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An Empirical Study of the Structure of the Patrol/Marking Motivational System in the Rat

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Received 2 June 1981

LEE, S., J. MITCHELL AND D. B. ADAMS. *An empirical study of the structure of the patrol/marking motivational system in the rat.* PHYSIOL BEHAV 32(4) 565–573, 1984.—The existence and structure of an hypothesized motivational system of patrol/marking was supported and elucidated by a behavioral study on untrained highly inbred laboratory rats. One rat (the "runner") was placed into a test chamber containing a wire-mesh running wheel flanked by two chambers, one of which contained another rat (the "target"). Four conditions of runners (socially-isolated males, socially-housed males, non-estrous females, and estrous females) were exposed to four types of targets (socially-housed males, non-estrous females, estrous females, and blank targets consisting of any empty target chamber). Also placed in the chamber was a Petri dish containing scent-markings of the target rat. The experiment was designed in a counterbalanced way with 10 replications and repeated two times in two separate years. As predicted from the hypothesis, scent-marking, sniffing the dish, locomotion (number of wheel revolutions), and approach (differential running towards the target) were all correlated with each other and varied in the same way as a function of the hormonal and experiential condition of the runner and the type of target. They were interpreted to reflect motor patterns of a single unitary patrol/marking motivational system. Grooming, on the other hand, did not correlate with the other behaviors and facial gland secretion was, therefore, rejected as a motor pattern of patrol/marking.

Strain differences Locomotor activity Patrol/marking motivational system

THIS study was designed to test the hypothesized hierarchical structure of patrol/marking behavior in the rat according to the theory of a patrol/marking motivational system. The various behaviors pertaining to patrol/marking have been described and called "patrolling" in males of a number of muroid rodent species, including mice [16], lemmings [9], Apodemus sp. [10], Psammomys sp. [17], Aethomys sp. [15], and Neotoma sp. [22]. It has been observed by many investigators that this behavior includes not only locomotion and investigation, but also scent-marking, that it is exhibited not only by dominant males, but also by estrous females, and that both sexes exhibit the behaviors maximally in the presence of conspecifics of the opposite sex [3].

The theory that there is a single, unified, hierarchically-organized, motivational system of patrol/marking has been developed on the basis of a comparative review of the agonistic behavior of muroid rodents [3], and its dependence upon gonadal hormones has been reviewed [4]. It has been proposed that the unity of the system is due to a single neural mechanism, the patrol/marking motivational mechanism, whose activation determines the level of patrol/marking motivation and, consequently, the performance and intensity of patrol/marking behaviors. This motivation is neither sexual nor aggressive, but it functions to advertise the reproductive state of the animal and to ascertain the reproductive state of other conspecific animals that it encounters.

The proposed hierarchical structure of the patrol/marking motivational system leads to specific, testable predictions about the motor patterns of patrol/marking and their stimulus and hormonal control. Since it has been proposed that all of the motor patterns (undirected locomotion, approach locomotion, stop-and-sniff behavior, facial-gland secretion, and scent-marking) are activated by a single unified motivational mechanism, it could be predicted that they should all be correlated in their occurrence. Stimuli, according to the theory, can have two different kinds of effects: (1) motivating effects upon the motivational mechanism itself which should affect all of the motor patterns equally; and (2) releasing or directing effects upon the motor patterns individually, which should affect one or several motor patterns without affecting the others.

Hormones, genetic factors, and motivational interactions, in the theory, should be able to affect the hierarchical system at any one of four different levels: (1) the analyzers of motivating stimuli; (2) the motivational mechanism; (3) the motor patterning mechanisms; or (4) the analyzers of releasing or directing stimuli. In the first two cases it would be predicted that they would affect all of the motor patterns of patrol/marking equally. In the latter two cases they would be expected to affect only certain motor patterns and not others. Finally, according to the theory it should be possible to distinguish between effects on motivating stimulus

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analyzers and effects on the motivational mechanism itself; the former should affect all patrol/marking motor patterns activated by that motivating stimulus and no other motivating stimulus; the latter should affect all patrol/marking regardless of the motivating stimuli that are operating in any particular instance.

The experiment was designed to test the theory by presenting male and female rats in various hormonal and motivational conditions with the various motivating stimuli of patrol/marking (independent variables) and measuring the various motor patterns of patrol/marking (dependent variables). The rat was placed in a test chamber with a scent-marked Petri dish (to elicit stop-and-sniff and scent-marking) and a running wheel (for the measurement of locomotion) in which the animal had the choice of running towards or away from a "target" rat. The target was located next to the running wheel so that the animal could "approach" the target by running on the wheel. Targets were chosen in order to present a range of different motivating stimuli: males, non-estrous females; estrous females; and control (blank) targets. Facial-gland secretion was measured indirectly in terms of frequency of facial grooming. A series of 14 predictions were tested corresponding to various aspects of the hypothetical structure of the patrol/marking motivational system.

The hypothesized unity of patrol/marking (i.e., its dependence on the activation of a single motivational mechanism) was tested with predictions 1–5. Correlation coefficients were computed among the five proposed motor patterns of patrol/marking that could be measured (stop-and-sniff, scent-marking, undirected locomotion, approach locomotion, and facial grooming) and it was predicted that they should all be significantly and positively correlated.

