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A STATISTICAL AND MOTIVATIONAL ANALYSIS OF THE SOCIAL BEHAVIORS OF THE MALE LABORATORY RAT

by

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INTRODUCTION

Isolation-induced fighting by resident male Norway rats against unfamiliar male intruders has been analyzed as a predictable sequence of behaviors involving relatively few acts and postures and culminating in a stereotyped bite-and-kick attack (GRANT, 1963; ADAMS, 1976). Perception of movement and olfactory stimuli from the intruder rat have been shown to be important in stimulating the attack by the resident rat (ALBERTS & GALEF, 1973). ADAMS (1976) has postulated that the combination of unfamiliar olfactory stimuli from the intruder and familiar olfactory stimuli from the resident's own scent-marking serve to trigger an offensive brain mechanism which mediates the attack. In response to that attack, the intruder displays stereotyped defensive postures which inhibit further attack. Recent research suggests that the defensive intruder may also inhibit attack by emitting a 25 KHz ultrasound (LUCIANO, 1974; SALES, 1972; LORE *et al.*, 1976).

The present study has been undertaken to analyze the behavior sequences of isolation-induced fighting more rigorously than in the previous studies by GRANT (1963) and ADAMS (1976). The present study, like previous ones, is based upon the detailed description and categorization of acts and postures in rodents completed by GRANT & MACKINTOSH (1963). According to that analysis, the rat and other rodents display a limited repertoire of acts and

postures during social interactions, and these can be reliably identified and noted by a trained observer. Unlike the previous work, which analyzed only certain acts and postures and some of their sequences, a computer technique is used here to analyze all acts and postures and their dyad sequences, and to determine and list all such sequences which would not be expected to occur at such frequency by chance. Transition analyses performed by computer are presented for all dyad sequences of interaction between the two animals as well as all dyad sequences of behaviours within each animal.

The present study also goes beyond previous work by reducing all of the non-random behavioral transition dyads to a few general patterns interpreted in terms of motivational mechanisms and motor patterning mechanisms with specifiable stimulus inputs and motor pattern outputs.

MATERIALS AND METHODS

The subjects were forty male laboratory rats consisting of hybrids of DA agouti, Fischer albino, and WAG-Rij albino rats, the parents of which had been used in an earlier study (ADAMS, 1976). All animals were weaned at 25 days of age and placed into 64 × 10 inch pens with their siblings. At 90 days of age the animals designated as home rats were isolated in a 32 × 10 inch cage, along with a Petri dish on the floor of the cage for the measurement of territorial marking. Other similar males to be used as intruders were caged together as groups of five in 14 × 24 inch cages.

Tests were conducted when the home rat had been isolated for five weeks, since previous work had shown that more fighting is obtained after this isolation period than after only one or three weeks isolation. An intruder of a different type of hybrid was introduced into the cage of the home rat during the red light conditions of a regular 12-hour simulated night cycle. Each home rat was tested once, i.e., there were forty tests in all.

Behaviors were recorded for both animals sequentially on a strip of moving paper for a period of twenty minutes. The forty tests were recorded by two independent observers, and inter-observer reliability was checked frequently. A scoring system of abbreviations was adapted from GRANT & MACKINTOSH's (1963) classification of acts and postures of laboratory rats, and included: sniff ano-genital region of the other animal (SA); sniff-back of the other animal (SB); sniff-tail of the other animal (ST); sniff-nose of the other animal (SN); sniff Petri dish (SD); crawl over the Petri dish (COD); explore the cage (X); crawl under the other animal (CU); crawl over other animal (CO); stretched attention posture (SAP); groom-self-face (GSF); groom-self-side (GSS); groom-self-ano-genital region (GSA); scratch (Sc); offensive sideways posture (OSP); full aggressive posture (FAP); bite-and-kick attack (B+K); upright posture (UP); boxing (Box); aggressive groom (GA); full submissive posture (Sub); defensive sideways posture (DSP); crouch (Cr); squeal (Sq); emission of 25 KHz ultrasound (Ult); rub (Rub); attempted mount (MA); approach (App); attend (Att); retreat (Ret); and flee (F).

The scoring system differed from that of GRANT & MACKINTOSH in several minor respects. The terms investigate, sniff, and nose were replaced by sniff-back, sniff-ano-genital region, sniff-nose, and sniff-tail, which we thought were more explicit descriptions of the same behaviors. The incipient flight and aggressive gestures listed by GRANT & MACKINTOSH as flag, evade, threat and thrust, were found to be very difficult to distinguish and record; hence only fully developed flight and aggressive behaviors

were noted instead. Self-grooming or "displacement grooming" of the previous authors was further differentiated into grooming of the face, side, or ano-genital region. The distinction between offensive and defensive upright posture was often difficult to make; therefore, upright posture was scored as only one behavior.

The identity of the animal producing ultrasound was usually determinable from the correspondence of the duration of the emitted ultrasound to the duration of the respiratory cycle of the vocalizing animal. The 25 KHz ultrasound which accompanies submission usually consists of a relatively long sustained pulse, corresponding to a relatively slow, sustained expiration by the vocalizing animal.

After each test, three separate behavior sequences were transcribed from each ethogram tape, two for the two individual animals, and one for the interaction between the two. Each act and posture, as it was transcribed, was given a prefix to indicate that it was performed by the home rat or intruder. This was possible since each of the independent observers had followed the same convention, recording the acts and postures of the home rat on the upper margin of the tape and those of the intruder on the lower margin. The two behavior sequences for the two individual animals were transcribed directly into the computer; disagreements between the data of the two observers being resolved by discussion. The interaction sequence was composed from the same tape of data and was transcribed into the computer as an alternating sequence: home rat act or posture; intruder act or posture; home rat ...; intruder ...; etc. Apparently simultaneous acts and postures ("ties") were not recorded as such; instead "ties" were broken by a random method and all data were entered as one serial sequence. The same act or posture by one rat was entered repeatedly if it continued steadily while the opponent changed from one act or posture to another, i.e., the interaction sequence was made up of an obligatory alternation of acts or postures by the home rat and intruder. Because of space limitations in the computer, only the first ten minutes of the total twenty recorded on each ethogram tape were transcribed. In sum, a total of 120 behavioral sequences, three from each test and ten minutes in length, were transcribed and stored on magnetic tape as data files on a DEC-10 digital computer.

Most acts and postures are discrete and posed no problem for transcription, but vocalization presents a special problem since it usually occurs simultaneously with other motor activities. For this reason ultrasound and squeal vocalizations were not transcribed as such. Instead, squeal was not transcribed at all; it usually coincided with the defensive response of the intruder when it was bitten. Ultrasound was transcribed in a behavioral complex with the accompanying act or posture: hence there was ultrasound upright posture, ultrasound crouch, ultrasound submissive posture, etc., as distinct from upright posture, crouch and full submissive posture without accompanying ultrasound. Ultrasound was analyzed, however, in the data processing stage as a single behavioral act; i.e., the various combinations of acts and postures with ultrasound were all treated as simply ultrasound. Similarly, the data analysis for specific acts and postures were later analyzed without regard to presence or absence of ultrasound. In other words each entry which included ultrasound was analyzed twice, once as ultrasound and a second time as a specific act or posture.

A system of computer programs coded in FORTRAN IV was written to analyze the data. Along with the data matrices which they produced, they are available on request from the first author. Behavior sequences were first analyzed to determine the mean frequency of individual acts and postures in each minute of the test for home rat and for intruder. Sets of matrices were then constructed to express the obtained and expected frequencies of behavioral transition dyads over the entire ten minute duration of the transcribed test. There were three types of matrices: obtained frequencies; expected frequencies; and ratio of obtained to expected frequencies. Each were expressed with 33 preceding acts and postures on one dimension and 33 following acts and postures on the other dimension. In all, twelve matrices were constructed and analyzed, each of

the three types done four times: for home rat to home rat, home rat to intruder, intruder to home rat, and intruder to intruder.

The ratio of obtained to expected frequency (transition ratio) was used as an indication of the nonrandom quality of a particular behavioral dyad. The expected frequency was determined from the matrix of obtained frequency by the method used in GRANT (1963); *i.e.*, it was computed as the ratio of the product of the row total times the column total divided by the grand total. A transition ratio of 1.00 would be expected if the transition from one act and posture to another were random. All transition ratios above 1.10 were tested for significance after construction of a 2 × 2 table about the cell of interest, the obtained transition frequency from act or posture A to act or posture B. The other cells were filled in with the obtained transition frequencies from A to all other acts and postures, from all other acts or postures to B, and from all other acts and postures to all other acts and postures. The significance level of the transition ratio was then obtained by a Chi-square test with Yates correction or by Fisher's Exact Test, if the expected value of the cell of interest was less than five.

An additional computer program was written and the data were analyzed to determine if there were significant reduction of statistical uncertainty by analysis of third and fourth order behavioral sequences. The program was based on the mathematics of information theory and was similar to that used on rhesus monkey behavioral interactions by ALTMANN (1965). Preliminary results indicated that most information reduction takes place on the second order sequence, however, and relatively little is added by consideration of higher order sequences. For that reason only second order sequences, *i.e.*, behavioral dyads, are considered in this paper.

Preliminary analysis indicated that a distinction was necessary between different types of nonrandom dyad effects: primary effects and higher order effects, *i.e.*, secondary, tertiary, *etc.* This results from the possibility that a behavioral act or posture may simultaneously affect both the succeeding act or posture within that animal and also the succeeding act or posture of the other animal. The possibility thus arises for indirect, "reflected" effects from one act to another within the behavioral sequence of one animal as a consequence of the interaction between the animals. For example, act A of one animal may not directly influence the following act B of that same animal, but act A may indirectly influence B by directly affecting act C of the opponent if act C also directly affects act B. In this case the transition ratio of the secondary effect A to B might be statistically significant, but it should be lower than those of primary effects A to C and C to B. Primary and higher order effects were determined by construction of all possible triangles in which one particular act or posture took part in significant transition dyads both within an animal and between two animals.

Two supplementary experiments were designed to test the hypothesis that bite-and-kick attacks would continue to occur at a high frequency if they were not inhibited by ultrasound. In the first experiment the intruder was prevented from producing ultrasound by surgical resection of the nerve supply to the larynx; this was accomplished by bilateral resections of the recurrent and phasolaryngeal nerves under sodium pentobarbitol anesthesia. After three days post-operative recovery, the muted animals did not produce ultrasound when handled roughly in a manner which had elicited ultrasound preoperatively. The second experiment involved preventing the home rat from hearing ultrasound. This was accomplished by rupturing the eardrum, destroying the middle ear ossicles with a blunt probe while the animal was under sodium pentobarbitol anesthesia and then plugging the ear canal with Audalin cement (Coe Laboratories, Chicago, Illinois) and sewing shut the outer ear canal. Three days post-operatively, no response was observed in these animals to a loud noise which had elicited a startle jump preoperatively.

Two muted intruders and two deafened home rats were tested pre-operatively and one week post-operatively, there being a total of eight tests in all. Bite-and-kick attack

had been recorded in each of the pre-operative sessions. Muted intruders were retested with the same home rat, and deafened home rats were tested with the same intruder both pre- and post-operatively. Ultrasound was monitored in these and in all other tests both aurally and visually using a Psyonics UMAR-2 ultrasonic receiver with microphone sensitivity between 20.5 and 24.5 KHz (Psyonics, New Brunswick, New Jersey).

