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BEHAVIOURAL STRATEGIES OF AGGRESSIVE AND NON-AGGRESSIVE MALE MICE IN
ACTIVE SHOCK AVOIDANCE

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ABSTRACT

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The hypothesis, partly based on findings in social interactions, that aggressive mice generally adopt an active behavioural strategy (cf fight-flight) in threatening situations, while non-aggressive ones generally assume a passive strategy (cf conservation-withdrawal) was tested using a two-way active shock avoidance paradigm. Overall, aggressive mice were found to be better active shock avoiders than non-aggressive animals, a finding that is consistent with our hypothesis. However, within the non-aggressive mice a clear dichotomy in high and low avoidance individuals was found. The high intertrial activity in the superior avoidance groups and the low activity in the poor avoidance group was interpreted as another indication of an active versus passive strategy respectively. Accordingly, it was concluded that not all non-aggressive mice assume a passive strategy, but that some mice adopt an active strategy, like all aggressive males.

key words individual differences aggression two-way active shock avoidance
behavioural strategies wild house mice

INTRODUCTION

The study of the integrated behavioural, neuroendocrine and physiological responses of animals and humans in answer to environmental challenges has been a main topic of psychological and biological stress research for many years. The two kind of responses that have originally been suggested and studied extensively are the flight-flight response as described by Cannon (1929) and the conservation-withdrawal response as reported by Engel and Schmale (1972). The flight-flight response is a behavioural pattern, characterized by increased activity and/or aggression in response to a challenging (social) situation. It is accompanied by the release of peripheral catecholamines, indicating a high sympathetic activity that prepares the organism to either fight or flight. Conservation-withdrawal is a response of an organism, characterized by restricted mobility, which is accompanied by an increase in adrenal-cortical activity. The behavioural withdrawal is probably a type of conservation of energy and corresponds to a

Selyean type of stress response (Selye, 1950, Henry and Stephens, 1977) The fight-flight and conservation-withdrawal response patterns are not strictly separate entities, but probably represent two ends of a continuum of adrenal-medullary and adrenal-cortical activity The classical view implies that the type of response pattern is largely situation-dependent, but evidence accumulates on an idiosyncrasy in response patterns, i.e. an individual consistency in type of response to any challenging event (Bohus et al., 1987, Frankenhaeuser and Gardell, 1971, Jones et al., 1970) Evidence has been reported that dominant male mice assume the Cannonian response pattern, whereas subordinate males adopt the Selyean pattern (Ely and Henry, 1978, Henry and Stephens, 1977) Since there is a clear positive correlation between social rank and the independently measured level of aggression (Blanchard et al., 1988, Fokkema, 1985, Oakeshott, 1974), it can be hypothesized that the aggression level of an individual is indicative for its type of response to all sorts of challenging situations This implies that aggressive individuals will adopt a fight-flight response in social interactions, but also in non-social challenging situations, whereas non-aggressive individuals will show conservation-withdrawal in all kinds of challenging circumstances

Male mice that have bidirectionally been selected for aggression for many generations (short and long attack latency, SAL and LAL line respectively, Van Oortmerssen and Bakker, 1981) show considerable differences in their behavioural response to male opponents In a resident-intruder paradigm males of the SAL line readily and persistently attack an opponent that intrudes their territory Males of the LAL line are very reluctant in this respect, their preparedness to attack is low and the duration of their aggressive acts is relatively short (Van Oortmerssen and Bakker, 1981, Van Oortmerssen et al. 1985, Benus, unpubl. results) Furthermore, when intruding into the territory of another male, some SAL individuals attack the resident and others show ample active defence, such as flight The prevalent response of LAL males upon introduction into the territory of another male is immobility (Benus, 1988) Accordingly, the active behavioural response of aggressive males resembles the fight-flight pattern and the passive behaviour of the non-aggressive animals seems to fit in with the conservation-withdrawal response Similar phenomena have been reported for TMD-S3 rats (Fokkema and Koolhaas, 1985, Koolhaas et al., 1986) and for tree shrews (Von Holst et al., 1983), suggesting that the individual differentiation in behavioural responses to social threats is valid across species One of the ways to test whether this individual differentiation extends to non-social situations is to investigate the active shock avoidance behaviour of the socially active, aggressive and the socially passive, non-aggressive mice Two-way active shock avoidance performance largely depends upon the amount of activity an animal still employs during this aversive task (cf. Driscoll, 1986) In rats it has been demonstrated that differences in avoidance performance, as between the Roman High and Low Avoidance strains (Bignami, 1965) and between the Spontaneously Hypertensive Rats and their normotensive controls (Knardahl and Sagvolden, 1982), are related to differences in offensive behaviour (Koolhaas, unpubl. results) This points to a trans-situational consistency in individual behavioural responses

