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BEHAVIOURAL STRATEGIES OF AGGRESSIVE AND NON-AGGRESSIVE MALE MICE IN RESPONSE TO INESCAPABLE SHOCK

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ABSTRACT

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The effect of exposure to inescapable long-duration shocks of moderate intensity on intershock activity and on subsequent escape or avoidance performance was studied in aggressive and non-aggressive male mice. The activity of the non-aggressive mice was severely suppressed during the inescapable shock session, while that of the aggressive males was hardly influenced. The decremental effect of prior shock exposure on subsequent response latency and activity in an active two-way escape or avoidance task was greater in the non-aggressive than in the aggressive mice. There was no evidence that learned inactivity or learned helplessness (an associative deficit) could explain the results. Instead, individual differences in behavioural strategy in response to threatening situations appeared to account for the effects of inescapable shock. Aggressive male mice predominantly adopted an active behavioural strategy in challenging situations, which resulted in persistent attempts to exercise control over the external situation and hence in a sustained tendency to initiate responses. Non-aggressive mice primarily assumed a passive strategy; their tendency to exercise control was low, which readily resulted in a reduced tendency to initiate responses.

key words: individual differences aggression response to inescapable shock behavioural strategies wild house mice

INTRODUCTION

Aggressive and non-aggressive male mice adopt active and passive behavioural strategies respectively in response to a social challenge (e.g. an intruder in their territory or attack by a conspecific male; Benus, 1988). The hypothesis that this differentiation extends to non-social situations has been tested by investigating the active shock avoidance performance of the socially active, aggressive and the socially passive, non-aggressive males (Benus et al., 1989). In accordance with our hypothesis, part of the non-aggressive males assumed a passive strategy and all aggressive mice adopted an active one. However, contrary to expectation some non-aggressive mice managed to control the demands of the shuttle task, implying that these individuals had adopted an active strategy. Nevertheless, it has been suggested that non-aggressive mice predominantly do adopt a passive behavioural strategy, unless effective control of the situation is easily perceived (control is defined here as a mastering of the external situation). Although it is not known why some non-aggressive mice should perceive the shuttle task as more easily controllable than others, this suggestion would implicate that in an uncontrollable situation all non-aggressive mice will assume a passive behavioural strategy, whereas the aggressive males will maintain their active behavioural strategy. By exposing the animals to inescapable shocks such an uncontrollable situation has been created.

The response of individuals to an inescapable shock session can be studied in two ways: 1) by analysis of the behaviour during the inescapable shock session and 2) by analysis of the behaviour following the inescapable shock session, e.g. in an escape/avoidance task. During an inescapable shock session both <u>intra</u>- and <u>inter</u>shock activity generally declines (Anisman et al., 1978; Anisman and Waller, 1972; Glazer and Weiss, 1976a). The consequence of exposure to inescapable shocks upon subsequent behaviour, for instance the acquisition of a conditioned escape and/or avoidance response, is a, well-documented, severe interference effect (for review see Maier and Seligman, 1976; Seligman and Weiss, 1980). Many differences in the magnitude of the deficit have been reported (Bracewell and Black, 1974; Feldt and McCann, 1977; Glazer and Weiss, 1976a; 1976b; Jackson et al., 1978; Kelsey, 1977; Maier and Testa, 1975; McCarty and Kopin, 1978; Overmier and Seligman, 1967), although little attention has been paid to individual differences in performance deficits following exposure to inescapable shocks. One such study revealed that the <u>inter</u>shock activity of an individual is a reliable predictor of subsequent avoidance performance (Anisman and Waller, 1972).

Our expectation was that during an inescapable shock session aggressive mice would have a higher intershock activity (active strategy) than non-aggressive mice (passive strategy). This difference in intershock activity may have its impact on subsequent escape and/or avoidance performance. If so, the deficit will be greater in the non-aggressive than in the aggressive male mice, since intershock activity positively correlates with subsequent performance in a controllable task (Anisman and Waller, 1972). Differences in intrashock activity were not predicted, since footshock induces a forced activity that does not reflect the behavioural strategy adopted (Benus et al., 1989).

