 24 h, at which time the dead mice were examined to see if they had been eaten.

Results

Table 1 presents the percentage of rats in each group who killed mice as a function of the time after the introduction of the mouse. It may be seen that nearly half the bulbectomized animals killed in the first hour of exposure to the mouse and 71.43% of Group B killed during the total 24-h observation period. None of the animals in the remaining groups killed mice. Thus

Table 1
Percentage of Ss in Each Group Killing Mice as a
Function of Time After Introduction of Mice

Group	Time				
	15 min	30 min	1 h	1½ h	2 h
Deafened	14.3	14.3	14.3	28.6	28.6
Bulbectomized	28.6	28.6	42.9	71.4	71.4
Enucleated	0	0	0	0	0
Operated Control	0	0	0	0	0
Unoperated Control	0	0	0	0	0

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olfactory bulbectomy produced a dramatic increase in mouse killing. These results were analyzed using a Fisher exact probability test (Siegel, 1956) and were found to be statistically reliable. The bulbectomized group differed reliably ($p < .02$ for each case) from the other groups in the number of mice killed. Each of the bulbectomized animals that killed ate all of the stimulus mouse within the 24-h period, leaving only fur and bones, with the exception of one animal who consumed only the brain of the stimulus mouse.

These findings are consistent with those of Myer (1964), Bugbee and Eichelman (1972), and Karli, Vergnes, and Didiergeorges (1969) showing that olfactory bulbectomy produces killing in nonkilling rats. These findings agree with Bugbee and Eichelman's (1972) report that enucleation and removal of vibrissae do not increase mouse killing, and further suggest that deafening has no effect on predatory aggression.

Karli et al (1969) have suggested that olfactory bulbectomy releases inhibition of mouse killing behavior. Such inhibition is presumed to be based on an olfactory similarity between mice and rats, which normally operates to inhibit predation of other (especially young) rats. Thus, the removal of the olfactory bulbs might be expected to result in a breakdown of the rat's differentiation between "rat pups" (including mice) and more appropriate prey.

EXPERIMENT II

The Karli et al theory suggests that olfactory bulbectomy increases mouse killing because the rat can no longer smell the mouse. However, Spector and Hull (1972) have reported that removal of the olfactory mucosa and afferents, with an intact olfactory bulb, fails to produce increases in mouse killing in animals that do not normally kill. This finding suggests that the mechanism of release of mouse killing which occurs when the olfactory bulb is removed is not just a simple elimination of the rat's ability to smell the mouse. It appears likely, however, that some manipulations which alter specific olfactory input to the rat, without olfactory bulb damage, can increase mouse killing. Myer (1964) has reported that baby rats, which are normally not killed by adult rats, may be killed if they are coated with lavender oil. If mice coated with lavender oil are also killed, then attempts to explain the mechanism of inhibition of killing and the release of such inhibition must also deal with this phenomenon.

Method

Subjects. The Ss were 20 naive male rats, 118 to 120 days old, from the same colony as those of the previous experiments.

Apparatus and Procedure. The stimuli were 20 male DBA mice, 258 to 259 days old. On Day 1, the mice were not coated with any scent, and the apparatus and procedure were identical to those of Experiment I, except for the time intervals employed. The cages were checked 10 min, 20 min, 30 min, 1 h, 2 h, 4 h, 22 h, 23 h, and 24 h after the mice were presented to the rats.

On Day 2 the apparatus and procedures were the same as on Day 1 except that the mice were coated with lavender oil immediately before being placed in the cages.

Lavender Oil Control. An additional five mice from the same population as those used in the experiment were coated with lavender oil and left alone in individual cages for 24 h to determine if lavender oil alone might have accounted for any deaths in the coated group. All of these lavender-oil control mice were living at the end of the 24-h period.

Results

There was no mouse killing on Day 1 when the mice were not scented with lavender oil. However, on Day 2 when the mice were coated with lavender oil, mouse killing did occur. At the end of the 24-h period, 60% of the rats had killed their mice. A McNemar test (Siegel, 1956) for the significance of changes indicated that this increase in mouse killing from Day 1 to Day 2 was significant [$\chi^2 = 10.08$, $df = 1$, $p < .01$]. This result clearly indicates that coating the mice with lavender oil increase mouse killing in the rat.