Factors that were proposed to operate directly upon the motivational mechanism were tested in predictions 6–9. Since it was proposed that hormones directly affect this mechanism, prediction 6 said that sex differences should be similar for all of the motor patterns, and prediction 7 said that estrous effects should be similar for all of the motor patterns. Since it was hypothesized that fear (submission or defense) directly affects the motivational mechanism, two other predictions followed: prediction 8 said that isolated males, who are more fearful, should have lower rates of all motor patterns than socially-housed males; and prediction 9 said that over the weeks of testing all of the motor patterns should increase in frequency as the rats habituated to the test situation and their level of fear was reduced.

Predictions 10–13 reflected the hypothesized structure of the sensory analyzers of motivating stimuli. Four sensory analyzers of motivating stimuli have been proposed: (1) an analyzer in both males and females that is tuned to unfamiliar conspecific odors; (2) an analyzer activated in males by androgens and tuned to estrogen-dependent pheromones of the target animal; (3) an analyzer activated in males by androgens, tuned to androgen-dependent pheromones of the target animal, which inhibits the patrol/marking mechanism; and (4) an analyzer activated in females by estrogens and tuned to androgen-dependent pheromones of the target animal. These analyzers have been proposed in order to explain previous findings that males and females respond to unfamiliar conspecifics [11,24] that males respond positively to estrous females [14,23] and negatively to other males [20] and that females respond positively to males [12]. Prediction 10 reflected the first of these analyzers and said that all of the motor patterns should be more frequent when the target was a conspecific than when it was a blank (i.e., an empty target chamber and a clean Petri dish). Prediction 11 reflected the second of these analyzers and said that all of the motor patterns should be more frequent in males to an estrous target than to a non-estrous female target. Prediction 12 reflected the third analyzer and said that there should be lower rates of all motor patterns to a male than to a non-estrous female target. And prediction 13 reflected the fourth analyzer and said that females should have higher rates of all motor patterns in response to a male than to a female target.

Genetic effects, it was hypothesized (prediction 14), should operate primarily upon the individual motor patterns. This was hypothesized on the basis of a survey of the motivational systems of agonistic behavior across various species of muroid rodents in which it was found that there are few differences in the basic organization of motivational systems and many differences in the particular motor patterns [3].

METHOD

The experiment was conducted twice, in successive years, using the same experimental design and apparatus and the same strains of rats. The two experiments were intended as replications, the only difference being the inclusion in the second experiment of two new noninvasive behavioral measures.

The subjects in each experiment were 50 adult laboratory rats, 30 males and 20 females. Half of the animals were pigmented rats of the DA highly inbred strain (DA rats) and half were albino rats of the Lewis highly inbred strain (Lewis rats). Twenty of the males and all of the females were housed in 81×25 cm cages as like-sexed pairs separated from each other by a wire-mesh screen (socially-housed rats). Each pair consisted of one DA and one Lewis rat. The remaining ten males were isolated in 25×25 cm cages with no visual or physical contact with other rats (isolated rats). All rats received ad lib food and water and were maintained in a light-dark cycle with white light from midnight until noon and constant red light illumination.

Before testing on any given day, the behavioral estrous state of the females was determined. The experimenter placed one of the two males from the adjoining cage into the female's cage. If a lordosis posture was adopted by one female when mounted by the male, she was judged to be in behavioral estrus (estrous rats). Estrous females were temporarily removed from the cage after having been mounted so that the other female in the cage could be tested. If no mounting was done by the introduced male after five minutes, the experimenter manually tested the females for lordosis [6]. If no lordosis occurred, the female was judged not to be in estrus (non-estrous rats).

Testing took place in a specially designed cage, 40.6 by 68.6 cm. On the back wall of the cage was a wire-mesh running wheel with diameter of 34.8 cm flanked by two "target chambers." Each target chamber was placed in such a way that by opening a partition that otherwise separated it from the wire-mesh running wheel, it was possible to expose the contents of the chamber to an animal that was on the wheel. Two fans were placed so that it was possible to blow air from one or the other through a target chamber and into the wheel. The test chamber was illuminated with red light rather than white light so that the animals could be observed during the testing which took place during the dark cycle.

Tests consisted of placing one rat into the main chamber (runner rat) and another rat into the target chamber adjacent to the wheel (target rat) and quantifying the subsequent be-

havior of the runner rat for 20 minutes. In addition to the two animals, a Petri dish from the home cage of the target animal was also placed on the floor in front of the wheel on the same side of the cage as the test chamber in which the target animal was placed. The Petri dish was already encrusted with the scent-marking material of the target animal and its partner from the home cage. The fan was turned on from the side of the cage as the target chamber in which the target rat was placed and the partition of that target chamber was opened. Thus, the runner was faced with a target rat in a target chamber on one side with the partition of the chamber opened and air blowing gently through it, and with a scent-marked Petri dish from the same animal on the floor in front of the test chamber on the same side.

Five types of behaviors were recorded in the runner rat: (1) The act of sniffing the scent-marked Petri dish (sniff dish); (2) the act of walking across the Petri-dish and making contact of the ano-genital region to the edge of the dish (marking); (3) each revolution of the running wheel regardless of direction (locomotion); (4) difference in the number of revolutions run towards the target minus number run away from the target (approach); and (5) each bout of facial grooming. Two additional sets of data were recorded in Experiment 2: the amount of time spent on the running wheel and the direction of entry each time the runner entered the running wheel from the main chamber of the test apparatus. These latter two measures enabled us to calculate (1) running speed (number of revolutions divided by time spent on wheel) and (2) differential entry towards the target (number of entries towards target minus number of entries away from the target). The latency of the first appearance of each behavior after the beginning of the test was also recorded. It was not possible to quantify the amount of scent-marking by directly weighing the deposited material.