METHODS

Subjects

Subjects were male wild house mice (Mus musculus domesticus) of selection lines for short attack latency (SAL line) and for long attack latency (LAL line). The SAL males came from the 31st, the LAL males from the 9th generation of selection. The mice were housed in plexiglas cages (17 x 11 x 13 cm) in a room with a 12:12 h LD cycle (dark from 12.30 h). Food and water were available ad libitum. The litters were weaned at 3-4 weeks. At the age of sexual maturity (6-8 weeks) the animals were paired male-female. At the age of 14 weeks the males were tested for their attack latency score (ALS; see van Oortmerssen and Bakker, 1981). Males of the SAL line with an ALS < 50 seconds and males of the LAL line with an ALS = 600 seconds (the maximum score) were used in the experiments. At the time of these experiments the subjects were 15-17 weeks of age. Only during the test period were the males separated from their females.

Apparatus

Inescapable shock session. The experimental chamber was one compartment of a shuttlebox. The compartment, measuring 23 x 20.5 x 20 cm, was equipped with a grid floor with an interbar distance of 0.9 cm. Scrambled shocks were delivered through the grid floor.

Escape or avoidance session. The experimental chamber was a shuttlebox, measuring 46 x 20.5 x 20 cm, with a grid floor (interbar distance of 0.9 cm). The box was divided in two compartments by an elastic barrier. This was done because a pilot experiment revealed that most subjects climbed any other barrier and stayed there. Punishment of this behaviour was considered as undesired, since it could interfere with the escape or avoidance task. In the avoidance task the conditioned stimulus (CS) was a light stimulus from a 15-W bulb, located on the ceiling of the apparatus. Scrambled shock (US) of 80 μA was delivered through the grid floor. The shock scrambler continuously produced background noise.

Procedure

Inescapable shock session. All testing was done between 13.00 and 16.00 h. Each individual (10 SAL and 10 LAL males) received 60 inescapable shocks of 6 s duration and an intensity of 80 μA (inescapably shocked groups). The intershock interval was 60 seconds. During every other shock the behavioural response was recorded - at 1, 3 and 5 s after shock onset - according to the definitions as described below:

no response	- no visible or audible response
flinch	- a sudden startling movement in which the animal's feet remain in contact with the grid
jerk	- a violent and sudden movement of the body and feet without a displacement of more than its own body length
run	- any movement of the animal forward or backward clearly more than its own body length
jump	- a response in which all 4 feet of the animal have left the grid floor

During the intershock intervals behavioural activity was recorded at 10, 20, 30, 40 and 50 s after shock onset according to the following definitions and numerical values (after Anisman and Waller, 1972) that were assigned to the behavioural categories:

0	- immobility
1	- sitting or crouching with head or whisker movements
2(a)	- grooming
2(b)	- upright; sniff (exploration)
3(a)	- walking or running (locomotion)
3(b)	- jumping

In this way qualitative behavioural observations resulted in a value of which the total sum per animal could be used for statistical analysis. To preserve the qualitative character of the observations distinctions were made between grooming and exploration and between locomotion and jumping. Twenty other individuals (10 SAL and 10 LAL males) were given the same procedure without administering shock (non-shocked groups).

Escape or avoidance task. Five males of both the shocked and the non-shocked group were tested in a two-way active shock escape task 24 h later. The other five males of both groups were tested in a two-way active shock avoidance task 24 h later. In these tasks an individual received 30 trials of escape or avoidance conditioning. Shocks of 80 μA were delivered. In the escape task the animal could terminate shock by shuttling to the adjacent compartment, thus ending the trial. In the avoidance task a 3-s CS preceded 20 s of paired CS and US presentation, unless the the animal terminated the CS (=avoidance) or CS/US (=escape) by shuttling to the adjacent compartment, thus ending the trial. In both tasks a 30-s intertrial interval preceded the next stimulus onset. Activity was recorded during the intertrial interval at 5, 15 and 25 seconds.

Statistics

Data are expressed as mean ± standard error (sem). When the frequencies of the discrete categories of shock-elicited behaviours were different between SAL and LAL mice, they were tested by the Chi-Square test (X^2; Siegel, 1956). Pair-wise comparisons of unrelated samples were done using the Mann-Whitney U test (MWU; Siegel, 1956). When the samples were related the Wilcoxon's Matched-Pairs test (WMP; Siegel, 1956) was used. The course of behaviour within a session was analyzed by analysis of variance for repeated measures (rANOVA; Kim and Kohout, 1975) with blocks of trials as the repeated factor. The effect of exposure to inescapable shocks on the behaviour during intershock intervals was analyzed by analysis of variance (ANOVA; Kim and Kohout, 1975). The p-values are two-tailed, unless otherwise stated.

