ACTA NEUROBIOL. EXP. 1988, 48: 145 - 159

IMMOBILITY REFLEX EVOKED BY VERTICAL LIFTING OF THE RAT

Renard KORCZYŃSKI and Piotr KORDA

Department of Neurophysiology, Nencki Institute of Experimental Biology
Pasteura 3, 02-093 Warsaw, Poland

Key words: immobility reflex, rat

Abstract. It is assumed that the immobility reflex (IR) evoked in adult rats by sensory stimulation does not exceed a few seconds. However, we easily achieved a longer lasting (up to 3 min or longer) immobility state in most of the tested rats when they were grasped by hand and lifted to a specific upright position. Twenty male rats originating from two different albino populations could remain immobilized continuously in such a position for average durations of 138 and 48 s respectively, while in 20 hooded male rats and 20 albino female rats the mean immobility durations were 138 s and 36 s, respectively. It is suggested that IR evoked in rats is homologous with similar reflexes in other species, the assumption that the rat is not useful for IR studies deserts reconsideration.

INTRODUCTION

The state of peculiar akinesis in animals, evoked solely by manipulation of their bodies followed by placing them in a specific position, was first described as early as the 17th century by Kircher (see 4), who called it "experimentum mirabile". Interest continues in the physiological mechanisms engaged in releasing and maintaining this state, which in the last decade, has been variously known as the immobility reflex, tonic immobility response, contact defense immobility, or cataleptic or hypnotic state. Among many species investigated to elucidate the mechanisms underlying this state, one may find surprisingly only a few studies on rats (2), which are (apart from mice) very convenient and the most frequently utilized species in psychophysiological investigations. This may be presumably due to general observation that evoking the immobility reflex (IR) (5) in adult but not senile rats by means of manual manipulation solely, without any pharmacological or surgical intervention, is unsatisfactory (5, 11, 12, 17, 18). Since it has not been possible to obtain the IR lasting longer than a few seconds in adult rats, while in rat pups the condition could be produced only during the first 15 days of life, it has been concluded that the rat as a species is not appropriate for IR studies.

Our preliminary observations of rats have not been fully consistent with this assumption. We found that some rats aged 40 - 80 days during "handling" and other procedures (e.g., while performing small cuts of the ears for the individual marking) remained unexpectedly immobilized and hyporeactive for even a few minutes, similar, if not identical, to IR described in other species. Such a reaction was repetitive and could be obtained only during specific manipulation of the rat's body and in the proper position only. Preliminary results also showed that IR occurred commonly in rats originating form various populations.

The goal of the present study was to investigate the possibility of evoking IR in adult laboratory rats. We also wanted to determine the duration, frequency of appearance and most typical physiological symptoms accompanying IR.

EXPERIMENT I

In the preliminary studies (8) we found significant individual differences in both the duration of immobility and the level of hyporeactivity in rats. The purpose of Experiment I was to test if our method was really sufficient to evoke IR and, secondly, if some differences in IR duration depended on accidental, small variations in the way of holding the rat by the experimenter and, eventually, to find the optimum body area to hold the animal.

Material and methods. The experiment was carried out on 20 mature, male albino rats, originating from two different breeding populations. Group 1 consisted of 10 male subjects from a randomly reproduced population, and Group 2 consisted of 10 Wistar males. One month before the start of the experiment individual number markings were made by means of small cuts on the ears. Beginning one week before the experiment, subjects were kept on a 12/12 h light/dark cycle in standard plastic cages, five rats per cage. The room temperature was 21° ± 2°C. The rats received standard laboratory food (Murigran) and water ad lib. The animals were handled once a week when their cages were changed.

Immobility of the rats was obtained by taking hold of the symmetrical fold of the skin in the neck area (see Figs. 1 and 2) with two fingers and then, gently but with relatively speed, lifting of animal up to a vertical position (about 50 cm above the floor), with continued the hand-holding.

