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Involvement of the Brain Catecholaminergic System in the Regulation of Dominant Behavior

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SEROVA, L. I. AND E. V. NAUMENKO. *Involvement of the brain catecholaminergic system in the regulation of dominant behavior.* PHARMACOL BIOCHEM BEHAV 53(2) 285–290, 1996. – The role of the brain catecholaminergic system in establishing dominant–subordinate relationships in mice of different genotypes was studied using inhibitors of tyrosine hydroxylase (α-methyl-p-tyrosine) or of dopamine-β-hydroxylase (FLA-57) or FLA-57 plus the dopamine precursor, DOPA. Demotion in all dominant and subdominant animals was associated with decreased noradrenaline levels, but the aggressive behavior of dominant male mice depended on the noradrenaline/dopamine ratio. Alterations in this relationship seem to have specific effects on social dominance in animals in the micropopulation, as drug-treated mice do not exhibit changes in their general activity. It can be concluded that brain catecholamines are of prime importance in maintenance of dominance.

Dominance Noradrenaline Dopamine Mice

CURRENT data testify both to the involvement of brain neurotransmitters in the regulation of behavior and to functional interrelations between parameters of brain neurochemistry and behavior (6,14,27,30,45,47). Analysis of the role of the central noradrenergic system in the modulation of aggression suggests excitatory noradrenaline control of different forms of aggressive behavior (18,20,27,42) and inhibitory effects on affective and predatory aggression (43,47). Most research on catecholamines in animals has focused on the regulation of aggression and defence (8) or on locomotion (35) as main features of dominant–subordinate behavior. The influence of catecholamines on the regulation of dominant behavior has been demonstrated by Miczek and Gold (1983), who found that the effect of amphetamine depends on social status; amphetamine-induced changes in antagonistic behavior, locomotion, and olfactory marking were selectively seen in dominant animals compared with subdominant and submissive monkeys. These behavioral effects seemed to be due to changes in the catecholaminergic systems upon which the drug acts.

Studies of social behavior show that the distribution of males in hierarchical classes is dependent on genotype and is nonrandom (40); in addition, males of various genotypes differ in their regional catecholamine levels. The data indicate an influence of genotype on the noradrenaline content of the olfactory bulb, hypothalamus, hippocampus, striatum, and brain stem. Our own previous work on different strains of mice (39) demonstrated that PT mice have both the highest brain noradrenaline levels and the highest percentage of dominant animals, while CBA mice, with low brain noradrenaline levels, rarely reach the dominant social rank in micropopulations. These results indicate that the genotype-dependent capacity for social dominance is related to the functioning of central noradrenergic neurons. Correlation analysis shows a strong intrastrain rank correlation between the noradrenaline levels in the striatum and brain stem and the percentage of dominant males in these murine strains (41). We suggest that the central noradrenergic system is involved in the coordination of the species-specific complex program of dominant behavior (5,13,37).

The goal of this article was to use pharmacological procedures to determine the effect of inhibitors of neurotransmitter biosynthesis on the manifestation of the dominant phenotype.

METHOD

Animals

Three-month-old (23–24 g) mice from inbred strains [A/He (n = 60), C57Bl/6J (n = 60), CBA/Lac (n = 60), DD (n = 60), YT (n = 60), and PT (n = 124)] were used. The animals were born and bred under natural illumination in the animal house of the Institute of Cytology and Genetics of the Russia Academy of Sciences and received food and water ad lib.

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Procedures

Mice were individually caged 5 days before the start of the experiments. To study hierarchic relationships, at 0800 h, six male mice (one per genotype) were grouped in special population cages; these were 74 cm long, 44 cm wide, and 17 cm high, divided by two partitions into three equal sized areas, these being a central corridor and two lateral areas, each of the latter being divided into three equal size compartments connected to the central corridor by a hole but separated one from the other. Individual and social mouse behavior were tested for 3 h immediately after grouping and for 3 h the next morning. Each test consisted of four 20-min observation periods, separated by 20-min intervals. Dominant-subordinate relationships were studied over a 2-day period, the time needed to establish the hierarchy (24,32). Dominant rank was determined by recording the individuals involved in unambiguous fight encounters resulting in one victorious and one defeated mouse. The male with the maximum number of victories who patrolled the cage corridor and showed aggressive towards other mice was classed as the dominant mouse (16). Animals were ranked as dominant if they exhibited such behavior on both test days. The male that ranked second in aggressiveness and social activity was classed as the subdominant mouse. Because the other four animals in each population group showed much less activity, their ranking could not be reliably assessed and they were, therefore, classed as subordinates. The latency period of the first attack and the total number of victories and defeats over the entire test period on the first day were scored.