RESULTS

BEHAVIORAL OVERVIEW

An overview of behaviors associated with attack during the course of a typical test may be obtained from Fig. 1, which gives the mean frequencies of selected acts and postures on a minute-by-minute basis for all forty tests in the study. In most respects, the obtained data are similar to those obtained by a slightly different technique in a previous study (ADAMS, 1976), in which simple presence or absence of a behavior was indicated for each minute without regard to frequency of occurrence. Both animals began the test with relatively high levels of olfactory investigation (sniff-ano-genital region and sniff Petri dish) and scent-marking (crawl-over-dish). At first the home rat tended to show more sniff-ano-genital region, while the intruder tended to show more sniff-dish and crawl-over-dish.

Offensive and defensive behaviors usually did not appear until several minutes into the test. Bite-and-kick, which was shown exclusively by the home rat, occurred primarily during minutes four through eight. Associated with the attack were increased levels of other aggressive behaviors (*e.g.,* offensive sideways posture) by the home rat and defensive behaviors, *e.g.,* submissive posture, upright posture, and ultrasound) by the home rat. Grooming frequencies increased during the test session, and groom-self-side increased more in the home rat than in the intruder.

To illustrate more directly the relation of bite-and-attack to the occurrence of other offensive and defensive behaviors, the mean frequencies of selected behaviors were plotted during the minutes before and after the initial bite-and-kick attack, as shown in Fig. 2. The obtained data were similar to those obtained in the previous study (ADAMS, 1976) in which simple presence or absence of a behavior in a given minute was indicated. Offensive sideways posture by the home rat increased dramatically in conjunction with bite-and-kick attack, while defensive behaviors of the intruder also increased during the minute in which the attack occurred. As had been found in the previous study, while the bite-and-kick attack occurred only once or twice, the other associated behaviors continued to be exhibited at high frequencies during subsequent minutes.

All behavioral transition dyads which occurred in frequency much higher than expected by chance (significance level .001) have been listed in Tables
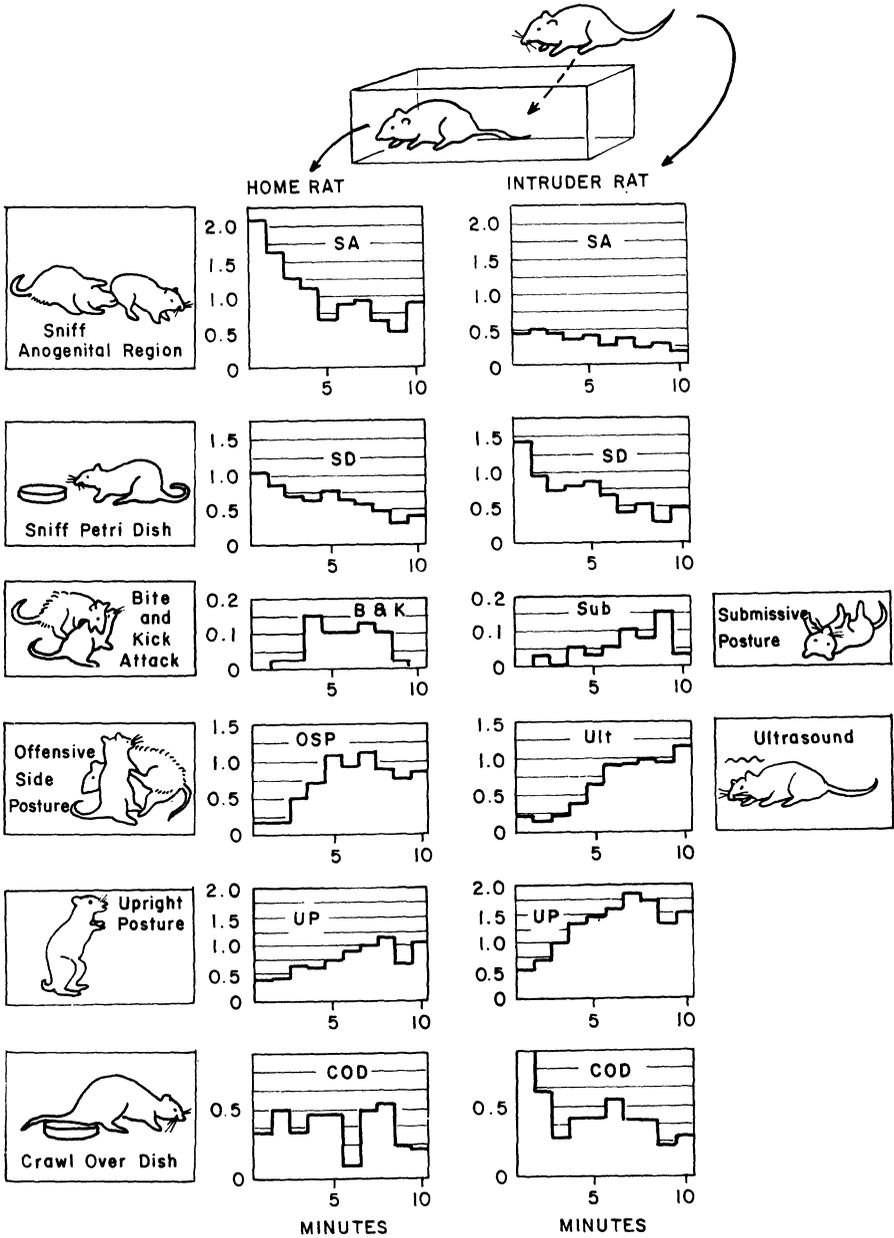
Fig. 1. Mean frequency of specific acts and postures on a minute-by-minute basis in isolation-induced fighting tests. Data from home rats shown on left and from intruder rats shown on right. Upright posture, for purposes of this analysis, calculated exclusive of boxing. Drawings in this and succeeding figures derived in part from GRANT & MACKINTOSH (1963).
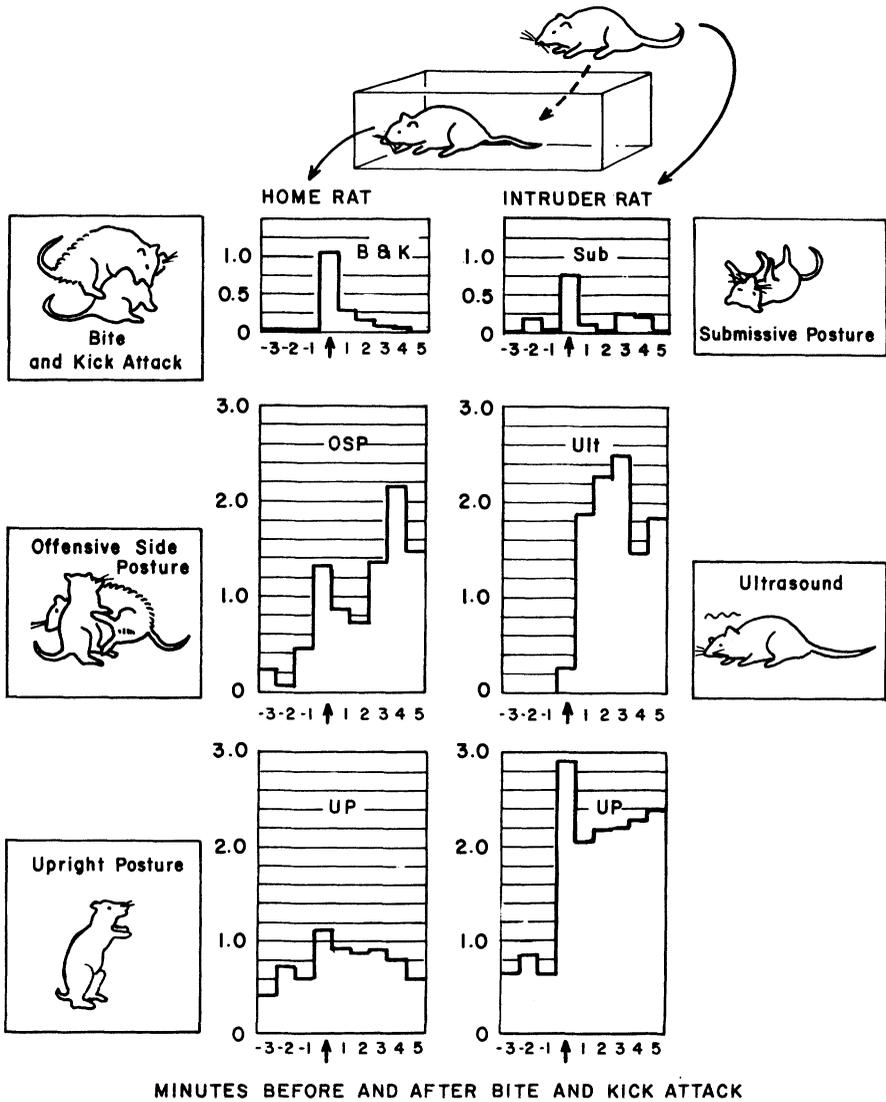
Fig. 2. Mean frequency of specific acts and postures on a minute-by-minute basis in isolation-induced fighting tests with the time scale based on minutes before, during, and after the initial bite and kick attack by the home rat. Data from tests in which bite and kick occurred, with home rats shown on left and intruder rats shown on right.

1-3. Since a total of 3,600 possible dyad permutations were examined, one would have expected only 4 to have occurred at this probability level by chance; the occurrence of 105, as listed in the tables, is prima facie evidence that there were non random processes involved in the behavioral sequences.

The data have been arranged into three tables, and categorized into several groups within those tables for preliminary analysis of the types of non random factors involved.

TABLE 1

Highly significant behavioral dyads within home rats

Exploratory and Marking Dyads				Grooming Dyads			
SD	→ COD	8.64	60	GSA	→ GSF	11.05	12
X	→ SAP	4.09	23	GSF	→ GSS	8.32	30
CU	→ SA	2.59	17	GSF	→ GSA	7.87	9
X	→ SN	2.46	66	GSS	→ GSF	4.08	14
X	→ SD	2.31	102				
SB	→ SA	1.90	103	Offense Dyads			
SA	→ ST	1.89	53	FAP	→ B & K	82.61	20
X	→ ST	1.75	81	OSP	→ FAP	4.16	11
SA	→ SB	1.74	94	OSP	→ OSP	3.82	80
ST	→ X	1.69	80	COD	→ OSP	2.87	22
ST	→ SA	1.66	47				
X	→ GSF	1.63	48	Defense Dyads			
SA	→ X	1.60	116	UP	→ Box	12.40	100
GSF	→ X	1.57	47	OSP	→ UP	2.55	50*
SD	→ X	1.54	68	Box	→ OSP	2.22	19*
X	→ SB	1.40	125	UP	→ OSP	1.74	34*
SB	→ X	1.38	125				

Note: First number is ratio of obtained to expected frequencies; second number is obtained frequency. Secondary and tertiary effects are indicated by asterisks.