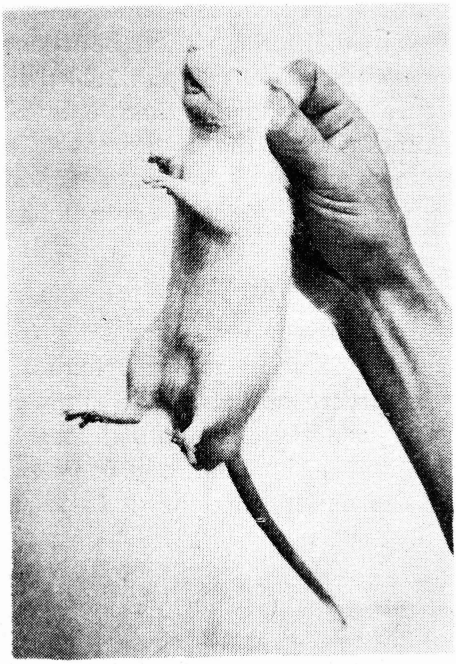

Fig. 1. A photograph of a hand-held rat immobilized by the method presented. Note linea alba on the ventral surface of the body, see text.

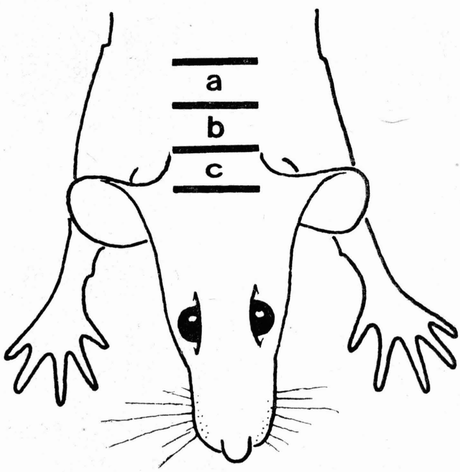

Fig. 2. Diagrammatic presentation of the three areas *a*, *b* and *c*, where the hand hold was applied.

Three partially overlapping areas of grip on the nucha (*a*, *b* and *c*) were tested (see Fig. 2). The *a* area was tested when the experimenter's fingers were situated on the third centimeter posterior to the line linking the posterior border of the ears, the *b* area was on the second centimeter, and the *c* area on the first centimeter. The effects of holding the animal in these three areas were tested 5 times, in random order, a total of 15 trials for each subject in the period between ages 3 - 9 months. The trials were performed between 1:00 and 3:00 p.m. Following a given trial, the next was repeated not earlier than 4 days later. Body weight was measured three times during the experiment. The IR duration was recorded from the moment the subject became immobile. The measurement was continued up to 180 s, which was the longest period arbitrarily selected by us, or it could be stopped earlier, the moment a strong defense reaction appeared.

Results. When the hand-held rat was immobile in a vertical position, various changes, such as defecation and/or urination, sometimes accompanying single body jerk were observed. We stopped the timing of immobility measurement, just when an animal manifested one of the struggle reactions: rotations around the long body axis, body ventroflexions and/or series of alternating flexions and extensions of the extre-

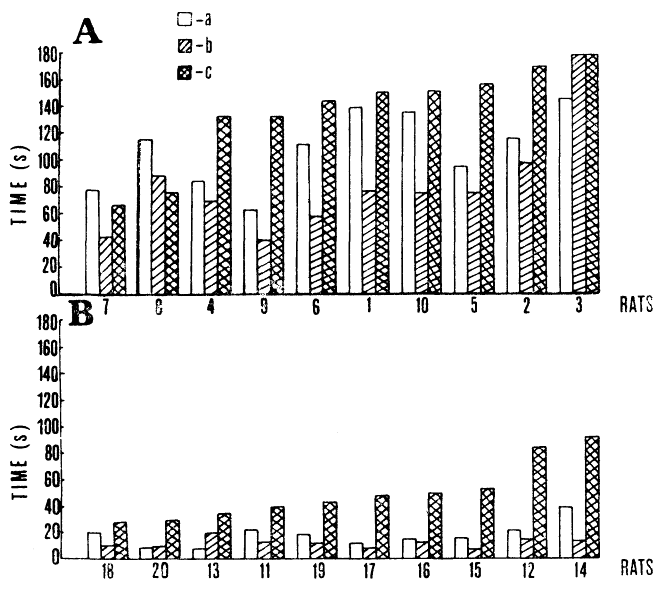

Fig. 3. Mean duration (from 5 trials) of IR for particular areas of hand-hold (*a*, *b*, *c*) in individual rats from Group 1 — *A* and Group 2 — *B*. The data ordered according to the increasing mean IR duration in the *c* area of hand-hold.