There were ten replications of the 32 experimental conditions in each experiment. The experiment conditions were orthogonal in a $2\times2\times2\times4$ design, consisting of two sexes of runners (male or female), two strains of runners (Lewis or DA), two conditions of runners (estrous or non-estrous females, isolated or socially-housed males), and four types of targets (estrous female, non-estrous female, socially-housed male, or blank). In the blank target condition the partition was opened and the fan was turned on, but no rat was placed in the target chamber; also, instead of a scent-marked Petri dish, a clean Petri dish was placed into the test chamber on the same side as the target chamber in use. The design was counterbalanced for order effects so that each experimental condition appeared at a different time during the eight weeks of testing in the ten replications. The side used for the target was also counterbalanced so that an equal number of tests were conducted towards the right and left sides. Runners and targets were taken from different cages so that a runner did not face a familiar target.

For two weeks prior to the experiment, all runner rats were given two "habituation" tests in the test chamber to reduce their fear of handling and exposure to the new situation. Other than this, the rats were untrained, in the sense that their only experience with a running wheel was during the course of the experiment. They were, however, sexually experienced because they were used daily to determine the estrous state of the females.

Statistical analyses were done with a computerized multiple analysis of variance using the SPSS repeated measures design (strain, sex, and condition as between subject factors and measure and target as within subject factors). Following the multiple analysis of variance (which included all of the various measures of behavior), individual analyses of variance were then performed on those measures that had proven significant.

RESULTS

Unity of Motivational System (Predictions 1–5)

Four of the five dependent variables were positively and significantly correlated with each other, as predicted would be the case if they represent motor patterns of a single motivational system. As shown in Table 1, marking, sniffing, locomotion (number of revolutions run), and approach (differential number of revolutions towards the target) were all correlated positively and significantly in both experiment 1 (Table 1A) and Experiment 2 (Table 1C). All correlations were greater than .40 (inclusive correlations) with the exception of locomotion in Experiment 2 whose correlations ranged from .27 to .45. However, when locomotion was measured in terms of running speed instead of number of revolutions run, the correlations were also above .40 for this set of relations as well (Table 1E).

Only one of the five predictions was contradicted. Facial grooming, in contradiction to the hypothesis, was not significantly correlated with any of the other dependent variables of patrol/marking in either experiment.

The dependent variables remained correlated even when the coefficients were recalculated in a different way to eliminate the influence of the main effects of the experiments. This was done by calculating correlation coefficients for each group of tests that were done under identical conditions of the independent variables and pooling the coefficients into a single mean value. These are shown in Table 1B and 1D as "exclusive correlations," i.e., correlation coefficients that were calculated exclusive of the main effects of the independent variables. As shown in Table 1, most of these correlations were above .30.

Factors Operating on Motivational Mechanism (Predictions 6–9)

The four correlated dependent variables of patrol/marking (marking, sniffing, locomotion, and approach) were all affected in the same way by the independent variables of sex, condition (housing in males and estrus in females), and order of testing. This confirmed predictions 6–9. The statistical significance of the effects were tested all together by a multiple analysis of variance including all four dependent variables and found to be significant in both experiments; then, individual analyses were performed for each of the dependent variables and they, too, were found to be significant (Table 2). Facial grooming, on the other hand, was not affected by any of the independent variables.

Results for three of the predictions are illustrated in Fig. 1. Confirming prediction 6, females had higher levels of all the dependent variables than males. Confirming prediction 7, estrous females had higher rates of patrol/marking than non-estrous females. The only exception was locomotion in Experiment 2 where there was apparently a ceiling effect; however, when running speed was calculated instead of number of revolutions run, there was a higher speed for estrous females in this case as well. Confirming prediction 8, socially-housed males had higher rates of patrol/marking than isolated males on all of the dependent variables.

Confirming prediction 9, all of the dependent variables of

TABLE 1
BEHAVIORAL CORRELATIONS

	Inclusive Correlations* (A) Experiment 1				Exclusive Correlations† (B) Experiment 1			
	Sniffing	Locomotion (Revolutions Run)	Approach (Running To Target)	Facial Grooming	Sniffing	Locomotion (Revolutions Run)	Approach (Running To Target)	Facial Grooming
Marking	.794	.489	.433	−.175	.742	.310	.287	−.099
Sniffing		.508	.436	−.023		.322	.232	+.067
Locomotion (Revolutions Run)			.682	−.213			.543	−.053
Approach (Running To Target)				−.171				−.081

	(C) Experiment 2				(D) Experiment 2			
	Sniffing	Locomotion (Revolutions Run)	Approach (Running To Target)	Facial Grooming	Sniffing	Locomotion (Revolutions Run)	Approach (Running To Target)	Facial Grooming
Marking	.735	.272	.463	−.022	.695	.344	.327	.100
Sniffing		.287	.447	−.025		.353	.299	.076
Locomotion (Revolutions Run)			.454	−.057			.686	.022
Approach (Running To Target)				−.016				.037

	(E) Experiment 2 (New Measures)			(F) Experiment 2 (New Measures)		
	Sniffing	Locomotion (Running Speed)	Approach (Differential Entry)	Sniffing	Locomotion (Running Speed)	Approach (Differential Entry)
Marking	.735	.510	.509	.695	.353	.225
Sniffing		.494	.473		.332	.221
Locomotion (Running Speed)			.400			.285

*Inclusive correlations calculated for all data together. All correlations over .170 are significant at $p<0.01$.
†Exclusive correlations calculated separately for each cell of experimental design in order to exclude design factors and then averaged.

patrol/marking increased steadily over the eight weeks of testing. The increases ranged from a low increase in locomotion in Experiment 2 (increased from 61 revolutions run in the first week to 75 in the last week) to a high increase in the differential number of revolutions toward the target (increased from 15 in week one to 33 in week eight). There was no change in the rate of facial grooming over the weeks of testing.