TABLE 2

Highly significant behavioral dyads within intruders

Exploratory and Marking Dyads				Defense and Submission Dyads			
SD	→ COD	5.67	101	Ult	→ Ult	15.94	44
X	→ SD	2.82	183	UP	→ Box	7.19	93
SA	→ SB	2.49	20	MA	→ UP	4.09	19*
ST	→ X	2.44	27	Cr	→ Ult	4.02	31
SB	→ SA	2.41	19	Cr	→ Cr	3.92	40
COD	→ X	2.22	92	Ult	→ Cr	3.89	31*
X	→ SN	1.86	33	Sub	→ UP	3.60	9*
X	→ GSF	1.77	45	DSP	→ UP	2.34	50*
SD	→ X	1.73	111	DSP	→ DSP	2.30	31*
X	→ SB	1.66	68	UP	→ Ult	2.00	30*
SB	→ X	1.53	61	Box	→ UP	1.95	25*
				Ult	→ UP	1.83	27*
Grooming Dyads				UP	→ Cr	1.82	36*
GSF	→ GSS	12.54	9				
GSF	→ GSA	9.03	9				
GSA	→ GSF	6.08	6				

Note: First number is ratio of obtained to expected frequencies; second number is obtained frequency. Secondary and tertiary effects are indicated by asterisks.

TABLE 3

Highly significant interaction behavioral dyads

Exploratory and Marking Dyads

SN	→ SN	11.96	41
SD	→ COD	2.51	25*
SD	← SD	2.12	36
ST	← X	1.54	156
ST	→ X	1.53	156
X	→ SD	1.49	85
SD	→ X	1.45	134
GSF	→ X	1.35	91
X	→ X	1.28	400
SD	← X	1.28	118
SB	← X	1.26	249
SA	→ X	1.25	202
SB	→ X	1.18	238
X	← X	1.16	359

Grooming Dyads

GSS	→ GSF	3.59	11
GSF	→ GSF	3.19	20
GSF	← GSF	2.57	16

Offense, Defense and Submission Dyads

FAP	→ Sub	47.83	11
B & K	→ Sub	47.06	8
Box	→ Box	26.98	100
B & K	← Sub	23.53	4*

Miscellaneous

App	→ Ret	18.76	30
App	← Ret	15.18	24
GSS	← Ult	3.30	17
GSS	→ Ult	3.08	17
GSS	→ SB	2.95	12

Offense, Defense and Submission Dyads (continued)

OSP	← SB	8.33	7
GA	→ Sub	8.22	6
UP	← MA	7.90	19
Box	← UP	7.07	87
Box	← Box	6.74	25
OSP	→ DSP	5.98	91
UP	→ UP	5.41	169
OSP	← MA	5.27	13
Ga	→ DSP	4.99	31
FAP	← DSP	4.17	7*
FAP	→ Cr	3.97	9
B & K	→ UP	3.69	11
GA	→ Cr	3.58	41
B & K	← Cr	3.52	9*
GA	← DSP	3.28	20*
OSP	→ UP	3.12	100
OSP	← DSP	2.88	43
OSP	← UP	2.65	84
UP	→ Box	2.56	21
UP	← UP	2.53	78
OSP	← Box	2.40	20
Ga	← Cr	2.14	24*
UP	← DSP	2.13	31

Note 1. Home rat always indicated first.

Note 2. First number is ratio of obtained to expected frequencies; second number is obtained frequency. Secondary and tertiary effects are indicated by asterisks.

HOME RAT DYADS

Within the home rat, there were 29 different highly significant behavioral transition dyads as have been listed in Table 1. All except four of these dyads may be conveniently represented in a single behavioral flowchart, shown in Figure 3, in which it may be seen that they break down into three categories: (1) exploration and scent-marking dyads; (2) grooming dyads; and (3) offense dyads. The other four dyads all involved defense behaviors which will be diagrammed later in other flowcharts.

The transition of exploratory and grooming dyads were generally symmetrical; *i.e.*, the ratio of obtained to expected frequency leading from one behavior to another was usually similar to that of the reverse sequence. There were two major exceptions which were asymmetrical: the sequence of sniff-nose to crawl-under to sniff-anogenital-region; and the sequence of explore cage to sniff-dish to crawl-over-dish.
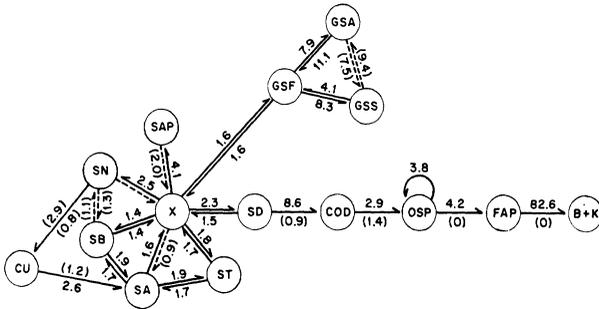

Fig. 3. Flow chart of highly significant and other related behavioral dyads within the home rat. All highly significant dyads except for two associated with retreat and several dyads associated with defense are illustrated here. Highly significant dyads (probability less than .001 by Chi Square) are indicated by solid arrows along with the ratio of obtained to expected value. Dyads which were not highly significant are indicated by dotted arrows or simply listed without an arrow and their ratio of obtained to expected value is placed in parentheses. See methods section in text for abbreviations of behaviors.

All of the possible transitions from one grooming act to another and most of the possible transitions among exploratory acts had relatively high if not significant, transition ratios. There were two major exceptions: exploration of the body of the opponent tended to move from one part of the animal to another adjoining part rather than skipping from head to tail, *etc.*, and the sequence of sniff-dish to crawl-over-dish was not linked with other exploratory acts.

There was a highly significant pair of symmetrical transition ratios linking explore cage and groom-self-face. The transition ratios between explore cage and other grooming acts were all about 1.00, however; *i.e.*, no greater than expected by chance.

Offense behavior, in contrast to exploration and grooming, was distinguished by the asymmetry of transition ratios and the restriction of transitions to only one highly probable sequence. That sequence consisted of repeated offensive sideways posture leading to full aggressive posture and then to bite-and-kick attack.

INTRUDER DYADS

Within the intruder, there were 27 different highly significant behavioral dyads as have been listed in Table 2. Of these dyads, 14 involved exploratory and grooming behaviors and may be conveniently represented in a single behavioral flowchart as shown in Fig. 4. Intruder rats did not show offense behaviors. The remaining 13 behavioral dyads all involved defense and submission behaviors which will be diagrammed in flowcharts to be presented later.
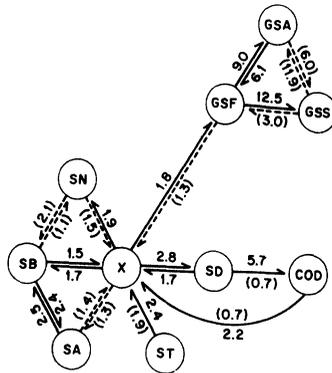

Fig. 4. Flow chart of highly significant and other related behavioral dyads within the intruder rat. All highly significant behavioral dyads are listed except for those associated with defense and submission. Conventions for significance level of behavioral dyads are same as in Fig. 3.

Similar to the data for home rats, the transition ratios of exploration and grooming within the intruders were mostly symmetrical, and most logically possible dyads were represented with relatively great, if not highly significant, transition ratios. There were even fewer exceptions than in the case of home rats: exploration of the body of the opponent moved from one adjoining part to another; and there was an asymmetrical sequence from explore cage to sniff-dish to crawl-over-dish to explore cage again. Also similar to the data for home rats, there was a highly significant set of symmetrical transition ratios between explore cage and groom-self-face, but the ratios between explore cage and other grooming acts averaged no greater than 1.00 which would be expected by chance.

INTERACTION DYADS

Between the home rat and intruder, there were 49 highly significant behavioral dyads as have been listed in Table 3. Simultaneous exploration or grooming by the two rats were represented by 17 highly significant dyads,

Five dyads have been classified as miscellaneous and will be considered separately. The largest and most important category included 27 dyads which involved offense or approach by one of the rats and defense or submission behavior by the other rat. For purposes of the present analysis, these dyads will be differentiated into 22 "primary effects" which are shown in Figs. 5 and 6, and five "secondary or tertiary effects" which will be analyzed later.
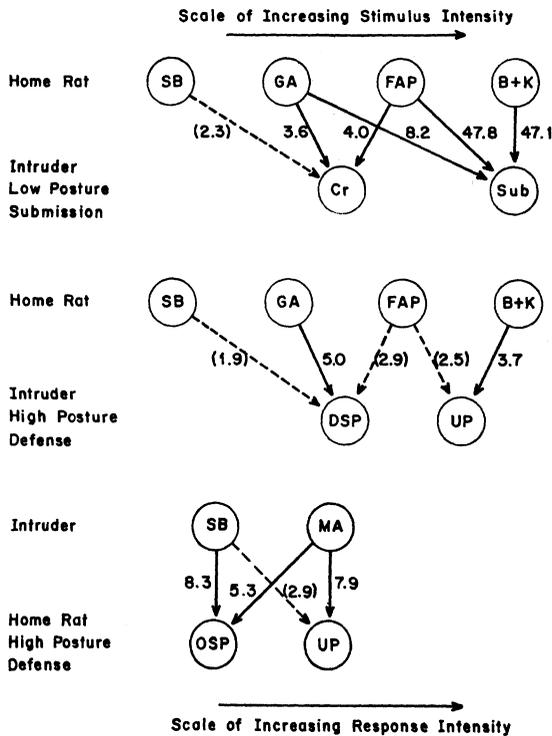

Fig. 5. Flow chart of highly significant and other related interaction behavioral dyads leading from tactile stimulation of the back by one rat to low posture submission and high posture defense by the other rat. Conventions for significance level of behavioral dyads are same as in Fig. 3. The following related but insignificant dyads of home rat to intruder behaviors are omitted from the figure for sake of clarity: (ratio of expected to obtained frequencies in parentheses) SB to Sub (0.0); B & K to Cr (1.5); SB to UP (0.6); GA to UP (0.8); and B & K to DSP (0.0).

Half of the primary effects consisted of an initial behavior involving tactile stimulation of the dorsal surface of the opponent by one animal and a succeeding behavior involving a low posture submission response or a high posture defense response by the opponent. These have been diagrammed in
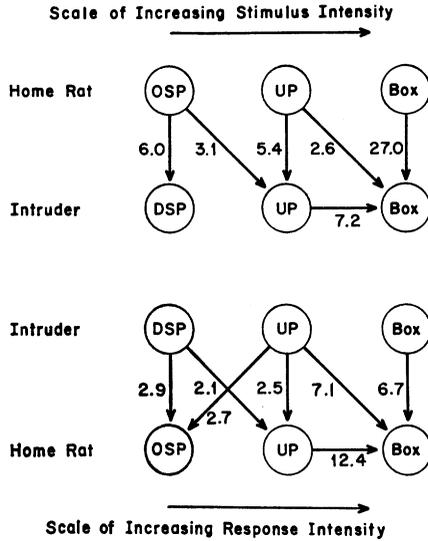
Fig. 6. Flow chart of highly significant interaction behavioral dyads leading from a high approach by one animal to a high posture defense by the opponent. Dyads from the home rat to the intruder are shown in the upper portion of the figure and from intruder to the home rat in the lower portion. The following insignificant but related behavioral dyads of home rat to intruder are omitted from the figure for sake of clarity (ratio of expected to obtained values in parentheses): OSP to Box (0.0); UP to DSP (0.6); Box to DSP (0.0); and Box to UP (0.4). The following behavioral dyads of intruder to home rat are omitted from the figure (ratio of expected to obtained values in parentheses): DSP to Box (0.0); Box to OSP (2.4); and Box to UP (1.2). Only the ratio for Box to OSP was statistically highly significant.