TABLE I

Mean durations (in s) of IR in rats from Group 1 ($n = 10$) and Group 2 ($n = 10$) under *a*, *b* and *c* areas of hand-hold in five consecutive trials. [a] trial when IR duration in *b* hand-hold was longer than in *c*; [b] trial when IR duration in *a* hold was longer than in *b*

Areas of hold	Group 1						Group 2					
	Trials					$\bar{x}$	Trials					$\bar{x}$
	1	2	3	4	5		1	2	3	4	5	
a	95.9	88.5	99.0	71.2	76.1	86.1	16.5[b]	12.4	7.7	12.5	10.5	11.9
b	121.1[a]	110.6	109.1	98.4	109.9	109.8	15.9	15.0	19.6	13.6	14.8	15.8
c	112.2	151.6	131.8	142.4	152.6	138.1	61.2	54.7	44.8	41.8	39.8	48.5

mities. These reactions were frequently accompanied by loud vocalization. IRs were obtained in all subjects from both groups on all 5 trials for each holding position for a total of 300 trials.

Area of hand-hold. Figure 3 and Table I present mean durations of IR for both groups obtained from the five trials for each of the hand-holding positions. The mean IR durations were longer in the hand-hold *c* than in the hand-hold *b* or *a* positions. Two-way analysis of variance (10) showed a holding effect ($F_{2;36} = 27.55$, $P < 0.001$). Duncan test confirmed that hand-hold *c* was significantly longest ($P < 0.001$)). In Group 1 this prevalence occurred in 4 trials and in Group 2 in 5 trials, i.e. in 9 out of 10 cases. Consequently, comparisons of the data obtained in holds *b* and *a* showed a longer mean IR duration in hold *b* than in *a*; in Group 1 in 5 cases and in Group 2 in 4 cases (9 out of 10 cases). The comparison of mean data from 5 trials for each of the three hand-holds applied also indicates that IR duration was longest in hold *c* for both groups (138 s and 48 s, respectively), shorter in *b* (110 s and 16 s) and shortest in *a* (86 s and 12 s).

Phenotypical differences. In both groups significant individual differences were observed (see Fig. 3 *A* and *B*). The mean individual time durations (from 5 trials) of IR in all hand-held positions were distributed in various divisions: in Group 1 — from 40 s to 180 s, and in Group 2 — from 8 s to 92 s. In position *c*, the data of the two extreme (minimum) individuals from Group 1 (No. 7 and No. 8) and the two extreme (maximum) data from the 2nd Group (No. 12 and No. 14) overlapped. Accordingly, the IR mean durations (see Table I) for particular rats (3 holding positions $\times$ 5 trials = 15), are, at least, twice as long in Group 1 as in Group 2. Predominantly, however the differences are manifold. Analysis of variance showed a group effect ($F_{1;18} = 65.77$, $P < 0.001$) and the interaction (hold $\times$ groups) was not significant. No disturbances in behavior and physical development of subjects were found during the entire experiment; normal increases of body weight were observed.

Discussion. The results indicated widespread appearance of IR in the rat produced by our method, and the holding position *c* allowed the longest IR duration. Accordingly, the area of holding and/or the head position in relation to the long body axis may be of essential importance for the IR duration. On the other hand, apart from great differences in the IR duration obtained in particular areas of holding and individual differences, significant differences were also observed between particular groups. They may indicate the importance of phenotypical differences in the IR duration.

EXPERIMENT II

The purpose of the Experiment II was to study the possibility of obtaining IR in male rats genetically different from those used in Experiment I and in female rats, as well as to perform a more detailed analysis of the features accompanying IR. It was also interesting to know the most frequently occurring external symptoms of IR.