In our previous study, we found that, in heterogeneous populations, highest dominance was displayed by males of the PT strain (39,40) and that they also comprised the majority of animals in the dominant and subdominant classes. In further experiments, only those populations in which PT males were dominant or subdominant were used, and only these PT mice were treated with drugs. After the animals' ranks had been determined, they were returned to their individual cages for a 6-day period. On the sixth day, dominant (n = 36) or subdominant (n = 24) mice received an intraperitoneal injection of drugs affecting catecholamine biosynthesis. All animals were then housed in the same group in population cages and their social behavior again noted.

Drugs affecting catecholamine biosynthesis were checked for their effect on both locomotion and brain catecholamine levels. Two identical groups (each n = 32; eight mice treated with α-MT, eight with FLA-57, eight with FLA-57 + L-DOPA, and eight with vehicle) were established; the first tested for locomotion and the second for brain levels of noradrenaline and dopamine. Locomotion was measured in a 5-min open-field test (4). Animals from group 2 were killed by decapitation. The brain was rapidly removed in the cold and dissected into two parts, the hemispheres and the brain stem, which were frozen at −70°C until analyzed fluorimetrically for catecholamine content (25).

Drugs

Tyrosine hydroxylase inhibitor (salt-acid methyl ester α-methyl-DL-tyrosine, α-MT, Serva) was dissolved in a physiological solution and injected at a dose of 120 mg/kg 7 h before testing (29). The dopamine-β-hydroxylase inhibitor (4-methylhomopiperasinilditiocarboxylic acid, FLA-57, Serva) was dissolved in 0.05% Tween 80 and injected at a dose of 75 mg/kg 6 h before testing (22). One hour before testing, a separate group of FLA-57–treated mice was injected with 40 mg/kg of the dopamine precursor, L-DOPA (3,4-dioxyphenylalanine, Reanal), dissolved in 0.05% Tween 80. Control mice were injected with vehicle.

Statistical Analysis

Statistical analysis of the results was performed using Student's t-test, Fisher's exact test and Wilcoxon s nonparametrical test.

RESULTS

The drugs used affected catecholamine biosynthesis and altered the brain noradrenaline/dopamine ratio (Fig. 1). Injection with α-MT was followed by a significant mean decrease of 30% in noradrenaline and dopamine, both in the brain stem ($p < 0.01$) and in the hemisphere ($p < 0.01$). FLA-57 injection caused a greater decrease in noradrenaline of, on average, 50% in the hemispheres ($p < 0.001$) and 70% in the brain stem ($p < 0.001$), while the dopamine concentration was unchanged. Mice with a low noradrenaline level receiving L-DOPA pretreatment showed a 30% increase in dopamine ($p < 0.05$) in the hemispheres and 50% in the brain stem ($p < 0.001$).

Analysis of the dominant-subordinate relationships revealed that virtually all animals receiving the three drug treatments were demoted from dominant or subdominant status to subordinate (Tables 1 and 2) and had a decreased number of victories (Table 3). In the dominant animals, α-MT treatment produced a significant decrease in aggression, but to a lesser extent than the other drugs. FLA-57–treated mice showed a dramatic reduction in fighting when compared with either controls or α-MT–treated animals. The combined use of FLA-57 and L-DOPA resulted in almost a complete loss of aggression, with the number of victories being significantly lower than in controls or animals treated with either α-MT or FLA-57. The number of victories of dominant animals in both the experimental and control groups was significantly lower than in intact animals (first testing). Subdominant animals given α-MT also showed a decreased number of victories, while animals treated with FLA-57 or FLA-57 plus L-DOPA showed no aggressiveness whatsoever. Concurrently with the reduction in victories, dominant males also showed a reduction in the number of defeats, this result being significant in the case of treatment with FLA-57, either alone or in combination with DOPA, while subdominant males showed no change in the number of defeats (Table 4). The latent period for the first attack of α-MT–treated mice increased significantly in both groups of high-ranking animals; in the dominant and subdominant males, the mean increased from 5.8 to 7.9 min ($p < 0.05$) and 10.5 to 15.0 min ($p < 0.05$), respectively. The latent period in mice treated with FLA-57, either alone or in combination with L-DOPA, could not be determined, as the number of attacks decreased markedly.