Factors Operating as Motivating Stimuli (Predictions 10–13)

Overall target effects, as tested by multiple analysis of variance, were significant in all cases except for running in Experiment 1, as shown in Table 2. When individual predictions were tested, however, only two of the four predictions were supported and a third was equivocal. There were no target effects on grooming.

Confirming prediction 10, there was always more patrol/marking when the target was another animal than when it was blank (i.e., when the Petri dish was clean and the target chamber was empty). The effects were all significant at better than a 0.05 probability by F-tests for marking, sniffing, locomotion, and approach on Experiment 1 and Experiment 2. Results are illustrated in Figs. 2 and 3 for males and females respectively.

Confirming prediction 11, males had higher levels of patrol/marking when the target was an estrous female than when it was non-estrous. This occurred in seven of the eight cases, the only exception being marking the Experiment 2. Although the individual F-tests were not significant, the overall trend (7 of 8) is significant by a sign test at a 0.05 probability level (one-tailed). Results are illustrated in Fig. 2.

Prediction 12 was that females would have higher levels of patrol/marking when the target was a male than when it was another female. In this regard there were two significant differences at a 0.05 probability level on F-tests: sniffing and approach, both in Experiment 1. Otherwise the expected effect was not found, as may be seen in Fig. 3.

Prediction 13 suggested that males would have less patrol/marking when the target was a male than when it was a

TABLE 2
MULTIPLE ANALYSES OF VARIANCE

			Strain†	Sex†	Condition†	Target‡
All variables together*	1981	F	26.9	242	41.9	4.35
		p	<0.001	<0.001	<0.001	<0.005
	1982	F	1.0	103	12.3	218
		p	n.s.	<0.001	<0.001	<0.001
1. Marking	1981	F	8.0	45.0	23.6	8.7
		p	<0.01	<0.001	<0.001	<0.001
	1982	F	8.7	34.6	7.0	10.0
		p	<0.01	<0.001	<0.01	<0.001
2. Sniffing	1981	F	0.02	49.1	28.9	19.6
		p	n.s.	<0.001	<0.001	<0.001
	1982	F	1.7	20.3	3.6	5.5
		p	n.s.	<0.001	<0.06	<0.001
3. Locomotion (Revolutions run)	1981	F	39.4	417	43.2	0.44
		p	<0.001	<0.001	<0.001	n.s.
	1982	F	5.9	152	13.8	3.6
		p	<0.02	<0.001	<0.001	<0.02
4. Approach (Differential running towards target)	1981	F	10.8	56.9	18.7	8.2
		p	<0.01	<0.001	<0.001	<0.001
	1982	F	0.003	27.9	5.8	4.2
		p	n.s.	<0.001	<0.02	<0.01
5. Locomotion (Running speed)	1982	F	0.53	124	23.3	3.2
		p	n.s.	<0.001	<0.001	<0.02
6. Approach (Differential entry towards target)	1982	F	0.56	13.2	4.5	6.6
		p	n.s.	<0.001	<0.05	<0.001

*Multiple analysis of variance for four dependent variables (1–4).
†$DF=1$.
‡Average F by multiple analysis of variance, repeated measures.

non-estrous female. This effect was not found, as may be seen in Fig. 2.

Target effects were the same for locomotion and approach no matter how they were measured. When running speed was calculated instead of number of revolutions run, there was no difference in the results. In all cases the running speed was slower to a blank target. Males ran faster to an estrous female than to a non-estrous female, and there was no difference in female running speed as a function of the sex of the target. When direction of entry into the wheel was calculated instead of the differential number of revolutions towards the target, the results were also similar. Females entered the wheel a greater proportion of the time towards a male target than towards a female target, and least often towards a blank target. Males entered the wheel more often towards an animate target than towards a blank target, and slightly more often towards an estrous female target than towards a non-estrous female target.

Genetic Factors

The results for strain effects confirmed prediction 14 that genetic factors should operate primarily upon motor patterns rather than upon the organization of the motivational system of patrol/marking.

There were a number of statistically significant differences as a function of strain, but these differences varied from one dependent variable (motor pattern) to another, and did not reflect an overall difference in patrol/marking. In Experiment 1, strain was a significant independent variable as measured by MANOVA on all of the dependent variables taken together (Table 2). Lewis rats had significantly more marking, locomotion, and approach as measured by individual F-tests ($p<0.01$ in all cases), and there was no significant difference in sniffing. In Experiment 2, on the other hand, there was no statistically significant effect of strain on the overall data. Measured by individual F-tests, however, there was significantly more marking by Lewis rats and more locomotion by DA rats. In both experiments there was significantly more facial grooming by DA than by Lewis rats, as measured by F-test ($p<0.01$).

There were no strain differences in any of the effects attributed to factors operating on the motivational mechanism (predictions 6–9) or factors operating on motivating stimuli (predictions 10–13). This was indicated by the lack of statistically significant interactions for any of the following in either experiment: strain by condition, strain by target, strain by condition by variable, and strain by target by variable ($p>0.05$ in all cases). Even the interactions of strain by sex and strain by sex by variables which were significant on the original MANOVA test, were no longer significant when computed on log-transformed data.