Fig. 5, where it may be seen that the intensity of the second behavior (the response) was a function of the intensity of the initial behavior (the stimulus). Initial behaviors which involved relatively weak stimulation of the back, head, or flank (sniff-back or aggressive groom) led to low intensity responses by the second rat (crouch or sideways posture). Initial behaviors which involved relatively strong stimulation of the dorsal surface (full aggressive posture, bite-and-kick attack, or attempted mount) led to high intensity responses by the second rat (full submissive posture or upright posture).

The other primary effects consisted of an initial behavior involving an elevated approach by one animal and a succeeding behavior involving a high posture defense response by the opponent. These have been diagrammed in Fig. 6, where it may be seen that the intensity of the second behavior was a function of the intensity of the initial behavior. Initial behaviors which involved an intermediate elevation of approach (offensive or defensive side-

ways posture) led to a lower intensity response offensive or defensive sideways posture or upright posture. Initial behaviors which involved a higher elevation of approach (upright posture) or an additional movement and tactile component (boxing) led to high intensity responses by the second rat (upright posture and boxing).

The data suggest that a distinction should be made between submission
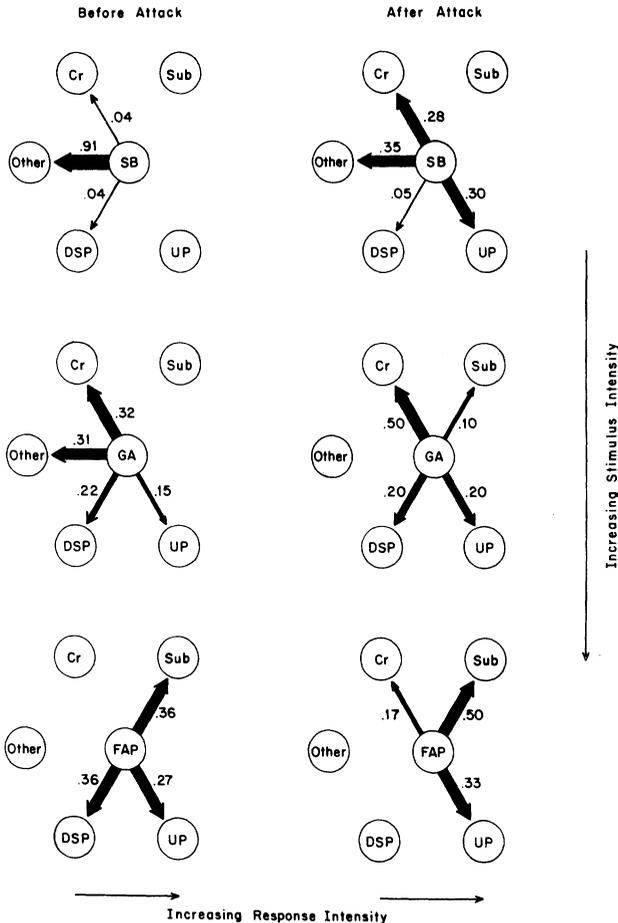
Fig. 7. Shift from low intensity to high intensity response by intruder to dorsal tactile stimulation by the home rat from the period preceding an attack to the period following an attack. Three types of home rat behavior which involve dorsal tactile stimulation are shown: sniff back (SB); aggressive groom (GA); and full aggressive posture (FAP); listed in order of increasing stimulus intensity. The proportion of each type of response by the intruder to these behaviors are shown for the five minutes preceding the initial bite and kick attack of a test (before attack) and the five minutes following the initial attack (after attack).
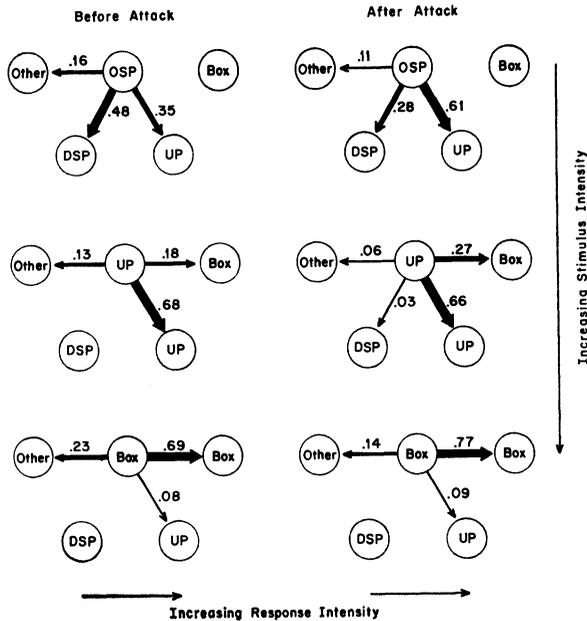
Fig. 8. Shift from low intensity to high intensity response by intruder to high posture approach by the home rat from the period preceding an attack to the period following an attack. Three types of high posture approach are shown: offensive sideways posture (OSP); upright posture (UP); and boxing (Box); listed in order of increasing stimulus intensity. The proportion of each type of response by the intruder to these behaviors are shown for the five minutes preceding the initial bite and kick attack of a test (before attack) and the five minutes following the initial attack (after attack).

and defense behaviors. Submission behavior occurs in response to dorsal tactile stimulation and consists of two postures, a low intensity crouch and a high intensity full submissive posture. Submission does not occur as a response to an elevated approach. Defense behaviors occur in response to either dorsal tactile stimulation or an elevated approach by the opponent, and consist of two postures, a low intensity sideways posture and a high intensity upright posture, which may include boxing movements of the fore-limbs at the highest intensity.

The level of intensity of submission and defense responses were also a function of prior attack by the opponent. If the animal had been attacked recently, the submission and defense behaviors were more likely to be of high intensity than if there had been no attack. Data on this question are shown in Figs. 7 and 8, which illustrate the shift from low intensity defense or submission responses prior to bite-and-kick attack to higher intensity responses after a bite-and-kick attack.

The potentiating effect of attack upon response to dorsal tactile stimulation is shown in Fig. 7. A weak level of tactile stimulation (sniff back) which did not lead to submission or defense behaviors before attack, did lead to crouch and upright posture frequently after attack. Other behaviors involving more intense tactile stimulation led to submissive and defensive responses prior to attack as well as after attack; hence the effects of attack were not as great in these cases. There was, however, a trend for aggressive groom to lead to more submissive and defensive behaviors after attack, and for the responses to be more intense. Similarly, full aggressive posture, which elicited low intensity responses prior to attack, elicited almost exclusively the high responses after attack.

The defense responses to an elevated approach were also potentiated by attack, as shown in Fig. 8. The greatest effect was again in the case of the least intense stimulus; offensive sideways posture led to upright posture by the opponent only 35% of the time prior to attack, but 61% of the time after the attack. The responses to upright posture and boxing were already relatively intense prior to attack; hence the intensity of response after attack could show only a slight increase.

The data from the potentiation of submission and defense behaviors by attack may be taken as a second, independent confirmation that these behaviors consist of several levels of response intensity. Submission, which consists of crouch at low levels, is potentiated by attack to full submissive behavior at high levels. Defense, which consists of sideways postures at low levels, is potentiated by attack to upright posture at higher levels, and to boxing at the highest level.

The home rat, more often than the intruder, was the initiator of mutual upright and boxing behaviors. As may be seen in Fig. 6, upright posture by both animals was more likely to have been initiated by home rat upright posture (ratio 5.4) than by intruder upright posture (ratio 2.5). Boxing in response to upright posture was more likely initiated by the home rat in response to the intruder (ratio 7.1) than vice versa (ratio 2.6). Finally, boxing by both animals was more likely to have been initiated by home rat boxing (ratio 27.0) than to have been initiated by intruder boxing (ratio 6.7).

The intruder frequently emitted ultrasound vocalization after being attacked by the home rat (see Fig. 2). The ultrasound was obtained most often in conjunction with crouch and full submissive posture and the transition ratio of crouch to ultrasound was highly significant. Ultrasound was sometimes obtained in conjunction with upright posture as well. It was often shown for many minutes in succession after an attack, and the transition ratio of ultrasound to ultrasound was highly significant.

Several other submission and defense dyads may be considered as primary effects. The behavior of crouch was often shown by intruders for many seconds and even minutes in succession; hence the transition ratio of crouch to crouch was highly significant for intruder rats. Upright posture by an animal often led directly into boxing behavior by the same animal, apparently as a result of any movement by the opponent rather than any particular act or posture on its part. Hence the transition ratio of upright posture to boxing was highly significant, both for home rats and intruder rats. In sum, the primary effects to tactile back stimulation, elevated approach, and those of sustained crouch and ultrasound, crouch to ultrasound, and upright posture to boxing account for 27 of the 44 highly significant defense and submission dyads.

All of the remaining 17 highly significant defense and submission dyads may be understood as statistical derivatives of the effects described thus far. These effects will be called "secondary" effects as distinguished from the previously described "primary" effects. By constructing a behavioral flowchart of significant primary sequences, one can obtain all of the secondary effects by completing the third side of any sequential triangle (Figs. 9 and 10). For example, given the significant dyads home rat FAP to home rat B&K and home rat FAP to intruder Sub in the primary attack sequence of Fig. 9A, one would also expect the third dyad, intruder Sub to home rat B&K to be a significant dyad as well. Since it is a statistical derivative, however, the transition ratio of Sub to B&K would be expected to be no greater than the lower of the two primary statistical transition ratios. This is confirmed for every secondary effect in Fig. 9B as well as most of the effects shown in Fig. 10B as well. Some of these effects might better be termed tertiary rather than secondary effects since one of the first two sides of the triangle is already a secondary effect. As one would predict, the tertiary effects are always still lower than the secondary effects. For example, building on the secondary effect described above, and the primary effect of home B&K to intruder UP, there is a tertiary effect of intruder Sub to intruder UP. The first two ratios are 23.5 and 3.7 respectively, and the derived tertiary effect has a ratio of only 3.6. Primary effects are indicated on the top portion of each figure and shown with double arrows. Secondary and tertiary effects are added on the bottom repetition of each figure and are shown as single arrows. Secondary and tertiary effects are asterisked in the tables.