Open-field test analysis of motor activity in male PT mice showed that the various treatments did not significantly alter the summed movement of the animals, the mean number of squares crossed by controls, α-MT-, FLA-57-, and FLA-57 + L-DOPA–treated mice being 201 ± 11.0, 189 ± 18.4, 222 ± 15.4, and 175 ± 20.0, respectively.

DISCUSSION

To alter the noradrenaline-dopamine balance in the brain, animals were treated with two inhibitors of catecholamine synthesis and with the dopamine precursor, L-DOPA. All experi-

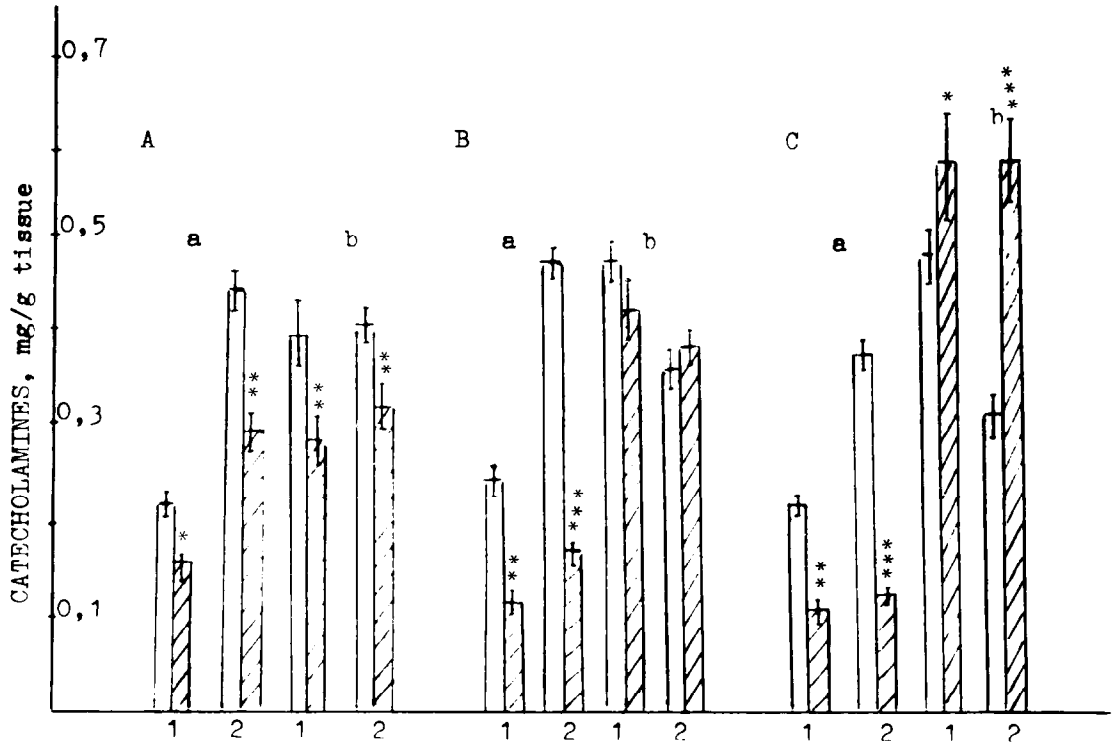

FIG. 1. Noradrenaline (a) and dopamine (b) concentrations (mean + SEM) in the hemispheres [1] and in the brain stem [2] after administration of α-MT (A), FLA-57 (B), or FLA-57 + L-DOPA (C). *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$ in comparison with controls. The white columns represent mean catecholamine levels after treatment with vehicle, the striped columns after drug administration.