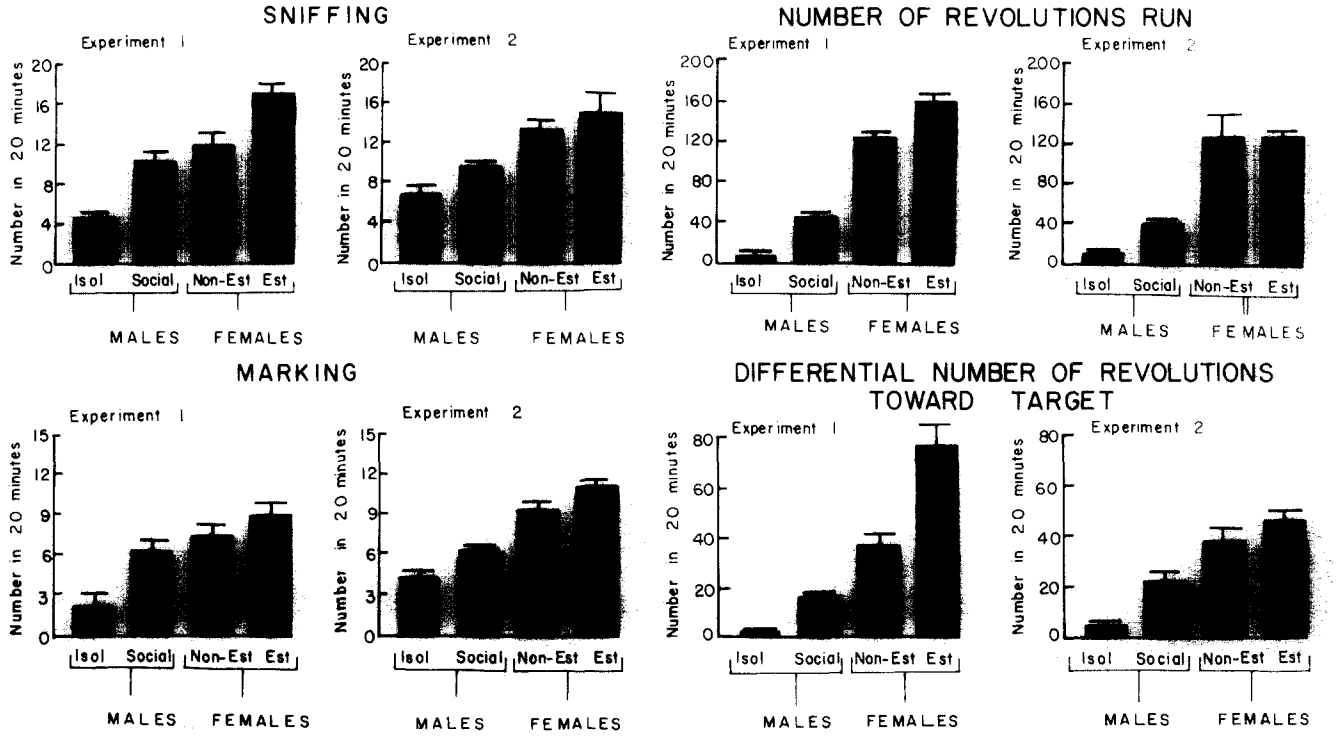

FIG. 1. Mean frequencies of dependent variables (motor patterns) of patrol/marking as a function of independent variables affecting the runner directly. The dependent variables are sniffing (number of times sniffing the Petri dish), marking (number of times of crawl-over-dish scent-marking), locomotion (number of revolutions run on running wheel), and approach (differential number of revolutions run towards the target). The independent variables are sex and condition of the runner (isolated versus socially-housed males and non-estrous versus estrous females). Data are shown separately for Experiment 1 and 2. Standard errors of the mean are shown on each column.