RESULTS

Intrashock behaviour

During the inescapable shock session (60 shocks) the intrashock behaviour of SAL males was significantly different from that of LAL mice (X^2=127.7, p<0.001). The number of no response, jerk and run responses differed significantly between the two groups (Table 1). Comparing the response rated at the first second of the shock (of 6 s duration) with that rated at the fifth second revealed an increase in number of no responses and number of jump responses in both lines (WMP; no response, SAL: T=10.5, ns, LAL: T=5.5, $p<0.05$; jump response, SAL: T=3, p=0.01, LAL: T=0, $p<0.001$). The number of flinches declined, but this was only significant in SAL mice (WMP, T=1.5, $p<0.01$). There were no differences in the number of jerk responses and only in LAL a significant decrease in number of run responses was found (WMP, T=6, p=0.025). The responses exhibited during the first 20 shocks of a session hardly differed from those during the last 20 shocks. The number of flinch responses increased in both lines (WMP; SAL: T=4, $p<0.02$, LAL: T=4, $p<0.02$) and, furthermore, the number of run responses decreased significantly in the SAL line (WMP, T=0, $p<0.001$).

	no resp	flinch	jerk	run	jump
SAL	6.7±1.4	30.8±5.9	13.6±2.5	28.7±2.2	10.2±2.8
LAL	3.3±0.8	25.3±4.6	2.9±0.6	40.7±4.2	17.8±4.9
p	0.05 U=25.0	ns	<0.01 U=4.5	<0.05 U=22.0	ns

Table 1. Responses during footshock in SAL and LAL male mice; per category of shock- elicited behaviour the mean number of responses (±sem) is given for the overall session. The p-values are obtained using the MWU test.

Intershock activity

Analysis of intershock activity (in blocks of 10 intervals) revealed a significant line (SAL, LAL; rANOVA, $F(1,36)=60.85$, $p<0.001$), treatment (inescapable shock, no shock; $F(1,36)=66.87$, $p<0.001$) and line x treatment effect ($F(1,36)=19.03$, $p<0.001$). As there was no significant change over time, in Fig. 1 the mean total activity during the entire session is shown.

More detailed analysis of the separate behavioural categories disclosed that exposure to inescapable shock affected all behavioural categories (ANOVA, $p<0.001$ for all cases), except jumping. There existed significant line x treatment interactions for immobility ($F(1,36)=21.50$, $p<0.001$), grooming ($F(1,36)=6.98$,

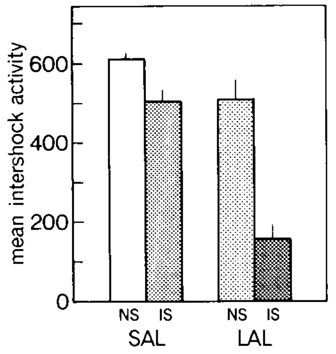

Fig. 1. Mean total intershock activity (±sem) in SAL and LAL mice during an inescapable shock session (IS) and mean total activity (±sem) in SAL and LAL mice in the shockbox without administering shock (NS).