Material and Methods. The experiment was carried out on two groups, each consisting of 20 rats: outbred hooded male rats (Group 3) and randomly reproduced albino female rats (Group 4). Starting one week before the experiment subjects were kept in the housing and feeding conditions described for Experiment I. IR was evoked by the method described in the previous experiment, only using exclusively the holding area *c*. The tests were performed three times at intervals of 14 and 7 days. The IR duration was measured up to the arbitrarily limited time of 180 s.

During the immobility state the following symptoms were recorded: tail erection, hissing expiration, rhythmical vocalization, hindlegs abduction, defecation and urination. Additionally in Group 3 vibrissae piloerection and piloerection along the white line (along the midline on the ventral surface of the body) were recorded (see Fig. 1). In both groups, defensive reactions in response to holding were noted. They consisted in attempts to escape, with or without vocalization.

Results. IR was obtained in all rats from both groups. Figure 4 shows that the IR duration was significantly longer in male hooded rats (Group 3) than in albino female rats (Group 4) two-way analysis of variance, $F_{1;38} = 225.76$, $P < 0.001$). The individual IR duration (the mean value from 3 trials) ranged from 99 s to 180 s in Group 3 and from 18 s to 68 s in Group 4. Accordingly, the lowest individual data for Group 3 were significantly higher than any data for Group 4. Moreover, the maximum duration (180 s) in 60 trials occurred in 35 cases in Group 3 (at least once in every subject) but in no rat from Group 4.

A statistically significant increase of mean IR duration on consecutive trials emerged (two-way analysis of variance, $F_{2;76} = 21.46$, $P < 0.001$) Duncan test confirmed differences between the first and other two trials ($P < 0.001$) and showed no systematic differences between the second and thrid trial in the rats from Group 3.

In both groups the most frequently occurring symptoms during IR (see Table II) were erection and rigidity of the tail, which was elevated $30° - 90°$ in relation to the long body axis, during the first stage of the trial. This symptom was observed in 92% in Group 3 and in

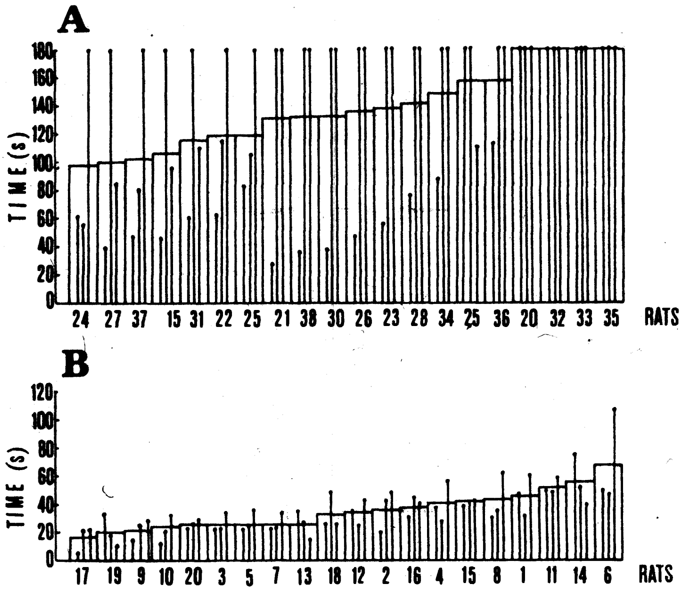

Fig. 4. Individual IR duration of the area of *c* hand-hold in rats from Group 3 — *A*, and Group 4 — *B*: mean time from three trials (open bars) and the time of particular trials (vertical lines). The data ordered as in Fig. 3.

85% in Group 4. Defecation, being found in 87% and 65% of trials, respectively was second in the order of frequency of occurrence. The "hissing" sound was in the 3rd position (68%) in Group 3 and on the 6th position (13%) in Group 4. The remaining three symptoms (vocalization, hindlegs abduction and urination) occurred in the same order of frequency in both groups: on the 4th, 5th and 6th position, and on the 3rd, 4th and 5th position in Groups 3 and 4 respectively. The respective percentages were as follows: 62, 30 and 25 for Group 3, and 63, 53 and 43 for Group 4.