Taken all together, the present findings and those of Spector and Hull (1972) present a very pretty puzzle. First, if coating the mouse with lavender oil and destruction of the rat's olfactory mucosa, both merely prevent the rat from smelling the mouse's "rat-like" odor, then both procedures should increase mouse killing by the rat. This however, has not been found. Also, if the removal of the rat's olfactory bulb merely eliminate smell, then olfactory bulb removal and destruction of the olfactory mucosa should have identical effects. Instead, the former increases mouse killing (Experiment I) while the latter does not (Spector & Hull, 1972). One possible solution to this problem involves the recognition that lavender oil does not simply eliminate the mouse's odor: instead it adds a very distinctive odor of its own. In considering the evolution of the inhibition mechanism, it seems likely that a programmed "command" which resulted in a failure to eat small animals with a "rat-like" smell would reduce cannibalism of young rats by their parents and thus increase survival probabilities for the offspring of rats carrying such a command. However, the ability to smell is not infrequently lost, for varying periods of time, in mammals. If the inhibition system were triggered only by a present "rat-like" odor, then a mother rat with a head cold should immediately cannibalize her own pups. An inhibition system released only by the presence of some "not rat" odor would eliminate instances of baby rat cannibalism by rats with impaired olfactory abilities, and would therefore produce (other things being equal) greater chances of reproductive success in these rats.

Such a mechanism is consonant with the present lavender oil findings and with the findings of Spector and Hull (1972). What, however, of the well documented phenomenon of mouse killing in bulbectomized rats? If these cannot smell anything then it might be expected that they would (in terms of the notions outlined above) kill nothing. One possibility,

which would explain these data as well as the Spector and Hull findings, is that the olfactory bulb is the locus—or at least one essential locus—of the inhibitory command. That is, an inhibitory mechanism must involve some anatomical loci and—without any direct evidence in either direction—it seems not unreasonable to assume that some aspect of the inhibition system may be damaged by olfactory bulb removal. Such removal would therefore render the inhibition system inoperative, such that odors, even if they could be processed, would be irrelevant. This formulation can thus account for all the otherwise puzzling phenomena in this area, and furthermore suggests an evolutionary mechanism for the acquisition of the inhibitory function.

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Ontogenetic changes in classification behavior

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A developmental study of free-classification behavior within the age range of 3-1/2 to 19 years indicates that categorical responses, which are characteristic of adult behavior, increase with age while overgeneralized responses, classifications including noncategorical instances, decrease with age. Overdiscriminated responses which are incomplete categorical classifications increase from 3-1/2 to 6 years and then decrease to 19 years of age. These results are discussed within a two-stage theory of conceptual development (Kendler, 1971).

This paper reports *selected* findings from a large-scale developmental study that was designed to investigate the two-stage theory of conceptual development (Kendler, 1971). This formulation, which is an outgrowth of discrimination shift studies (Kendler & Kendler, 1962; 1970), postulates that, at early ages, the mechanism of stimulus generalization guides classification performance while later on mediational mechanisms in the form of implicit representational responses control such performance. During the early period of the mediational stage, it is additionally assumed that Ss form narrow concepts and only later do they become capable of forming broad concepts that are characteristic of adult behavior (Saltz & Siegel, 1967).

METHOD

Subjects

A total of 192 Ss, 32 at six different age levels, are described in Table 1. An additional 22 Ss were eliminated, 3 for E's error; 16 Ss from the three youngest age levels who refused to finish the experiment, 2 who failed to complete the experiment due to illness, and one 3-year-old who could not solve all the practice problems. The 3- and 4-year-old children were drawn from private nursery schools; the elementary school children, from the public school system in Goleta, California, and the college

students from introductory psychology classes at the University of California, Santa Barbara. Analysis of variance of the children's Peabody Picture Vocabulary Test (PPVT) scores (Dunn, 1959) failed to indicate any significant age-related difference in intelligence over age [$F(4,155) = 1.47, p > .20$].

Procedure

Each S was confronted with a sequence of eight successive classification tasks, four of which involved two-dimensional stimuli (Fig. 1), the results of which are reported in this paper. The remaining four tasks involved stimulus patterns with binary values of four characteristics (e.g., a schematic drawing of a human face with two values of the eyes, nose, mouth, and moustache). The results obtained with these stimuli will not be reported because of unanticipated and insuperable difficulties in developing satisfactory response measures.

Table 1
Description of Ss at Each Age Level

Age in Months		Number		PPVT IQ	
Mean	Range	Male	Female	Mean	SD
42.4	36-47	14	18	115.9	13.5
54.1	49-59	14	18	112.6	9.9
69.5	65-76	12	20	112.2	7.2
97.4	85-110	18	14	109.3	13.5
144.2	131-156	15	17	110.0	14.8
225.7	215-247	9	23	-	-