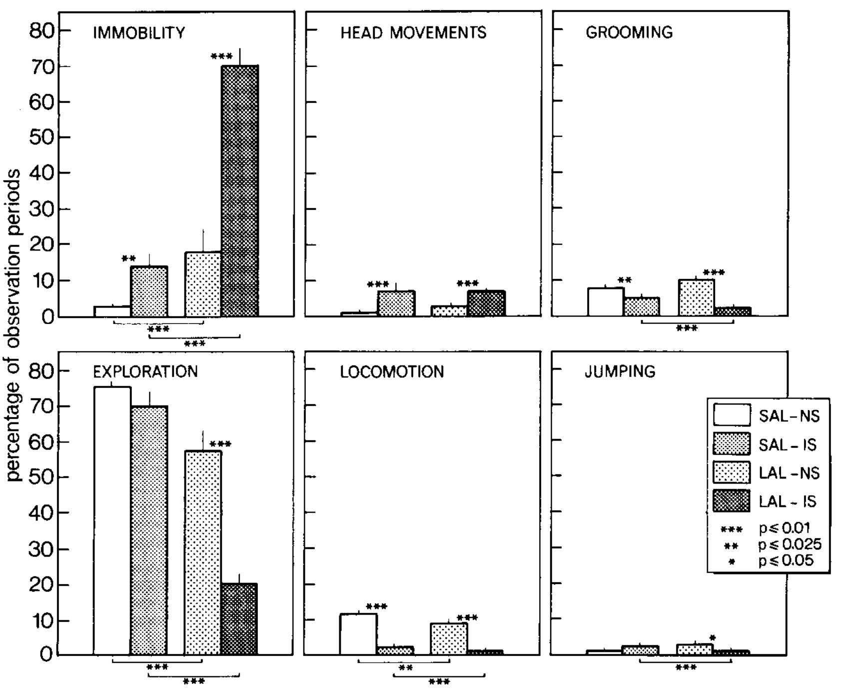

Fig. 2. Mean percentage (±sem) of periods that immobility, head movements, grooming, exploration, locomotion and jumping were observed in SAL and LAL mice, both during an inescapable shock session (IS) and during a non-shock session (NS). The p-values were obtained using the MWU-test.

p=0.01) and exploration (F(1,36)=19.43, p<0.001), indicating that the effect of exposure to inescapable shock was larger in the LAL than in the SAL line. Pair-wise comparisons of the data are shown in Fig. 2. The most obvious result was the enormous difference in immobility and exploration between the LAL and SAL mice during the inescapable shock session.

Effect on escape/avoidance performance

Analysis of the effect of prior shock exposure (PSE) on subsequent escape performance revealed a significant line (rANOVA, F(1,15)=5.78, p=0.03) and treatment effect (F(1,15)=3.65, p<0.04, one-tailed; Fig. 3a). Further analysis showed that only within the LAL line PSE significantly lengthened escape latencies (MWU, U=3, p=0.056).

Analysis of the effect of PSE on subsequent avoidance performance (response latencies) revealed no significant line or treatment effect, although there was a trend for PSE to lengthen response latencies in the LAL, but not in the SAL line (Fig. 3b).

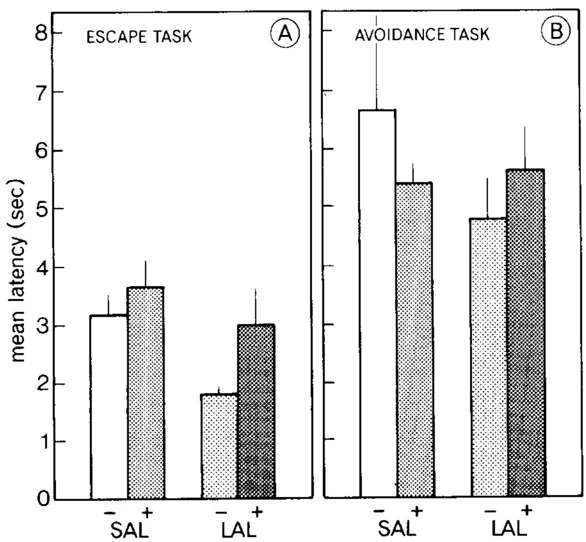

Fig. 3. (a) Mean escape latencies per block of 6 trials in an escape task and (b) mean response latencies per block of 6 trials in an avoidance task in SAL and LAL mice following exposure to inescapable shocks (+PSE) and without prior shock exposure (-PSE).

However, the effect of PSE on the number of avoidance responses was highly significant (rANOVA, $F(1,16)=9.71$, $p<0.01$), an effect that differed markedly between the two lines as there existed a significant line x treatment interaction ($F(1,16)=9.71$, $p<0.01$, Fig. 4). Since there was no significant change over time the total number of avoidances per
individual was calculated. Following PSE the SAL males showed significantly more avoidances per 30 trials than the LAL mice (5.5±0.1 and 1.1±0.5 respectively; MWU, U=2.0, p=0.03). Without PSE the avoidance levels were similar for both lines (SAL: 1.5±0.5, LAL: 1.2±0.4 avoidances/30 trials). So PSE had a remarkable incremental effect on the number of avoidances in the SAL line (MWU, U=0, p=0.01). This effect was especially clear-cut in the first block of 6 trials (Fig. 4).

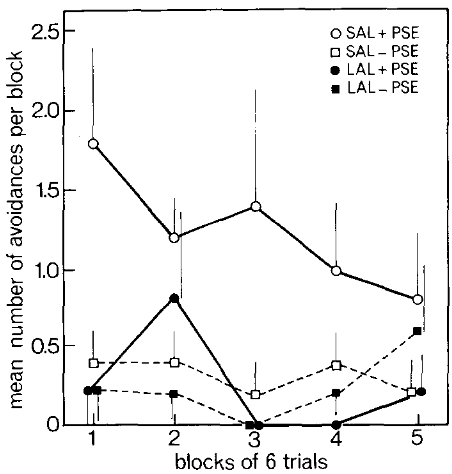

Fig. 4. Mean number of avoidances per block of 6 trials in SAL and LAL mice following exposure to inescapable shocks (+PSE) and without prior shock exposure (-PSE).