The other symptoms, not mentioned in Table II, included piloerection along the white line and vibrissae piloerection, which were both recorded only in Group 3. The former piloerection seen along the long body axis on the ventral surface, occurred in 82% of trials while the later, when the vibrissae were at the angle of 90° to the long body axis (or more rostrally), was observed in 50%. Defensive reactions were observed in both groups before evoking IR as a result of holding the rat's neck and occurred in Group 3 — 25 times (42%) and in Group 4 — 9 times (15%).

The data in Table II, ordered as in Fig. 4 in relation to the increasing mean IR duration, showed no correlation between IR duration and the frequency of occurrence of any symptoms recorded. It was also the case

Table II

The appearance of some typical symptoms in 3 trials of IR in particular rats from 2 groups. The individual data (each from 3 trials) ordered as in Fig. 3. [a] short-lasting series of high pitched sounds emitted synchronically with expiration; [b] short-lasting series of sibilant sounds emitted synchnronically with expiration

Group 3

Symptoms \ Rats	24	27	37	19	31	22	25	21	38	30	26	23	28	34	29	36	20	32	33	35	Σ	%
Tail erection	3	3	1	3	3	3	3	3	3	1	3	3	3	3	3	2	3	3	3	3	55	91.7
Defecation	3	3	2	2	3	3	3	2	1	3	3	3	3	3	2	3	2	3	2	3	52	86.7
Hissing[b]	1	2	2	2	3	1	2	2	1	1	2	2	3	2	3	3	3	3	2	3	41	68.3
Vocalization[a]	2	1	1	1	2	2	3	2	0	1	2	2	1	3	2	2	3	2	1	2	37	61.7
Hindlegs abduction	1	1	0	2	0	1	1	1	2	1	0	0	0	0	1	0	2	2	2	1	18	30.0
Urination	1	1	1	1	0	1	0	0	2	2	0	0	0	1	1	0	0	1	2	1	15	25.0

Group 4

Symptoms \ Rats	17	19	9	10	20	3	5	7	13	18	12	2	16	4	15	8	1	11	14	6	Σ	%
Tail erection	3	3	3	2	3	2	2	3	3	3	3	2	3	1	3	2	3	2	2	3	51	85.0
Defecation	2	3	2	1	1	2	0	3	3	3	1	2	2	0	2	3	2	3	2	1	39	65.0
Vocalization[a]	2	3	2	3	3	0	0	0	3	1	2	3	2	0	2	3	1	3	3	2	38	63.3
Hindlegs abduction	1	0	2	1	0	1	2	3	1	1	2	1	2	2	2	3	2	3	1	2	32	53.3
Urination	2	1	1	2	2	0	1	3	2	3	1	3	2	0	1	2	0	0	0	0	26	43.3
Hissing[b]	0	0	0	1	0	0	0	1	0	0	0	0	0	1	1	2	0	0	0	2	8	13.3

with respect to the other symptoms described above but not included in Table II.

The dynamics of the occurrence of symptoms accompanying IR allows us to distinguish three, partially overlapping, stages. During the first stage, lasting 30 - 45 s, a state of increased tonus of skeletal muscles was observed, accompanied by the tail rigidity and erection, and a tendency to abduct the extremities (especially hindlegs) with frequent concomitant defecation. In the second stage, a progressing hypotony of skeletal muscles and temporary sibilant expiration were observed. The second stage evolved into the third stage, characterized by a repetitive increase in the skeletal muscle tonus, although not always equal to the initial level. However in some rats of Group 3, after 100 - 120 s the third stage was found to run a different course. That is, instead of an increase in the muscle tonus, a decrease in the tonus and an increase in hyporeactivity were observed. The progress of such a reaction resulted in "hypotonic" immobility, which was characterized by adduction of all extremities with flexion in both proximal and distant joints and tail atony.