mental treatments resulted in a significant reduction in brain noradrenaline. In contrast, the effect on dopamine levels was drug dependent, with a decrease following administration of the tyrosine hydroxylase inhibitor, no change following administration of the dopamine-β-hydroxylase inhibitor and an increase following combined use of the dopamine-β-hydroxylase inhibitor and the dopamine precursor. These data agree with those from other groups who have studied catecholamine levels in the brain after administration of analogous preparations for other purposes (1,22,29). The social behavior of the treated male mice showed an important change: irrespective of variations in dopamine levels, the social status of previously dominant or subdominant mice, whose noradrenaline levels had been decreased by treatment, was reduced, i.e., they became subordinates. It has been suggested that central adrenergic mechanisms play an important, or even the major, role in the appearence of dominant behavior. The results of our pharmacological study are in agreement with our previous investigation of the genetic correlation between neurotransmitters and dominance behavior in male mice of different strains (40,41). A strong intrastrain rank correlation was found between the level of noradrenaline and tyrosine hydroxylase activity in the striatum, hypocampus, and brain stem and the percentage of dominant males. There was no significant correlation between dominant behavior and brain dopamine or serotonin metabolism. The aggression of dominant

TABLE 1

ALTERATION IN SOCIAL RANK OF DOMINANT PT STRAIN MICE AFTER ADMINISTRATION OF DRUGS AFFECTING CATECHOLAMINE SYNTHESIS

	Number of Mice	
Experimental Series	Dominants	Subordinates
Control	9	0
α-MT	1	8*
FLA-57	0	9*
FLA-57 + L-DOPA	0	9*

*$p < 0.025$.

TABLE 2

ALTERATION IN SOCIAL RANK OF SUBDOMINANT PT STRAIN MICE AFTER ADMINISTRATION OF DRUGS AFFECTING CATECHOLAMINE SYNTHESIS

	Number of Mice	
Experimental Series	Subdominant	Subordinate
Control	6	0
α-MT	0	5*
FLA-57	0	6*
FLA-57 + L-DOPA	0	6*

*$p < 0.025$.

TABLE 3

NUMBER OF VICTORIES IN PT STRAIN MALES AFTER ADMINISTRATION OF DRUGS AFFECTING CATECHOLAMINE SYNTHESIS

Experimental Series	Number of Victories $\bar{x}$ (x_{min} – x_{max}) Dominants	Subdominants
Intact (first testing)	23.3 (15–47) [36]	10 (2–12) [24]
Control	15.7 (8–34) [9]!	6.6 (1–12) [6]
α-MT	8.6 (0–23) [9]*!	2.6 (0–6) [6]†
FLA-57	1.0 (0–3) [9]*!	0 [6]*
FLA-57 + L-DOPA	0.1 (0–1) [9]*(*)!	0 [6]*

The number of animals is given in brackets; *$p < 0.01$, †$p < 0.05$ in comparison with controls; (*)$p < 0.05$ in comparison with FLA-57-treated animals, !$p < 0.01$ in comparison with intact animals.

and subdominant PT mice with lowered noradrenaline levels was also reduced, with a dramatic drop in the number of victories as the difference between the levels of noradrenaline and dopamine increased.

Administration of the tyrosine hydroxylase inhibitor decreased the levels of both noradrenaline and dopamine and was followed by a reduction in victories of the previously dominant mice. Treatment with the dopamine-β-hydroxylase inhibitor resulted in unchanged brain dopamine levels but decreased levels of noradrenaline. In these animals, the reduction both in brain noradrenaline levels and in victories was greater than in animals receiving tyrosine hydroxylase inhibitor treatment. In subdominant animals, with either normal or elevated brain dopamine levels, a decrease in noradrenaline content completely suppressed their capability for dominance. Dominants with decreased brain noradrenaline levels and increased dopamine levels showed a 10-fold reduction in victories. Using different models of aggression, an influence of the noradrenaline system on aggression has been shown. Inhibition of noradrenaline uptake by desimipramine increases aggression in long-term isolated mice; this effect is eliminated by adrenoceptor antagonists or lesions of the noradrenergic system induced by the noradrenergic neurotoxin DSP-4 (27). In contrast, the chronic reduction in brain noradrenaline content induced by DSP-4 increases aggressive behavior in rat intruders in the model intruder–resident paradigm (47). This is in agreement with our previous data showing increased aggression in dominant PT mice, using 6OHDA *define* (38). However, in this study, the destruction of noradrenergic neurons 3 weeks before behavior testing potentiated the development of postsynaptic membrane hypersensitivity (22), so an increase in numbers of attacks might be due to chronic alterations of neuronal neurochemistry. A complex interaction in the regulation of foot shock aggression behavior between dopamine- and noradrenaline-containing neurons in the CNS has been described by several authors (3,9,17,30,34). Aggressive behavior was inhibited by several neuroleptics without any effect on dopaminergic neurotransmission (26). However, the effect on clonidine-induced aggressiveness depends on the dose used, the genotype of the mice and the genotype-dependent presence of physiologically functional D_1 dopamine receptors (30) and α_1-adrenoceptors (46). Based on our data, we suggest that the balance between noradrenaline and dopamine is important in maintaining intermale aggressive behavior in mice with genetically determined dominant behavior.