Effect on intertrial activity

In the escape task PSE had no significant effect on intertrial activity. However, there was an overall difference in intertrial activity between the two lines (rANOVA, $F(1,15)=4.73$, $p=0.04$), which appeared to be more salient after PSE than without

PSE (Fig. 5a). Analysis indicates that intertrial activity significantly decreased over blocks of intervals ($F(4,60)=3.26$, $p=0.02$).

In the avoidance task PSE differently affected intertrial activity in the SAL and LAL line (rANOVA, $F(1,16)=9.12$, $p<0.01$), an effect which also differed over the course of time ($F(4,64)=3.24$, $p<0.02$; Fig. 5b). Subsequent analysis disclosed no differences between SAL and LAL mice without PSE, but following PSE the intertrial activity differed markedly between the SAL and LAL males ($F(1,8)=65.49$, $p<0.001$), which held for the last four trial blocks (MWU, $U=2$, $p=0.03$; $U=0$, $p<0.01$; $U=0$, $p<0.01$; $U=0$, $p<0.01$). Only within the LAL line PSE significantly affected intertrial activity ($F(1,8)=7.42$, $p=0.025$).

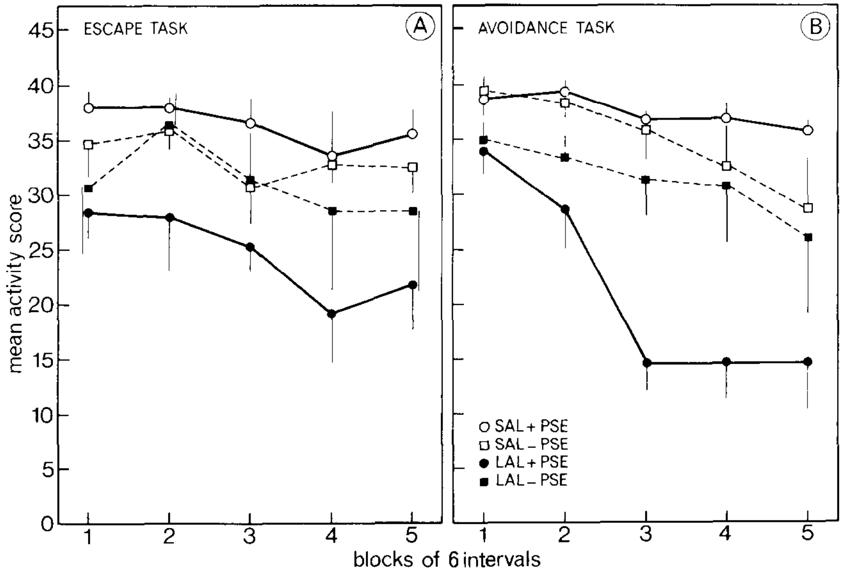

Fig. 5. (a) Mean activity score per block of 6 intertrial intervals in an escape task and (b) mean activity score per block of 6 intertrial intervals in an avoidance task in SAL and LAL mice following exposure to inescapable shocks (+PSE) and without prior shock exposure (-PSE).

DISCUSSION

The present study shows that, as expected, aggressive and non-aggressive male mice differ in their response to an inescapable shock session. This is manifest in the large difference in intershock activity between the two types of individuals; aggressive mice sustain their exploratory activity, while non-aggressive ones become mainly immobile. Exposure to the shockbox without administering shock does in fact also show an influence of the strategy adopted. The relatively high level of immobility in the non-aggressive males is indicative of their passive strategy with which they react to the exposure to a novel cage (a potentially threatening situation). The same reluctancy in the behaviour of the non-aggressive mice has been found in their entrance of a novel cage or a novel complex environment (Polman, 1986; Van Oortmerssen et al., 1985).