Among the miscellaneous interaction dyads which were highly significant were a symmetrical pair of dyads involving approach by the home rat and retreat by the intruder. The transition ratios were particularly high for

these two dyads: 18.8 for the dyad initiated by the home rat; and 15.2 for the dyad initiated by the intruder.
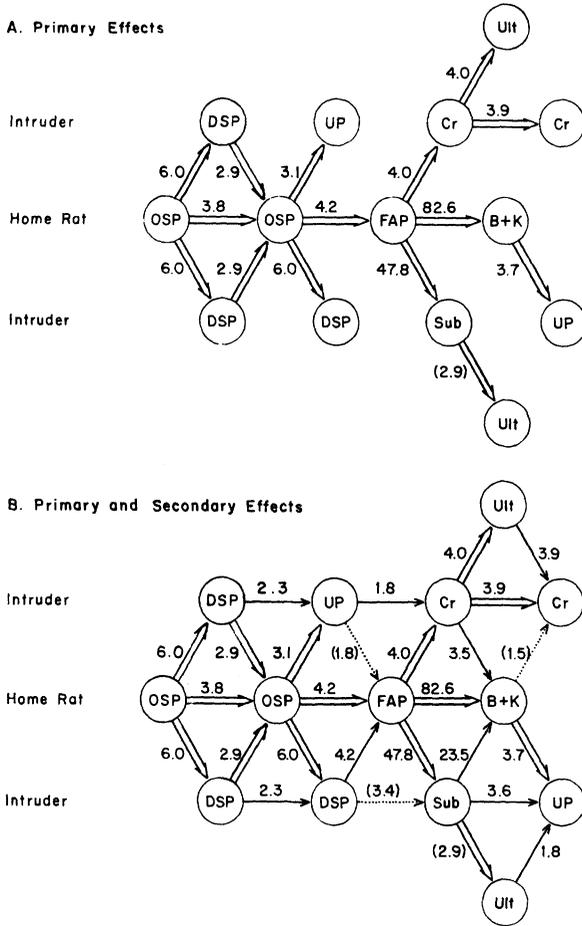

Fig. 9. Prediction of secondary and tertiary statistical transitions based upon the primary offense sequence and consequent defense behaviors by the intruder. In (A) a composite diagram has been constructed from all the primary offense sequence (see Figure 3), all of the defense responses elicited by those offense behaviors (see Figures 5 and 7), and several defense to defense or submission to submission tranitions which are also apparently primary effects. In (B) all of the possible triangular lines have been filled in between pairs of behaviors which are each elicited by the same third behavior. Primary effects are indicated by double arrows, highly significant secondary effects are indicated by solid single arrows, and insignificant secondary effects are indicated by dotted arrows. Ratio of obtained to expected frequency is indicated next to each appropriate arrow, with insignificant ratios placed within parentheses.

A. Primary Effects
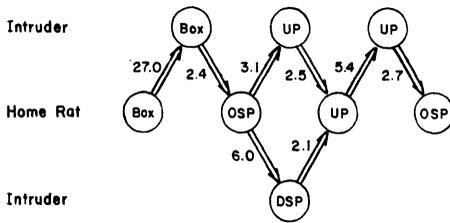
B. Secondary Effects
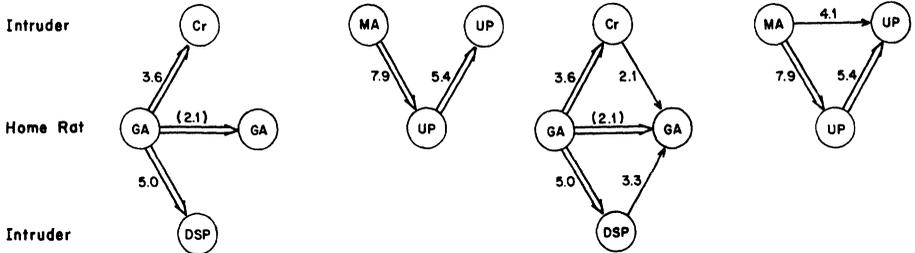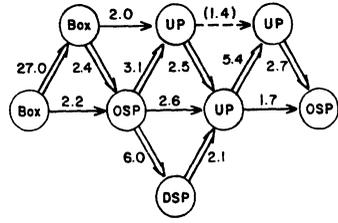
Fig. 10. Prediction of secondary statistical transitions based upon high posture defense interactions, repetition of aggressive groom by the home rat, and effect of mounting behavior by the intruder rat. In the top portion of the figure, the primary effects are shown. In the bottom portion of the figure the various triangular lines have been filled in to predict secondary effects. Notation is same as in Fig. 9.

Another symmetrical pair of interaction dyads involved groom-self-side by the home rat and ultrasound by the intruder. The transition ratios were 3.1 for the dyad initiated by the home rat and 3.3 for the dyad initiated by the intruder. As will be discussed later, these effects may be interpreted in terms of the inhibitory function of ultrasound, and the possibility that groom-self-side is a "displacement" activity in place of other inhibited behaviors.

The only other highly significant interaction dyad was from groom-self-side by the home rat to sniff-back by the intruder. The latter will be discussed in terms of the possible function of groom-self-side behavior for the airborne diffusion of glandular odors, a function which would stimulate approach and sniff by the opponent.

A few details should be noted concerning the highly significant interaction dyads which involved simultaneous grooming behavior by the two rats or simultaneous exploratory and scent-marking behavior by the two rats. In most cases the transition ratios were lower than the corresponding transition ratios for grooming and exploration within the home rat and the intruder. One exception, however, involved the dyad of sniff-nose by the home rat

to sniff-nose by the intruder, which had the remarkably high transition ratio of 11.96. In many cases the initial behavior was cage exploration by one animal and the succeeding behavior involved sniffing the body of the exploring animal by its opponent. In some respects these dyads may be understood as special cases of the interaction dyad, retreat to approach, *i.e.*, the exploring animal may be perceived by its opponent as if it were in retreat, which may stimulate an approach and sniffing by the opponent. One such dyad led to a curious secondary effect. Sniff-dish by the intruder was often followed immediately by sniff-dish by the home rat which was following it around (ratio: 2.1). Since the intruder sniff-dish also led to intruder crawl-over-dish (ratio: 5.7), one often found a secondary effect leading from home rat sniff-dish to intruder crawl-over-dish (ratio: 2.5).

ULTRASOUND INHIBITION OF ATTACK

Data from the present study have allowed a simple statistical test for previous assertions by other investigators that ultrasound emission by an intruder serves to inhibit attack by a home rat. A comparison was made of the transition probabilities from crouch, upright posture, and full submissive posture (the three behaviors most often associated with ultrasound) to a bite-and-kick attack by the opponent as a function of whether or not they were accompanied by ultrasound. The hypothesis was sustained. When not accompanied by ultrasound, these behaviors led to bite-and-kick attack 18 times out of a possible 756. When accompanied by ultrasound, on the other hand, they never led to a bite-and-kick attack out of a possible 296 occurrences. The difference is significant by a Chi Square Test. It is not due simply to the fact that ultrasound occurs almost exclusively after the first attack, for in 8 of the 18 cases in which the behaviors without ultrasound led to attack, the attack was the second, third, or fourth attack of the test session.

Most intruders began to emit ultrasound after having been attacked, and most home rats showed only one or two bite-and-kick attacks in a test session. From these facts, one might hypothesize that bite-and-kick attacks would be likely to continue at a high frequency if they were not inhibited by ultrasound. Data from supplementary experiments do not confirm this hypothesis, however. In cases where the intruder was rendered incapable of producing ultrasound after surgical resection of the nerve supply to the larynx, and in cases where the home rat was rendered incapable of hearing ultrasound after destroying the middle ear and plugging it with cement, there were still the same number of bite-and-kick attacks during post-operative test sessions as there had been during pre-operative test sessions.

DISCUSSION

In the results section it proved possible to reduce the large number of statistically significant transitional dyads to a relatively small number of primary effects; in the following discussion section, a further reduction will be attempted, and the primary effects will be considered as the results of the dynamic relationships of a few hierarchically organized mechanisms which are thought to correspond to the neural organization of behavior.

The attempt to explain complex behavioral interactions in terms of a few hierarchically organized mechanisms is not new. The present analysis owes much to the work of ethologists such as LORENZ (1950), TINBERGEN (1951), LEYHAUSEN (LORENZ & LEYHAUSEN, 1973), and BAERENDS (1976). For example, the distinctions between three functions of stimuli, releasing, directing, and motivating, and between two functions of actions, appetitive and consummatory, may be found in TINBERGEN (1951). Also, the distinction between motivational mechanisms and motor patterning mechanisms corresponds roughly to his distinction between central excitatory mechanisms and innate releasing mechanisms. The present analysis is not intended to correspond completely to any particular theory, however; these partial correspondences are mentioned as acknowledgement of our general intellectual debt to the tradition of ethology.

Basic to the present analysis is a distinction between motivational mechanisms and motor patterning mechanisms. Motivational mechanisms are hypothesized to receive activating inputs from motivating stimuli: exteroceptive stimuli, interoceptive stimuli, and hormonal activation. Their output is hypothesized to activate motor patterning mechanisms. Motor patterning mechanisms, in addition to receiving input from motivational mechanisms, are hypothesized to receive inputs as a result of two types of activating stimuli: releasing stimuli and directing stimuli. The output of a motor patterning mechanisms is a particular motor pattern, which is an observable component of behavior. Releasing stimuli may trigger the release of the motor pattern, depending upon the quality of the stimulus. Directing stimuli may orient the motor pattern in space, depending upon the spatial information of the stimuli. The expression of some motor patterns may depend upon a simultaneous confluence of all three types of activation upon the motor patterning mechanism: input from one or more motivational mechanisms; input from appropriate releasing stimuli; and input from appropriate directing stimuli. An example of this might be the bite-and-kick attack. Expression of other motor patterns, *e.g.*, piloerection, might require only a motivational input.

It should be noted that according to the present analysis, a discrete motor

patterning mechanism may be under the influence of more than one motivational mechanism. In this case the motor pattern which it organizes may be said to be ambivalent (cf. GRANT & MACKINTOSH, 1963). In other words, mere presence of the motor pattern does not tell the experimenter which of the two possible motivational mechanisms are active. It should also be noted that a particular physical stimulus may function simultaneously as motivating, releasing or directing, depending upon the information processing in the brain of the animal.

The authors believe that these motivational and motor patterning mechanisms correspond to neural mechanisms which organize behavior. An example of one motivational mechanism, its neural substrate, its motor patterning mechanisms and motor outputs was presented by one of the authors in a previous publication (EDWARDS & ADAMS, 1974) and the activity of single neurons have been recorded which are believed to be part of the mechanism (POND, SINNAMON & ADAMS, 1977). In the publications cited, the motivational mechanism was called a "patterning mechanism" and the motor outputs were called "patterned reflexes."

In order to explain the present data, five basic motivational mechanisms are postulated: exploration and scent-marking; grooming; offense; defense; and submission. The first two mechanisms follow rather directly from the data shown in Figs. 3 and 4 in which a number of different behaviors are temporally related in a symmetrical manner. Offense and defense were characterized as "hypothetical neural mechanisms" in a previous study (ADAMS, 1976), and the distinction is maintained here. Finally, data from the present study suggest that a motivational mechanism of submission should be distinguished from that of defense even though they may each be activated by similar stimuli, and they may both ward off attack. Presumably there are many other motivational mechanisms in the rat as well as those discussed here, e.g., maternal behavior, prey-catching, sleep, etc., but only five appear to be active under the circumstances of inter-male social encounters.

Exploration and Scent-Marking.

The various acts and postures involved in exploration and scent-marking behavior (crawl-over-dish) have been considered here as reflections of a single underlying motivational mechanism, and several motor patterning mechanisms and motor patterns which are differentiated by continually changing orientation towards different objects in the environment. In other words, once the motivational mechanism is activated by motivational stimuli, the motor patterns of behavior unfold in a sequence determined by the directing stimuli from the environment which attract the animal from one

moving object or odorous object to another. Since the moving objects and odorous objects in the environment may be arranged in any spatial order, the specific acts and postures also occur in any order. Transition ratios for particular dyads are symmetrical and any act may follow any other act. In fact, the exceptions to the rule are as instructive as the examples of it. The exploration of the body of the opponent tends to be ordered by the invariant spatial relationships of the body; hence exploration precedes from one part of the body to an adjacent part rather than skipping from head to tail or vice versa. Similarly, the progression of explore to sniff-dish to crawl-over-dish proceeds in a set order determined by the spatial relationship between the rat and the Petri dish as the rat approaches and passes over it. The rat approaches the dish, sniffs it, passes over it, lowering the body and urinating slightly. Only if the rat were to walk backwards, which is rarely seen, would one find crawl-over-dish preceding or in isolation from sniff-dish.