We believe that all the applied drugs have a specific effect on the dominance behavior of mice. This is supported by the experiments showing changes in locomotion in the open-field test in which none of the drugs had any effect. We believe that changes in brain catecholamine levels disrupt the specific consolidatory effect of the noradrenergic system in the establishment of the dominant behavioral phenotype. The increased dopamine level in dominants with a lowered noradrenaline level was followed by a gradual decrease in the number of defeats, although the number of victories also declined. One reason for the reduction in the number of defeats is the reduction in social activity and aggressive behavior of dominants treated with FLA or FLA plus DOPA. The number of defeats is determined not only by the aggressive behavior of the dominant mice but also by the behavior of subordinate animals: their fear, pain from previous bites, and other behavioral elements learned during the establishment of the hierarchic structure in the population (7,21,38).

Another reason for the decline in the number of defeats in all experimental groups is prior social experience (12). This may be related to the memory of the animals previously defeated by the dominant male during the preliminary testing stage. In the case of territorial aggression (7), it has been suggested that the experience of intruders changes aggressive behavior by decreasing the resident's fear of strangers. The influence of social experience on offensive and defensive behavior has been discussed in detail by several investigators (2,10–12,23). It is also possible that, when the animals are placed back in the group, the dominant exerts an influence over other mice in the population by various means of communication, such as odor (15,31,44), vocalization, etc., which may change after treatment. However, in the present study, these features was not taken into account.

Quite different results were seen in populations in which the subdominant animal was treated. In these animals the change in brain catecholamine levels did not affect the number of defeats. The reason for this is unclear, but it may result from the fact that subordinate animals do not play a leading part in establishing the hierarchic structure, which means that, when the animals are regrouped, this community process goes on as before, i.e., other members, mainly the dominant, do not change their attitude to the subdominant and subordinate animals. However, the reason still remains unclear and requires further detailed experimentation.

Thus, the brain catecholaminergic systems are important in the regulation of dominant behavior. Because the decrease in brain noradrenaline levels is followed by an marked decline in aggressiveness and subsequent social demotion, it may be

TABLE 4

NUMBER OF DEFEATS OF PT STRAIN MALES AFTER ADMINISTRATION OF DRUGS AFFECTING CATECHOLAMINE SYNTHESIS

Experimental Series	Number of Defeats $\bar{x}$ (x_{min} – x_{max}) Min Dominants	Max Subdominants
Intact (first testing)	5.1 (0–8) [36]	15.3 (3–15) [24]
Control	2.5 (0–8) [9]	9.1 (6–14) [6]
α-MT	2.0 (0–8) [9]	7.3 (4–17) [6]
FLA-57	0.8 (0–4) [9]*	8.1 (2–13) [6]
FLA-57 + L-DOPA	0.6 (0–3) [9]*	6.8 (1–17) [6]

*$p < 0.01$ in comparison with controls.

concluded that the noradrenergic system plays the leading role in the regulation of neurochemical brain processes involved in the establishment of dominant behavior. At the same time, the number of attacks resulting in victories depends not only on the absolute decrease in the noradrenaline level but also on the noradrenaline–dopamine ratio. An increase in dopamine levels in male mice with lowered levels of noradrenaline causes a decline in their aggressiveness in the micropopulation.

In addition, it is known that the regional distribution of catecholamines in the brain (19,33,40) and the number of catecholaminergic neurons (36) are controlled by genotype, suggesting that genotypically controlled factors regulate the relationship between noradrenergic and dopaminergic mechanisms in the animal predisposed to dominant behavior.

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