Discussion. IR obtained in all rats from both groups and on all 120 trials supports the assumption about the universality of the occurrence of this response to the method applied presently and it was also obtained reliably in females. The great differences in the IR duration between sexes, were not, however, sufficient to reach any conclusions concerning sex effect on IR duration. Groups 3 and 4 differed not only with respect to sex, but to phenotype as well. The great phenotypical differences which were found in different populations of albino rats, (Experiment I) could be expressed more between genetically different color types of rats. Therefore, the effects of differences due to both sex and phenotype could accumulate.

It is convenient to analyze the origins of these differences when one compares the results of Groups 3 and 4 with the appropriate data of Experiment I, Groups 1 and 2 of the holding position *c*. Such a comparison demonstrates that the mean duration of IR in hooded rats (Group 3) is not shorter than the respective IR duration in randomly bred albino males of Group 1, but it is more than twice as long as inbred albino males of Group 2. Moreover, the "maximum" IR duration (180 s) in rats from Group 3 was obtained in 37 cases in 60 trials, but in Group 1 only 25 times and in Group 2 once in 50 trials. The respective IR durations in albino females (Group 4) were significantly shorter than in albino males from Group 1. They were, however, similar to those in males of Group 2; the "maximum" IR duration was never observed in subjects from Group 4. So, taking into account that a long duration of IR makes the strain more suitable for studies of this problem, it may be concluded that male hooded rats and outbred albino rats are more useful than both males and females originating from the Wistar strain. However, the results of this comparative analysis should be taken with caution, because the experimental conditions of Experiment I (15 trials) and Experiment II (3 trials) were different. On the other hand, the population differences in susceptibility to IR in different animal species were found also in other studies (see 2).

The analysis of IR accompanying symptoms indicate dynamic changes in tonus of both striped and smooth muscles. The erection of the tail, occurring nearly in all cases (106 in 120 trials in both groups), indicate an increased tonus of the long axis muscles. It was especially strong in the first stage of IR when hindleg abduction was seen (the last resulting from the increased tonus of the muscles abducting the thighs). However defecations, observed predominantly in the first stage but occasionally in the second one too, may reflect atony of the anus constrictor muscles and/or increased peristalsis of the large intestine, although the consistency of faeces was nearly unchanged. Similarly the occurrence of urination indicates changes of tonus in the muscles of the bladder. It seems that long lasting series of sibilant, high pitched sounds synchronized with expirations, occurred in the first stage, reflected transitory changes either in tonus of the pallatum molle or epiglottic muscles. The long-lasting piloerection along the linea alba and vibrissae piloerection indicate the changes of the tonus of the autonomic system.

In turn, any of these vegetative changes (e.g. piloerection, defecation, urination) as well as various forms of motor inactivity, are frequently observed during emotional excitation in spontaneously behaving mammals. It is possible that in the model presented these symptoms were the aftereffects of a fear reaction, evoked by the experimenter in the "introductory" stage, but this possibility needs further investigation.

GENERAL DISCUSSION

The data presented have shown that there does exist a method of manipulation of the adult rat's body allowing the evoking of a peculiar immobile state with a relative lack of responsiveness. We were able to evoke such a state in all rats tested from various populations.

With the method of evoking IR employed it was not possible to separate precisely the time necessary to induce immobility from the duration of the immobility "proper". Similar difficulties were described by other researchers (2, 5). In our experiments, the rats were held continuously while immobile by the proper grip. However in some cases, the motor defensive reactions of rats, being probably an expression of the "freedom reflex" (15), when they did occur in the elevated rat subsequently disappeared within 2 - 3 s typically and exceptionally 20 s. So, the IR duration recorded in these rare cases, included also a few seconds of restraint which occurred before the "proper" immobility state. On the other hand, IR lasting 180 s was observed in a great number of trials, which were terminated, although, the IR could have been continued. In sum, we suppose that an estimation of the IR duration was sufficiently precise.

It is known from other studies (5, 11, 12) that IR, as a result of restraint, can be induced in rat pups until 10 day of age, but not in adult rats. So one may doubt if IR, evoked by us in adult rats, is really analogous or homologous with the reaction described in the literature in other species, such as the tonic immobility reaction, animal catalepsy and so on.