The stimuli which activate the motivational mechanism (motivational stimuli) and which orient the specific motor patterns (releasing and directing stimuli) appear to be similar and to involve the perception of unfamiliar rat odors. Since the cage is encrusted with scent-marking odors of the home rat, its odors are already familiar to the home rat but unfamiliar to the intruder; thus when the session begins, the exploration by the intruder is guided and oriented by cage odors, and exploration by the home rat is guided by odors of the intruder. As the session progresses, the tempo of locomotion involved in the exploration and scent-marking increases, suggesting that the additional unfamiliar odors encountered during the exploration further activate the motivational mechanism of exploration in general. Also, the rats soon exchange roles with the home rat sniffing the cage as well as the intruder and the intruder sniffing the home rat as well as the cage.

Other types of stimuli may affect exploration and scent-marking. Exploration involves approach locomotion, but when the rat has approached within "sniffing" distance of the object or opponent, its locomotion stops and the distance is maintained during the sniffing behavior; the releasing stimuli for this apparent locomotor inhibition may involve stimuli from the vibrissae. Another set of stimuli, perhaps from the ventral surface of the animal, may be involved in releasing the urination of crawl-over-dish. Finally, data from the previous study (ADAMS, 1976) suggest that pain may be an inhibitor of the motivational mechanism for exploration and scent-marking, since these behaviors are greatly reduced in frequency after an animal has been attacked. Alternative explanations are possible, however; pain-elicited defense and submission acts and postures might reduce exploration by behavioral com-

petition; or these other motivational mechanisms might interact directly with the exploratory motivational mechanism.

The specific motor patterning mechanisms which are activated by exploration and marking may include approach locomotion, sniff, crawl-over-object, and facial gland secretion. Evidence for facial gland secretion will be discussed in terms of grooming behavior. The motor patterns of sniff and crawl-over-object are to some extent mutually exclusive: following an approach, a rat may inhibit its locomotion, maintain a distance from the object, and sniff; or alternatively, it may continue the approach and pass over, under or beside the object or opponent and deposit urine during the passage (crawl-over-dish or crawl-over behavior). Approach locomotion may be activated by other motivational mechanisms as well as exploration and scent-marking, *e.g.*, the offense motivational mechanism, which may help explain one asymmetrical dyad which is present in home rats but not intruder rats. Unlike the intruder, which halts at sniff-nose, the home rat often continues its approach to the intruder, sniffs its nose, passes under the body (crawl-under) and sniffs the ano-genital region of the intruder. This sequence may be interpreted as a consequence of joint activation of approach by both exploratory and offense mechanisms.

G r o o m i n g .

Many details of the data in this study can be explained by postulating that both the motivational stimuli and the directing stimuli for grooming consist of tactile sensations associated with secretion from specialized scent-glands on the body surface. The motivational effects of these stimuli, it is suggested, are general and active the motivational mechanism of grooming without predisposing the rat to any one particular grooming act; the directing effects of these stimuli, however, are postulated to be specific for that part of the body where the scent glands are active.

At least three types of scent-gland appear to be involved in the motivation and orientation of grooming: facial glands in the eye and mouth region (QUAY, 1965; THIESSEN *et al.*, 1976); sebaceous glands of the flank (GRANT & MACKINTOSH, 1963); and glands in the ano-genital region associated with the urinary tract (ORTMANN, 1960). Data from the present study suggest that the facial glands are activated by way of the exploratory and scent-marking motivational mechanism, and that the flank glands are activated by way of the offense motivational mechanism, while those in the ano-genital region may be activated by way of the sexual motivational mechanism.

The distinction between motivational and directing aspects of stimuli from

scent-gland activation enables one to explain the following data. On the one hand, the transition probabilities for self-grooming dyads were symmetrical and all logically possible dyads had great, or highly significant transition ratios, which suggest that there is a single motivational mechanism for grooming and that all self-grooming acts are equally affected by the motivational stimuli of grooming. On the other hand, there were major differences in the occurrence of different acts and postures oriented towards different parts of the body, suggesting that there are diverse directing stimuli of grooming responsible for the different orientations and that they are influenced by various other motivational mechanisms. Groom-self-side and scratch were more frequent in home rats than in intruders; they may be explained by the activation of flank gland secretion by way of the offense motivational mechanism which was activated only in home rats. Groom-self-anogenital region was particularly frequent following mounting or attempted mounting behavior, reflecting the postulated activation of ano-genital glands by way of sexual motivation. Groom-self-face was often associated with exploratory behavior, e.g., the highly significant dyads of groom-self-face to and from exploration which reflects the postulated activation of facial gland secretion by way of the exploratory and scent-marking motivational mechanism. Finally, whereas exploratory and scent-marking behaviors were highest in frequency at the beginning of a test session, grooming behaviors became higher in frequency towards the end of a test session, reflecting the activation of scent-gland secretion by way of motivational mechanisms which became active during the course of the test.

Self-grooming might also be called "self-anointing" insofar as it functions to spread the secretions of the glands onto the surface of the body where they have a greater area for diffusion into the air. EISENBERG & KLEIMAN (1972) have described such self-anointing behavior in a variety of mammalian species, although it has not usually been applied to the analysis of grooming in the rat. The "self-anointing" effect would explain why groom-self-side by the home rat leads to sniff-back by the intruder rat, one of the highly significant dyads hitherto unexplained in the present study; i.e., the groom-self-side diffuses odors from the flank gland which direct the exploratory behavior of the opponent and causes the behavior of sniff-back. The "self-anointing" effect may also help explain the highly signiifcant dyad of sniff-nose to sniff-nose; i.e., exploratory behavior is accompanied by facial gland secretion and by groom-self-face which diffuses odors which may direct the exploration of both animals towards sniffing the facial region of the opponent.

The motor patterning mechanisms of rub and aggressive groom may be

considered as ambivalent, activated partly by grooming and partly by other motivational mechanisms. Rub may be jointly activated by grooming and offense. The former would explain why it seems to be associated with groom-self-side and secretion of glands on the flank; the latter would explain why it is shown only by home rats (ADAMS, 1976). Aggressive groom may result from the combined motor patterns of approach (activated by exploration and/or offense) and grooming (activated by glandular secretion of the grooming animal). It would be more common in the home rat because of its stronger approach tendencies (offense motivated approach) and its stronger grooming tendencies (due to secretion from flank glands).

Offense.

In the previous study (ADAMS, 1976) it was suggested that there is a brain mechanism for offense behavior, that its motivating stimuli are the combination of unfamiliar odors from the opponent rat and familiar odors from the scent-markings in the home cage, and that it leads to various motor output patterns including full aggressive posture and bite-and-kick attack, offensive sideways posture, and rub. Data from the present study suggest several additions and changes in this formulation.

The significant transition ratio from sniff-dish to crawl-over-dish to offensive sideways posture may be interpreted as indirect evidence in favor of the hypothesis that olfactory comparisons provide primary motivating stimuli for offense. Sniff-dish provides olfactory stimuli from previous scent-marking in the home cage, and, as has been pointed out, it usually occurs during the course of the home rat's olfactory investigation of the intruder rat as it follows the latter around the cage; hence both parts of the olfactory comparison are completed at that point. Sniff-dish does not lead directly to offensive sideways posture, however, since crawl-over-dish intervenes, due to the strong link between sniff-dish and crawl-over-dish.

Other facilitating and inhibiting stimuli may affect the offense motivational mechanism. It has been suggested that the crouch posture is an effective inhibitor of attack because of removal of facilitatory cues of movement; this would correlate with findings by previous investigators that movement of the opponent can stimulate or intensify attack (CALHOUN, 1962; ALBERTS & GALEF, 1973). Data from the present study along with those of previous studies (SALES, 1972; LUCIANO, 1974; LORE et al., 1976) also suggest that ultrasound inhibits offense.

The motor patterning mechanisms activated by offense may produce approach locomotion, the attack sequence (full aggressive posture to bite-and-kick attack), rub, and "high posture" (offensive sideways posture and

upright posture and boxing. These motor patterning mechanisms are probably activated by more than one motivational mechanism, however, in many cases. Approach locomotion may be influenced by both offense and exploratory motivation and may be associated with behaviors other than attack or offsensive sideways posture. Rub may be activated by grooming as well as offense, and directed by stimuli from the scent glands of the flank. The motor patterning mechanism of high posture (offensive sideways posture and upright posture) may be under joint activation of offense and defense, which may explain why the home rat is more likely to initiate high postures than is the intruder. Boxing may also be considered as a hybrid motor pattern involving the high posture with the addition of a locomotor and locomotor placing component in the forelimbs due to offense activation. For this reason boxing also is usually initiated by the home rat. Offensive sideways posture may also be considered as a hybrid act; it is similar to the defensive sideways posture of the intruder but with additional components of approach and piloerection due to offense activation.

There is an asymmetrical relationship between offensive sideways posture (OSP) and the attack sequence of full aggressive posture to bite-and-kick attack, with the former leading to the latter but not vice versa. The transition from OSP to attack may simply reflect temporal pattering since they are both activated by way of the same motivational mechanism of offense. Once the attack has occurred, however, the offense motivational mechanism seems as if it were "discharged" for the moment. Offensive sideways posture often does not begin again for several seconds. The next bite-and-kick attack, if it occurs at all, does not usually come until two or three minutes later. And bite-and-kick attack may cease altogether, even if there is no inhibition from ultrasound. This phenomenon may be comparable to the refractory period observed following ejaculation in sexual behavior and suggests that bite-and-kick is a consummatory act in the terms of TINBERGEN (1951).

The motivational mechanism of offense, as observed here, is apparently dependent upon testosterone and relative social isolation. It is not shown by isolated female laboratory rats in this test situation, although it may be seen in females of some species of rats (BARNETT, 1975). The motivational mechanisms of offense may be active in other test situations, however, where it is under the control of different hormonal and motivating stimuli. In competitive fighting, pairs of food-deprived female rats without social isolation show all the motor patterns of offense including the offensive sideways posture, the bite-and-kick attack and piloerection (ZOOK & ADAMS, 1974). Lactating females also show all of these behaviors during maternal nest defense, although other motor patterns may be present as well (GALLAND, ODMARK & ADAMS, unpublished observations).

Defense.

In the previous paper (ADAMS, 1976) it was suggested that the observed behavioral dyad of offensive sideways posture by the home rat leading to upright posture by the intruder indicated that upright posture was a defensive response to "threat." For the present analysis, however, the term "threat" is not sufficiently precise. Instead, it is proposed that the motivational mechanism of defense, which activates the high postures as one possible motor pattern, is stimulated by one of two precise and quantifiable types of motivational stimuli: (1) tactile stimulation of the dorsal surface of the body; and (2) visual or vibrissal stimulation by an approaching object at a certain elevation above the horizontal plane, such as an approaching rat in sideways or upright posture. A brain mechanism comparable to the latter has been described in elegant detail for the toad (EWERT, 1972). The motivational mechanism would be further activated or sensitized by pain stimulation and by the amount of movement (e.g., boxing with forelimbs) exhibited by the opponent.