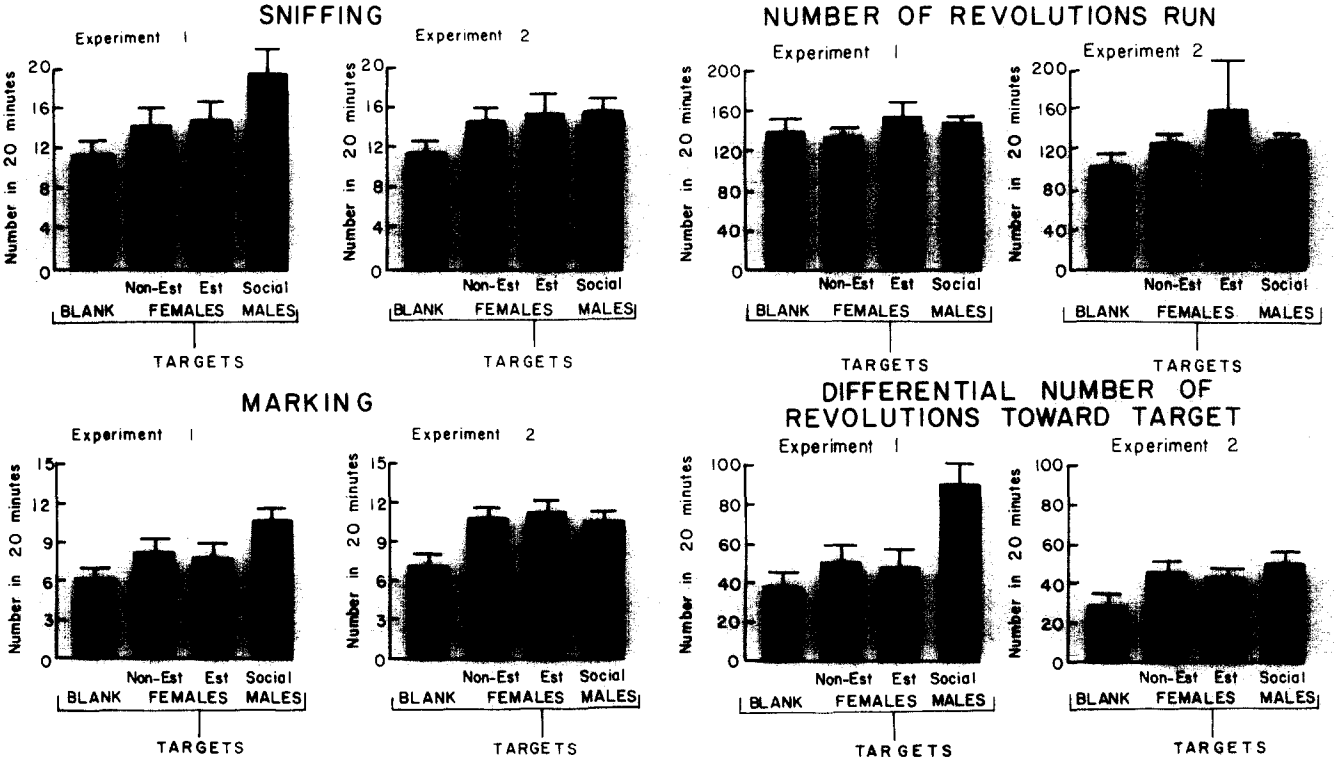

FIG. 2. Patrol/marking in females. Mean frequencies of dependent variables (motor patterns) of patrol/marking as a function of the type of target. Dependent variables described in caption for Fig. 1. Independent variables are blank target (control condition), non-estrous female target, estrous female target, and male target. Data are shown separately for Experiment 1 and 2. Standard errors of the mean are shown on each column.

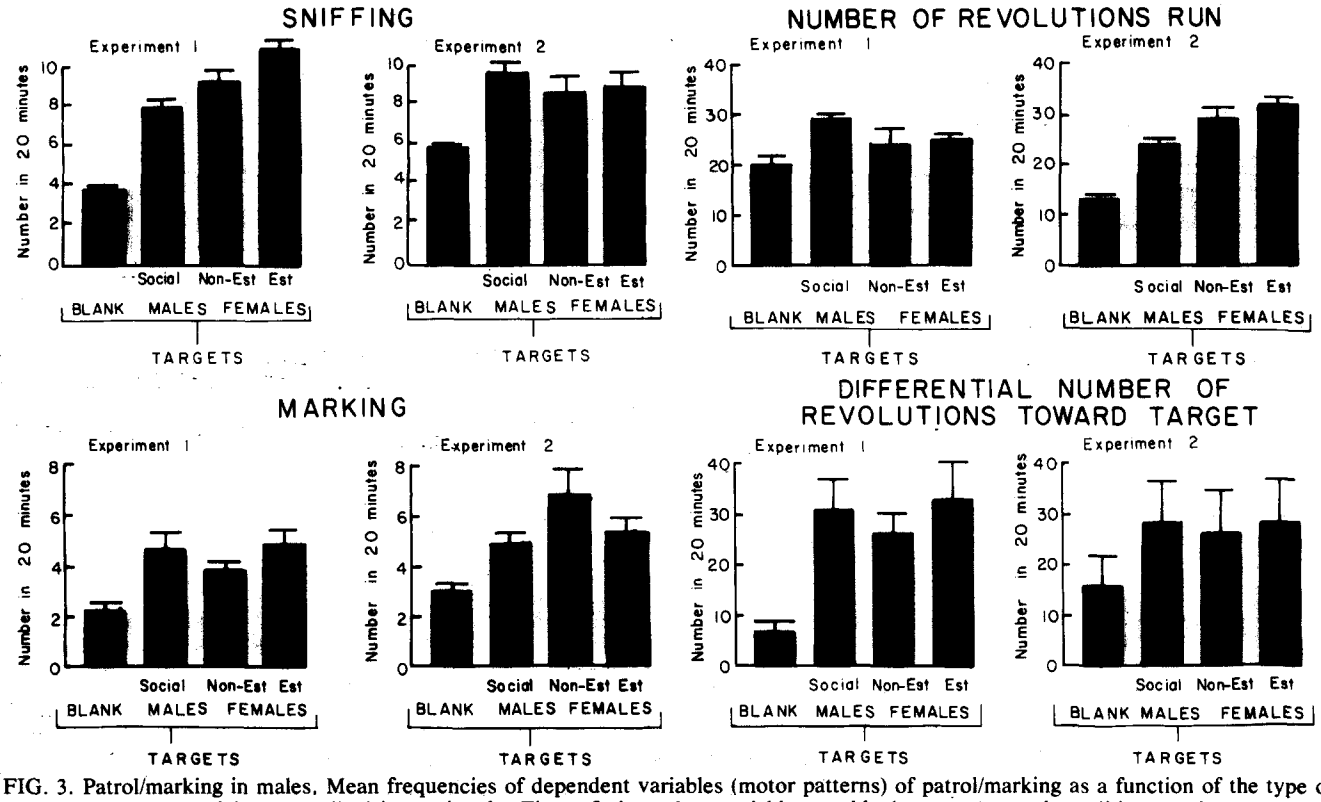

FIG. 3. Patrol/marking in males. Mean frequencies of dependent variables (motor patterns) of patrol/marking as a function of the type of target. Dependent variables described in caption for Fig. 1. Independent variables are blank target (control condition), male target, non-estrous female target, and estrous female target. Data are shown separately for Experiment 1 and 2. Standard errors of the mean are shown on each column.