The lack of a dichotomy within the non-aggressive mice, as previously been found in response to the controllable active shock avoidance task (some non-aggressive mice adopted a passive strategy, whereas others adopted an active strategy; Benus et al., 1989) indicates that the controllability of a situation may indeed interfere with the adoption of a passive strategy. The rational for this can probably be found in the importance for an individual to have control over environmental events (Overmier et al., 1980; Seligman and Weiss, 1980; Weiss, 1968). It has not only been demonstrated that the absence of control has extremely deleterious effects on several physiological parameters (Laudenslager et al., 1983; Sklar and Anisman, 1979; Weiss, 1968), but also that animals prefer to exercise control over acceptance of even non-aversive events (Overmier et al., 1980; cf. Knapp et al., 1959; Osborne, 1977; Singh, 1970). Therefore, it is reasonable to accept that non-aggressive mice also will have a tendency to exert control, especially when control is easily perceived and/or executed.

The influence of prior shock exposure (PSE) on controllable escape or avoidance tasks was not exceedingly clear, which may have been caused by the small group size (n=5). Despite this handicap it is obvious that, whenever it existed, a deteriorating effect of PSE was only apparent in the non-aggressive group (escape latencies and intertrial activity in the avoidance task).

In the aggressive mice the only effect of PSE was its unexpected, facilatory influence on the number of avoidance responses. It remains obscure how this effect should be interpreted, but a suggestion by Anisman and Waller (1972) may be relevant. They have suggested that increased fear, without a concomittant increase in freezing, inceases the probability of an avoidance response. As the activity level of the aggressive animals was not suppressed due to PSE, increased fear established during the inescapable shock session may result in a higher level of avoidance.

There are various hypotheses that may account for the decremental effects of PSE. The most widely adopted ones are the learned inactivity and the learned helplessness hypotheses. The learned inactivity hypothesis asserts that a subject learns to be inactive during inescapable shocks of long duration, which interferes with subsequent performance in an active escape or avoidance task (Glazer and Weiss, 1976b). This learning to be inactive is suggested to be due to the biphasic nature of the motor response during shocks of long duration. A peak of activity at the time of shock initiation is followed by a decline in the amount of movement as shock continues. This results in inactivity at the instant of shock termination (Glazer and Weiss, 1976b). However, although response topographies during shock differ significantly between aggressive and non-aggressive mice, there is no indication that in either type of individual prolonged shock results in greater passivity as shock continues. In addition, intrashock activity does not change as trials progress. Thus, learned inactivity cannot account for the interference effect whenever it is seen in the non-aggressive male mice. The learned helplessness hypothesis states that animals learn during the inescapable shocks that onset and offset of shock are independent of their own behaviour. This results in three deficits: (1) a motivational deficit - a decreased tendency to initiate responses, (2) a cognitive deficit - having learned that shock termination is unrelated to behaviour proactively interferes with learning the relation between responding and shock in the controllable task, and (3) an emotional deficit - fear that is established due to the uncontrollability of the situation may lead to depression (Maier and Seligman, 1976; Seligman, 1975). Whether (and to what extent) these three deficits contribute to the interference effect in our non-aggressive mice is not clear from the data. It is unlikely that PSE has resulted in an associative deficit, as the aggressive males do not show a decremental effect in performance, and we have no indications that aggressive and non-aggressive mice differ in learning ability (Benus, 1988). However, it is conceivable that individuals differ in the extent to which a motivational and/or emotional deficit arises. For instance, the active behavioural strategy of the aggressive mice may result in persistent attempts (despite their ineffectiveness) to control the situation, leading to a sustained tendency to initiate responses. The passive strategy assumed by the non-aggressive males reflects a lack of initiating attempts to exercise control or to readily "give up trying". This results in a deficit to initiate responses. In this respect it is noteworthy that the conservation-withdrawal response (passive strategy) is suggested to be more closely related to depression than the fight-flight response (Henry and Stephens, 1977).

The general conclusion from our experiments is that on one end of a continuum individuals predominantly show an active response to aversive situations. In a social setting they react offensively or with flight (Benus, 1988); in non-social situations they react with active avoidance of a controllable shock (Benus et al., 1989) and with sustained activity during an uncontrollable task. On the other end of the continuum individuals prepotently show a passive behavioural response, but under certain conditions also are able to adopt an active strategy. In social situations passive animals are non-aggressive and react with immobility when confronted with a resident male (Benus, 1988); in a controllable non-social situation they react either with active avoidance or passive endurance (Benus et al., 1989) and in an uncontrollable task they unambiguously fall into a passive strategy. The rigid behavioural strategy of the aggressive males suggests a high and persistent tendency to exercise control, whereas the more flexible behavioural strategy of the non-aggressive mice is indicative of a lower and/or less persistent tendency to exert control.

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