There are several motor patterning mechanisms activated by defense motivation, as well as gradations of intensity within their motor patterns and hybrid acts and postures when other motor patterns are simultaneously activated by way of other motivational mechanisms. In the present study, only high posture motor patterns were observed, but if one conducts similar tests in a larger arena, flight may be observed. High posture motor patterns may be observed at three levels of intensity, from the lowest intensity defensive sideways posture, through upright posture, to the highest intensity boxing behavior. Hybrid acts and postures may also be formed when there is simultaneous offensive motivation: the motor pattern of sideways posture may be accompanied by motor patterns of approach and piloerection, producing offensive sideways posture; and the motor pattern of upright posture may be accompanied by offense-motivated locomotor movements of the forelimbs producing boxing. The low posture motor patterns of crouch and full submissive posture are *not* activated by way of defense, however, since they are never seen in reaction to a high approach by the opponent. Instead, they are activated by way of the motivational mechanism of submission, to be described below.

There are important theoretical consequences of the hypothesis that the motor patterns of high posture are ambivalent, reflecting activation from offense as well as defense motivational mechanisms. GRANT & MACKINTOSH (1963) noting that upright posture and boxing by home rats had an additional approach component, made a distinction between offensive upright posture and defensive upright posture. The present analysis is somewhat similar

although we differ from GRANT (1963) since we propose that the sideways postures are less intense forms of the high posture defense than are the upright postures.

The high posture motor pattern, motivated by defense, is the major component of behavior elicited by electrically shocking the feet of two rats in a small enclosed cage. The brain mechanisms of this shock-elicited fighting have been more intensively studied than those of any other behavior analyzed here. EDWARDS & ADAMS (1974) have suggested that the cells of the motivational mechanism are located in and lateral to the midbrain central gray. Single unit recording from cells in this region have shown them to be maximally active during the behavior (POND, SINNAMON & ADAMS, 1977). Afferent inputs from the vibrissae have been shown to be the most critical kind of sensory stimulation involved (THOR et al., 1974). Although boxing is most conveniently elicited by footshock and is greatly potentiated by attack, it does not require pain or pain sensitization. It is seen in home rats as well as intruders, in non-bitten intruders as well as bitten intruders, and in naive rats that have been raised in social isolation (ADAMS, 1976).

Submission.

The motor patterns seen in submission are the low posture patterns of crouch and full submissive posture, in contrast to the high posture patterns seen in defense. In our previous work, we had not distinguished these two motivational mechanisms since they are each stimulated on some occasions by tactile stimulation of the back and they are each potentiated by pain. One critical piece of data suggests that they be distinguished, however; whereas the motor patterns of defense may be seen following high approach motivating stimuli, the motor patterns of submission are never seen in response to a high approach.

Although it is convenient to distinguish defense and submission as separate motivational mechanisms in terms of the present data, one can entertain an alternative hypothesis. If one postulates that the high approach stimuli function as releasing stimuli rather than motivational stimuli, then one can consider high postures and low postures as motor patterns organized by separate motor patterning mechanisms both under the influence of a single motivational system, which one may call defense. In such a formulation, high approach stimuli elicit only high posture responses because they function as releasing stimuli for the motor patterning mechanism of high postures, but not as releasing stimuli for low postures. Given the present data, it seems premature to reject either of these two alternative hypotheses.

The low posture motor patterns of submission are characterized by motor inhibition. Crouch, which occurs at a lower intensity, consists primarily of an inhibition of skeletal movement. The full submissive posture, which occurs at a higher intensity, may also contain strong inhibition, especially in the case of catalepsy (see GRANT & MACKINTOSH, 1963). The animal progresses from crouch at low intensity to full submissive posture at high intensity by rolling away from the opponent and onto its back. The tactile stimulation of the back which results from this new posture provides additional input to the submission motivational mechanism, *i.e.*, a positive feedback process ensues. This positive feedback may explain the catalepsy sometimes seen during isolation induced fighting, and it may be related to the more general phenomenon of "animal hypnosis" which is evoked by holding an animal on its back (RATNER, 1967).

Prolonged low posture responses are usually accompanied by ultrasound emission, suggesting that ultrasound emission may be considered as a motor pattern of the submission motivational mechanism.

The finding that ultrasound emission inhibits approach and attack confirms previous reports by SALES (1972), LUCIANO (1974), and LORE *et al.* (1976). The ultrasound is usually more effective than specific submissive or defensive postures in inhibiting attack, perhaps because it is emitted for relatively long periods of time, up to several minutes in duration. The evolution of ultrasound inhibition may be an example of the retention of infantile patterns among adults and their use as attack inhibitors, as has been noted previously in many vertebrates by many ethologists including LORENZ (1960). Young rat pups can inhibit the approach of adult rats by emission of ultrasound (NOIROT, 1973).

The statistical concurrence of groom-self-side by the home rat and ultrasound by the intruder may be due to ultrasound inhibition of attack. Both these behaviors would be expected to be high after an attack, the former because of flank gland secretion activated by way of offense ,the latter as part of submissive behavior activated by the pain of the attack. Furthermore, attack behaviors would be inhibited by the ultrasound, leaving little behavioral alternative to compete with the groom-self-side behavior. This might be cited as an example of "displacement."

Other Motivational Mechanisms and Behavioral Dyads.

Most of the acts and postures and most of the highly significant behavioral dyads obtained in the present study have been explained in terms of the five

motivational mechanisms discussed above. Some details have not yet been discussed, however.

The occurrence of mounting and attempted mounting behavior by the intruder suggest that there was some activation of sexual motivation in the intruder rats.

The strong, symmetrical dyad of home rat approach and intruder rat retreat has not been explained in terms of motivational mechanisms. It is possible that the sequence of home rat approach to intruder retreat might in some cases be a special case of defense behavior in which the retreat is the aborted initiation of flight behavior, but flight is precluded by the small size of the cage. The opposite sequence, that of intruder retreat to home rat approach might be a special case of offense behavior in which the approach is an aborted initiation of chasing behavior, but chasing is similarly precluded by the small size of the cage. Variations on these themes may be reflected in the number of highly significant dyads involving intruder exploration of cage and home rat exploration (*i.e.*, following) of the intruder.

The highly significant dyads of exploration and grooming within each rat have been explained in terms of motivational mechanisms, but the significant dyads of interaction between the rats requires further explanation. Exploration by each animal was most frequent at the beginning of the test, while grooming behaviors by each animal were most frequent towards the end of the test session. Since offense and defense or submission behaviors were seen in combination, it may be argued that exploratory and grooming behaviors must have occurred often at the same time in the two rats simply by a process of elimination; *i.e.*, there were no other competing behaviors at that time, while at other times there were competing behaviors for both animals at once.

GENERAL DISCUSSION

The motivating stimuli, motivational mechanisms, and motor patterning mechanisms of behavior discussed above have been summarized in Fig. 11. Releasing and directing stimuli are not shown. Below the motor patterning mechanism are listed all of the various acts and postures observed in the present study except for attempted mount which would have required the addition of a sixth motivational mechanism for sexual behavior. Acts and postures which are hybrid combinations of more than one motor pattern are listed under each appropriate motor patterning mechanism.

Certain paradoxical relationships may be seen clearly in this summary figure. Motor patterns may be activated by way of more than one motivational mechanism: rub is activated by way of both groom and offense; approach is activated by way of both offense and explore; high postures are activated by
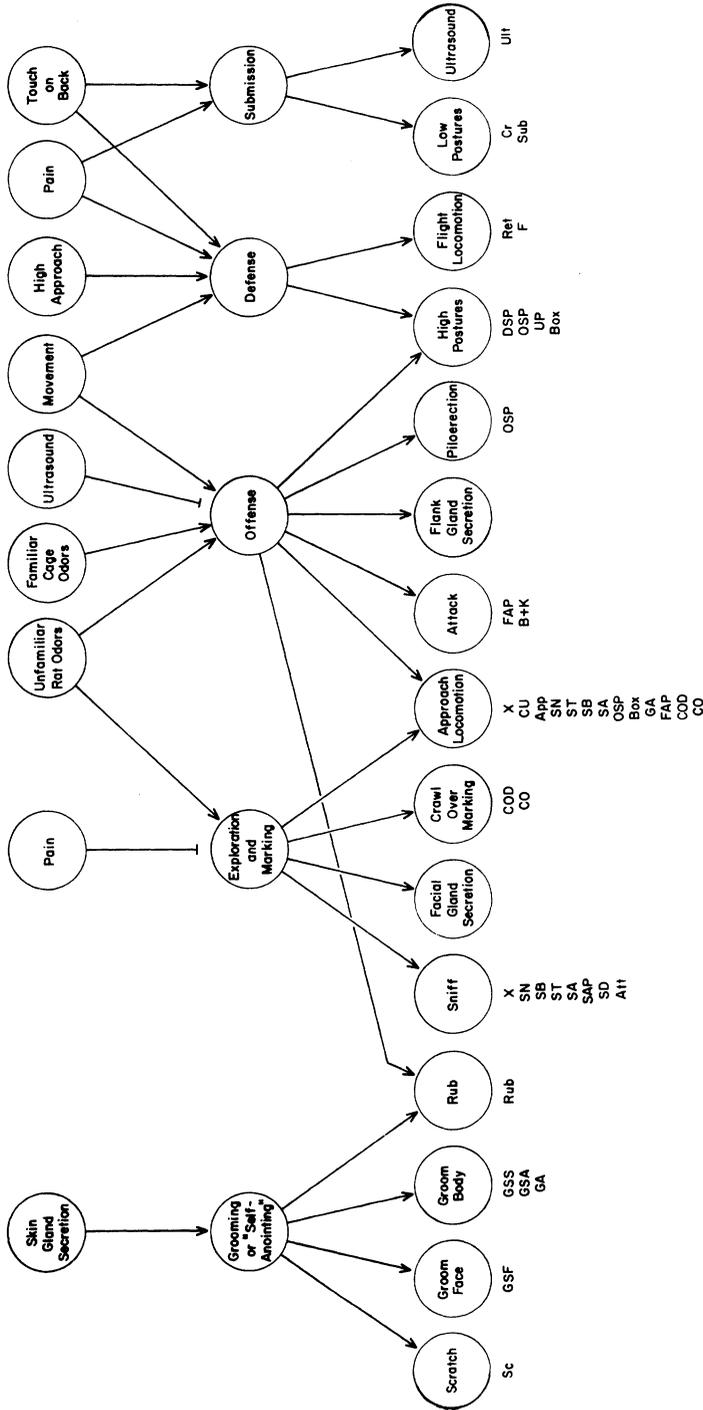
Fig. 11. Motivational mechanisms involved in isolation-induced fighting and defense. Top row of factors: motivational stimuli. Second row of factors: motivational mechanisms. Third row of factors: motor patterning mechanisms. Acts and postures are listed below the motor patterning mechanisms involved in each one. Note that some acts and postures involve more than one motor pattern. Directing and releasing stimuli are not shown; they are presumed to act upon the motor patterning mechanisms.

way of both offense and defense. Various stimuli may serve as motivating stimuli for more than one motivational mechanism: pain potentiates both submission and defense, while inhibiting exploration and marking; unfamiliar rat odors potentiate both offense and exploration and marking; and dorsal tactile stimulation activates both submission and defense.