Interactions

There were remarkably few significant interactions among the variables, and instead they were independent for the most part. As mentioned above, interactions involving strain were not significant. Also, the following additional interactions were not significant at a 0.05 significance level in either experiment: sex by condition, sex by target, condition by target, and condition by target by variable. In fact of the 24 possible interactions at this level in the two experiments, only two were significant in either experiment: sex by condition by target in Experiment 1 and sex by target by variable in Experiment 1; while neither of these was significant in Experiment 2.

DISCUSSION

Since most of the predictions were confirmed, it is possible to support the theory that there is a motivational system of patrol/marking with a structure as shown in Fig. 4. Central to the structure is the hypothesized motivational mechanism of patrol/marking which is responsible for the unified activation of the system. Radiating towards it are facilitating inputs from three sensory analyzers for motivating stimuli and radiating away from it are hypothetical connections to four motor patterning mechanisms corresponding to the four motor patterns of patrol/marking confirmed by this study.

There are two modifications in the figure from its original presentation in previous publications [3,4]. Because of the failure of prediction 5, and the fact that facial grooming was not affected by the various motivating stimuli, hormonal factors or fear in the same way as other motor patterns, facial gland secretion cannot be included as a motor pattern of patrol/marking. Also, because of the failure to confirm prediction 13, it is not possible to support the existence of a motivating stimulus analyzer activated in males by androgens, tuned to androgen-dependent pheromones and inhibitory of patrol/marking. Our results are in contradiction to those of previous studies that have shown that male mice fail to patrol areas that have been patrolled by other males [20] and that male rats show less approach, sniffing, and scent-marking to intact males than to castrated males [12]. Further study is needed to resolve this apparent contradiction.

The unity of the patrol/marking motivational system and existence of a patrol/marking motivational mechanism responsible for its unity is supported by the significant positive intercorrelations of sniffing, marking, locomotion, and approach. Further confirmation of the theory depends upon more direct investigation of the neural structures critical for these behaviors [2]. We have been able to find neurons in the medial preoptic area of the male rat that respond during running towards the estrous female target, but not during other types of running such as escape from the experimenter or running towards a water reward [26]. Whether or not these are neurons of the hypothetical motivational mechanism of patrol/marking cannot be determined until we have more data on the entire neural system involved.

There are two reasons why one would not expect higher correlations, even among the measures of patrol/marking. First is the problem of response competition. All other things being equal, one should expect negative correlations of certain behaviors simply because of this. For example, the more

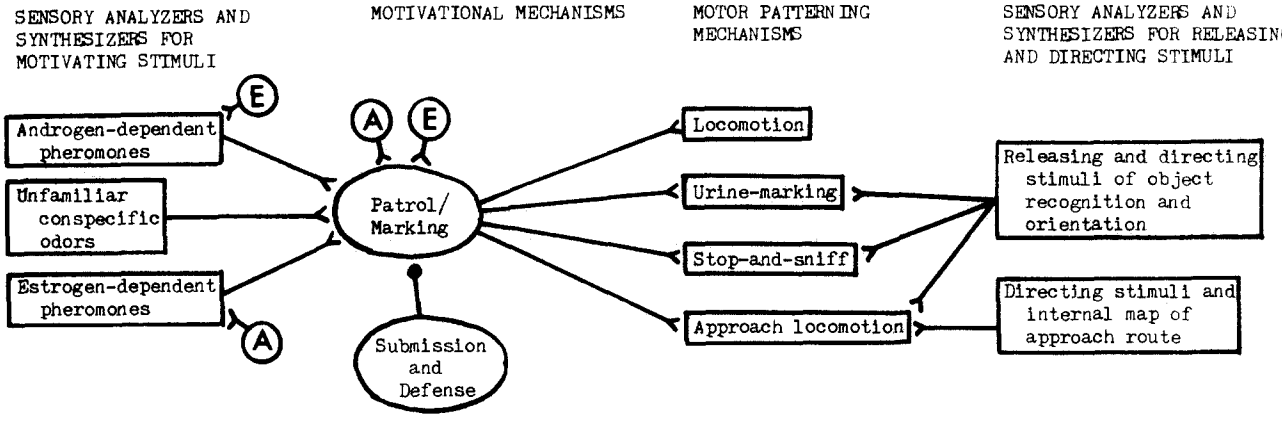

FIG. 4. Hypothetical structure of patrol/marking motivational system pertaining to variables recorded in this study. Sensory analyzers of motivating stimuli, motivational mechanism of patrol/marking, motor patterning mechanisms, and sensory analyzers of releasing and directing stimuli are shown from left to right, respectively. Figure derived from reference [4]. "E" refers to site of action of estrogens and "A" to site of action of androgens. Arrows with forked endings are facilitative, while arrows with filled circle endings are inhibitory.

time an animal spends in wheel running, the less time it should have for sniffing and marking the dish or grooming the face. This is particularly evident in the case of estrous females who ran up to 262 meters during a 20 minute test: in fact, the lowest correlation was between locomotion and marking or sniffing, and the correlation was improved as one would predict when instead of number of revolutions run, the measure of running speed was used. As one would predict from a response competition hypothesis, those measures that did not compete: locomotion and approach, and marking and sniffing, had higher correlations than did the others. Also, as one would predict from this, given that facial gland secretion is apparently not a motor pattern of patrol/marking, most of the correlations with grooming were negative.