Studies of numerous investigators have shown that in evoking IR in different species of vertebrates an important role is played by stimuli which excite both labyrinth and kinestetic systems, and also tactile stimuli on the skin in the neck and/or spine area (1, 2, 5, 7, 9, 12, 17, 18). These data are in agreement with the commonly employed methods of evoking IR in which both restraint and body inversions are used as a rule.

So, coming back to the question of to what degree our method is similar to those described above, the following points should be taken into account. The differences between sensory inputs during the "introductory" stage and the "proper" immobility are more spectacular in conventional models than in our model. In the former the experimenter's participation in manual restraint of animal movements takes place during the introductory stage only. Thereafter an active experimenter's participation is replaced by putting an animal in an other, unsual, special position or even putting in a special apparatus, convenient for supporting such position. It is of importance that such a position is an origin of specific, sensory input, necessary to support immobility state. In the model presented now, the experimenter took part, by hand manipulation, in both stages i.e., in the introductory and proper. Therefore, the sensory inputs are apparently similar in both stages. In fact, however, sensory inputs differed significantly during respective stages. In the introductory stage, the animal was pressed to the baseground, caught by the neck skin and lifted up. Such polysensory stimulation was not present in the "proper" immobility stage, when the animal has been only held by the neck skin in a vertical, stable position. So, in the second stage the experimenter's participation was restricted mainly to a mechanical role, i.e., supporting the vertical position of the animal between the fingers.

It is also possible to evoke the IR reflex by using special forceps but the effect is weaker. The reason for such a difference is not known up to now. It is possible that the pincer localization by forceps is not sufficiently precise or the pincer itself is more traumatic. The other possibility is that when the animal is hand-held invisible, involuntary tremors of the experimenter's hand and fingers serve as an origin of additional stimulation. So, taking into account all these features of the compared experimental procedures, we do not have a sufficient basis for full estimation of the differences between conventional methods and the one presented now.

It ought to be added that Ratner (13), characterizing such a peculiar reaction, listed the following circumstances as the criteria permitting differentiation of it from other physiological states of immobility: (i) the immobility of the animal occurs as a result of taking it into hands or other form of animal restraint (accompanied or not by the application of rhythmical sensory stimulation); (ii) the immobility lasts longer than a moment and it is accompanied by a specific body position; (iii) during immobility, time reactivity of the animal onto exteroceptive stimuli is decreased in comparison to the normal state.

Recently, a large body of evidence has been accumulated in support of the predatory theory (3, 13, 14), whereby the influence of the predator or predator-like stimuli (including the experimenter) plays the key role. Apart from the suggested phylogenetic origins of this reaction, such as passive defense of the prey (3), it is possible, especially in mammals, to take into account also the ontogenetic origins. It is of interest that immobility occurs naturally in juvenile subjects of various species of mammals when they are carried across or retrieved by mothers.

The description of our method shows that polymodal sensory stimulation of the animal is the inherent feature, namely: (i) tactile stimuli, the hand-hold of the animal by the skin fold on the neck area and subsequent lifting of the animal result in both pressure on the skin and its distention; (ii) labyrinth stimuli, lifting the animal vertically against the force of gravity in the upright position; (iii) kinestetic stimuli, changed proprioceptive stimulation from the skeletal muscles resulting from lifting the animal above the floor and position change from the horizontal to the vertical; (iv) predator-like stimuli, which in our method of holding of the neck and consecutive lifting up of the subject against the force of gravity relatively well imitate the predatory attack.

The results obtained have shown significant similarities of psycho-neurological mechanisms underlying IR described by other authors in various species of homoiothermic animals. It is suggested that this method of evoking IR in adult rats will be useful in studies on this phenomenon. It also seems that a commonly accepted assumption about the rat as a species not suitable for the studies on IR ought to be modified.

The authors wish to express their thanks to Mrs. Krystyna Koperska for her skillful technical assistance. This investigation was supported by Project CPBP 04.01.606 and 609 of the Polish Academy of Sciences.

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Accepted 8 February 1988