Whereas motivational stimuli act upon motivational mechanisms in a general fashion, directing stimuli act upon specific motor patterns with information about spatial localization. For example, afferent stimuli from secreting scent glands function both as motivational stimuli for grooming (no spatial localization necessary) and also as directing and releasing stimuli for scratching or grooming of left or right flank, grooming of face, etc., depending upon the spatial localization of the directing stimuli. Similarly, approach and sniff motor patterns activated by way of exploration and marking are oriented by the localization of directing stimuli from the cage and the other animal. The orientation of attack and of high postures also depend upon specific directing stimuli, the nature of which has yet to be established.

Various motor patterns themselves produce stimuli which may feed back to the behaving organism or provide stimulus cues to the opponent. Thus, for example, the secretion by the flank glands which is postulated to result from offense activation may, in turn, activate grooming, which in turn, will combine with offense to activate rub behavior. Similarly, submissive posture provides dorsal tactile stimulation which may intensify the low posture defense activation in a positive feedback loop.

No doubt the rat has many other motivational mechanisms, motivating stimuli, and motor patterning mechanisms besides those discussed here, but with the exception of sexual motivation involved in attempted mounting by intruders, the other motivational mechanisms of the rat do not appear to be active during tests for isolation-induced fighting. Regarding motivating stimuli, it has been pointed out that the offense motivational mechanisms may be activated by other types of motivating stimuli in other types of test conditions such as those of competitive fighting and maternal nest defense. Regarding other motor patterns, it has been pointed out that flight, which is a motor pattern activated by way of defense, is not seen under the present test conditions because the cage is too small. Similarly, biting, which may often be seen in association with the boxing behavior elicited by shock-elicited fighting, isolation-induced fighting by wild rats, and attack by lactating females is not seen under the present circumstances except in the bite-and-kick attack .

It has proved possible to explain practically all of the 105 highly significant

behavioral transitions observed from two rats in the isolation-induced fighting situation by means of only five motivational mechanisms. One might argue that this is less impressive because of the confined space in which the tests were conducted, the use of laboratory rats, and the artificial nature of the confrontation. Yet, except for sexual and maternal behaviors, most of the social behaviors reported by CALHOUN (1962) in his extensive study of wild rats in a large outdoor pen over a three-year time period find their equivalents in the behaviors observed in the present study.

The precise and potentially quantifiable specification of motivational, releasing and directing stimuli and motor patterns of behavior should make it possible to analyze these behaviors at the level of single neuron recording in both sensory and motor outflow systems. Since the neural mechanisms of locomotion are increasingly well understood at the level of individual neuronal circuits (ADAMS, in preparation), and since many of the motor patterns in the present study may be seen as locomotor movements or variants, one may predict that it will become possible to analyze the brain mechanisms of social behavior at a new level of neuronal specificity. Similarly, one might hope for a new level of specificity in the analysis of the integrating mechanisms of behavior. It may be proposed that the motivational mechanisms postulated in Fig. 11 will correspond with identifiable populations of neurons in the brain such as those implicated by EDWARDS & ADAMS (1974) for defense motivation. One would also expect the various circles in Fig. 11 to correspond to unitary aspects of rat behavior which differ from one inbred strain to another and which would assort according to predictable genetic ratios. If so, then the present analysis will be more than a conceptual framework for some data; it will provide a rough picture of the behavioral mechanisms themselves. The critical tests must come from future research on the neurophysiology and behavior genetics of social behavior in the rat.

SUMMARY

The behavior sequences of male rats during tests for isolation-induced fighting were analyzed by computer. All transitional dyads which were highly significant (probability less than .001 by chance) were listed in tables and categorized. Most highly significant transition dyads fell into five categories: exploration and scent-marking; grooming; defense and submission; offense, and approach and retreat. All of these categories were obtained for sequences within the home rat, within the intruder rat, and between the two rats except for the following: offense sequences were seen only in the home rat; approach and retreat sequences were seen only in interactions; and interaction sequences usually involved combinations of offense with defense or submission rather than simple offense sequences or simple defense-submission sequences.

Further analysis of exploration and scent-marking dyads suggested that the various acts and postures all reflect a single underlying motivational mechanism which activates motor patterning mechanisms whose motor patterns are directed by continually changing

orientation towards different objects in the environment. The ratios of obtained to expected frequency of transition from one act or posture to another were usually symmetrical and most of the possible dyads were observed in frequencies greater than expected by chance.

Analysis of grooming dyads also suggested that these acts and postures reflect a single underlying motivational mechanism which activates motor patterning mechanisms through which directing stimuli orient grooming towards various parts of the animal's own body or the body of the opponent. Within self-grooming most of the possible dyads were observed at frequencies greater than expected by chance, and the transition ratios were symmetrical. It was suggested that these behaviors all facilitate the broadcast diffusion of odors from scent glands on the face, flank, and ano-genital region, that the motivational mechanism is activated by sensations arising from these glands which are differentially activated by way of other motivational mechanisms, and that self-grooming might also be characterized as "self-anointing".

Offense behaviors of the home rat tended to follow an asymmetrical sequence: from sniff-dish and crawl-over-dish to repeated offensive sideways posture to full aggressive posture to bite-and-kick attack, with the latter act followed by a refractory period. The frequent initiation of the sequence by sniff-dish behavior was taken as evidence that an offense motivational mechanism is activated by comparison of strange rat odors with familiar home cage odors. A number of acts and postures were considered to be ambivalent or hybrids of motor patterns produced by patterning mechanisms simultaneously activated by offense and other motivational mechanisms. These include aggressive groom and rub (grooming and offense), crawl-under (exploration and offense), and offensive sidoeways posture, upright posture and boxing (both offense and defense).

A detailed analysis of the many dyads from offense behavior to defense and submissive behaviors led to the following hypothesis. There are probably two different motivational mechanisms, defense and submission, which are activated by stimuli associated with attack by the opponent, dorsal tactile stimulation or an elevated approach. Both defense and submission are elicited by dorsal tactile stimulation and both are potentiated following subjection to attack. Defense, but not submission, may also be elicited by a high approach of the opponent. The motor patterns of defense are flight in a large enclosure, or high postures in a confined space. The high postures are usually of low intensity (sideways posture) if the motivating stimuli are of low intensity and if the motivational mechanism is not sensitized by previous attack. They are usually of high intensity (upright postures) if the motivating stimuli are of high intensity or if the motivational mechanisms has been sensitized by attack. The submissive postures may also be of low intensity (crouch) or high intensity (full submissive posture) depending upon intensity of motivating stimuli and sensitization by pain. Submission often includes the emission of a 25 kilo herz ultrasound cry which inhibits further attack by the opponent. An alternative hypothesis was considered: that submission and defense are sets of motor patterning mechanisms, each activated by a single motivation mechanism but differentiated by different releasing stimuli.

In addition to the primary significant transitional dyads mediated by five motivational mechanisms, there were also many secondary and tertiary transitional dyads obtained as a result of the temporal correspondence of two different acts or postures each elicited as primary effects from another behavioral act or posture which preceded both of them. These secondary and tertiary effects, less significant than the primary effects, could be demonstrated by triangulation in flowcharts of the behaviors.

Practically all of the 105 highly significant behavioral transition dyads in the tests could be explained as primary effects due to the action of only five basic motivational mechanisms and the secondary or tertiary effects based on these primary effects. The five motivational mechanisms were identified as: exploration and scent-marking; grooming, offense; defense; and submission. A model was presented which included

these five motivational mechanisms, their critical stimulus inputs (motivational stimuli), the motor patterning mechanisms which they activate and which receive separate input from releasing and directing stimuli. Specific acts and postures could be understood as simple or complex combinations of motor patterns which were produced by motor patterning mechanisms activated by single or multiple combinations of motivational mechanisms.

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RÉSUMÉ

Les séquences des comportments de Rats mâles au cours de tests de combat résultant d'isolements ont été analysées par ordinateur. Des tableaux par catégories de toutes les dyades de transition qui avaient une signification considérable ont été établis. Les dyades de transition les plus significatives entraient dans cinq catégories de comportement: exploration et marquage par l'urine; toilettage; défense et soumission, offense, approches et reculs.

Des analyses plus poussées des dyades d'exploration et de marquage ont révélé que les divers actes et postures reflètent tous un seul mécanisme de motivation à la base. Ce mécanisme active des schémas moteurs, différenciés par une orientation envers les différents objets du milieu, laquelle change continuellement. Les rapports entre la fréquence obtenue et la fréquence attendue de transition d'un acte ou d'une posture à un ou une autre ont été en général symmétriques, et la plupart des dyades possibles se sont manifestés plus fréquemment que l'on ne l'aurait prédit si l'on avait procédé par hasard.

Une analyse des dyades de toilettage a fourni des conclusions similaires à celles de l'exploration. Cela mène à formuler l'hypothèse que tous ces comportements facilitent la diffusion d'odeurs à partir des glandes odorantes de la tête, du flanc et des régions ano-génitales.

Les comportements offensifs du Rat „résident" tendaient à suivre une séquence asymmétrique, du reniflage du plat et du passage par-dessus le plat à la posture pleinement agressive, à l'attaque, à la morsure et au coup de patte. Le fait que le comportement nommé „reniflage du plat" commençait fréquemment la séquence offensive nous a mené à conclure qu'un mécanisme de motivation offensive est mis en action par la comparaison d'odeurs de rats étrangers avec les odeurs de la cage „résidentielle".

Une analyse détaillée des nombreuses dyades, celles du comportement offensif et des comportements défensifs et des comportements soumis, a amené les conclusions suivantes: il y deux mécanismes différents de défense et de soumission, activés tous deux par l'attaque et par une stimulation liée à l'attaque. Dans les cas du comportement défensif, la stimulation liée à l'attaque inclut la stimulation tactile du dos aussi bien que l'approche à partir d'une position plus élevée. Dans le cas d'un comportement soumis, le seul stimulus efficace est la stimulation tactile du dos. Les schémas moteurs de défense consistent en postures „accroupies" si les stimuli de motivation ne sont pas intensifs et si le mécanisme défensif n'est pas sensibilisé par l'attaque. Ils consistent en postures „dressées" si les stimuli de motivation sont intensifs ou si le mécanisme défensif est sensibilisé par l'attaque. Les schémas moteurs de soumission consistent de même en deux postures une posture „figée" (à basse intensité) et une posture pleinement soumisse (à haute intensité).

En plus de dyades primaires de transition qui reflètent les cinq mécanismes de motivation, il y a des dyades secondaires et tertiaires qui reflètent la correspondance temporelle entre deux actes ou postures différents, dont chacun est causé par un premier acte ou première posture qui les précède tous les deux. Il était possible d'établir ces dyades secondaires et tertiaires — toujours moins significatives que les dyades primaires — par un processus de triangulation, à partir d'un schéma de toutes les dyades primaires.

Un schéma des cinq mecanismes de motivation a été présenté : (1) exploration et marquage par l'urine; (2) toilettage; (3) offense; (4) défense; (5) soumission. Leurs divers stimuli motivationnels et leurs schémas moteurs ont été spécifiés précisément. Les actes et postures spécifiques de comportement social ont été expliqués comme des combinaisons simples ou complexes de schémas moteurs qui sont activés par des combinations simples ou complexes d'activation par les mécanismes de motivation.