A second reason not to expect higher correlations is the difference in releasing and directing stimuli for the various motor patterns. The releasing and directing stimuli from the Petri dish and from the target animal are somewhat different; for example, vomeronasal stimulation might be expected from the sniffing and occasional licking of the Petri dish, but not from the air stream odors from the target chamber. This, too, leads one to expect higher correlations of behaviors sharing the same target, i.e., marking and sniffing, on the one hand, and locomotion and approach, on the other hand.

The direct activation of the patrol/marking motivational mechanism by estrogens, as illustrated in Fig. 4, is supported by results bearing on predictions 6 and 7. Higher rates of patrol/marking by females than males (prediction 6) can be explained simply in terms of the balance of effects of estrogens and androgens. Although both estrogens in females and androgens in males facilitate locomotor behavior [7], the effects of estrogens may be stronger than those of androgens, as indicated by the extreme case of the estrous female. The estrous effect, itself, confirming prediction 7, is consistent with many classical observations of increased locomotion and scent-marking during estrus under field conditions [13] and in laboratory settings [8,28].

The inhibition of the patrol/marking mechanism by submission and defense (fear) which was proposed in a previous study on the basis of a very different type of data [1], could explain several effects found in the present experiment. It could help account for the decreased patrol/marking of isolated rats since previous studies have shown that isolation increases fearfulness [19,27]. Also it could account for the increasing levels of patrol/marking over the successive weeks of testing as the animals became habituated to handling and to the test apparatus (prediction 9). Since both handling and exposure to a new situation (neophobia) would be expected to produce defense [3], the habituation of defense in later tests as the animals became accustomed to the handling and the apparatus would be expected to allow higher levels of patrol/marking. The effect proposed here is similar to the effect of defense (fear) upon offense behavior as measured in another recent experiment [25].

The higher rates of patrol/marking by socially-housed than by isolated males (prediction 8) could also have been related to higher androgen levels in the former, since androgens, it is hypothesized, directly facilitate the motivational mechanism. It has been shown that males with access to females, even if only their odors, have higher levels of luteinizing hormone and androgens than isolated males [21]. Unfortunately, although we attempted to measure androgen levels from these animals in a companion experiment, the data were not interpretable.

Support for the structure of motivating stimulus analyzers is somewhat equivocal in the present experiment. The confirmation of prediction 10, that patrol/marking was greater to conspecific stimuli than to blank stimuli, supports the existence of an analyzer tuned to conspecific odors. These results do not test the hypothesis that unfamiliar conspecific stimuli are more effective than familiar conspecific stimuli.

The evidence for cross-sexed target effects (i.e., predictions 11 and 12) are rather weak in the present experiment, in contrast to the strong evidence reported by previous investigators on which the hypothesis was formed (e.g., [12, 14, 23]). There may be several reasons for this. For one thing, it has been shown that male preference for estrous female odors is partly learned [23], and it is also possible that the female preference for males has a learned component. It is possible that in the present experiment, where the runner is never allowed to make physical contact with the target, the conditions for such learning are not fully present. Another possible reason might be the nature of the stimuli involved. It may be that the scent-markings on the Petri dish and the air currents with the target odors do not convey the full impact of possible motivating stimuli.

The differential effects of strain differences, exerted upon some motor patterns and not upon others, confirm prediction 14 and support the hypothesis that genetic variance is greater with respect to motor patterning mechanisms than to motivating stimuli or motivational mechanism. This hypothesis is further supported by the lack of any interaction of strain with the other effects found in the study, all of which pertained to motivating stimuli or the motivational mechanism. These findings support the hypothesis that the fundamental structure of motivational systems of social behavior is remarkably stable across muroid rodent species and that most so-called "species-specific" differences consist of details in the motor-patterning mechanisms [3].

In conclusion, the present study supports the theory that there is a motivational system of social behavior in muroid rodents that is neither aggressive nor sexual. Patrol/marking may be looked upon as a system of behavior that advertises the reproductive state of the individual [4]. The estrous female advertises her sexual receptivity. The territorial male advertises his "ownership" of the territory and his sexual availability to nearby females. It may be compared to the bobbing and dewlap display of lizards which at times appears to be "an attitude that is not courtship and yet does not seem strong enough to be considered fighting" [18], and also to the display of primates that seems neither sexual nor aggressive [5]. The extent to which such "neutral" systems of social behavior are common throughout the vertebrates has yet to be determined.

ACKNOWLEDGEMENTS

The authors wish to thank Carlton Barnswell, Jill Bogdan, Elaine Bryant, Edward Chang, Susan Chao, Michelle Dukes, Carroll Fields, Frederick Gordon, Betsy Heartfield, Beverly Hutt, David Kauff, Jean Sook Lew, Sharon Marable, Marianne Milton, Raphael Ornstein, Fred Pelzman, Bitsy Robinson, Miriam Stern, Gregory Ward, and Steven Zendell for their careful and patient work on the project which was done during two courses at Wesleyan University.

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