similar to a fight-flight and conservation-withdrawal pattern, to any threatening stimulus. Therefore, the socially active, aggressive mice are expected to be superior in active shock avoidance performance to the socially passive, non-aggressive males.

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 (17x11x13 cm) in a room with an artificial 12/12 h LD cycle (dark from 12:30 h). Food (standard laboratory chow, Hope Farms AM2) and water were available ad lib. The animals were weaned at 3-4 weeks of age. 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 old. Only during the test period the males were separated from their females.

Apparatus

Shock threshold The experimental chamber was one compartment of a shuttlebox. This compartment measured 23 x 20.5 x 20 cm and had a grid floor with an interbar distance of 0.9 cm. Scrambled shocks were delivered through the grid floor. The shock scrambler gave a continuous background noise, which prevented conditioning effects from the clicks of the resistor box switch.

Avoidance conditioning 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 into 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 avoidance task. The conditioned stimulus (CS) was a light stimulus from a 15-W bulb, on the ceiling of the apparatus. Scrambled shock (US) of 200 μ A was delivered through the grid floor.

Procedure

Shock threshold Testing was done between 13:00 and 16:00 h. Fifteen SAL and fifteen LAL males were used in this experiment. A mouse was placed in the shock compartment and the schedule of foot shock delivery was started one minute later. Each shock intensity was presented twice. The schedule of shock delivery was as follows:

20 - 60 - 35 - 10 - 80 - 50 - 80 - 10 - 50 - 60 - 20 - 35 (μ A)

Shock duration was 1 s and the interval between the shocks was at least 15 s. Shock was given only when the animal had all 4 paws on the grid. Although current thresholds are a very arbitrary entity, due to the large dependence on previous shock experience, comparison of arbitrary thresholds can reveal valuable information on differences in

shock sensitivity Shock threshold was determined in the following way

X_s = shock threshold

X = lowest intensity at which the animal responded

Y = lowest but one intensity at which the animal responded

If the animal showed a response (irrespective of the kind of response) upon the first presentation of that particular intensity, then $X_s = X$ If the animal showed a response only upon second presentation, then $X_s = X + 0.5(Y - X)$

Avoidance conditioning All testing was done between 13 00 and 16 00 h Two other groups of SAL ($n=9$) and LAL ($n=16$) males were used Each subject received 5 consecutive days of signalled two-way active avoidance conditioning Each daily session consisted of 30 trials in which a 7-s CS preceded 20 seconds of paired CS and US presentation, unless the animal terminated the CS (=avoidance) or CS/US (=escape) by shuttling to the adjacent compartment, thus ending the trial A 90-s intertrial interval preceded the next stimulus onset Spontaneous crossings to the adjacent compartment during the intertrial interval were recorded as intertrial crossings (ITCs)

Statistics

Data are expressed as mean \pm standard error (sem) Comparisons of two unrelated samples were done using the Mann-Whitney U test (MWU, Siegel, 1956) Avoidance acquisition was analyzed by analysis of variance for repeated measures (rANOVA) with the five days of testing as repeated factor (Kim and Kohout, 1975) Whether the number of avoiders versus non-avoiders was different between two unrelated groups was tested by the Chi-Square test (X^2 , Siegel, 1956) The p-values are two-tailed, unless otherwise stated

RESULTS

Shock threshold The threshold to react to electric footshock was higher in LAL than in SAL males (38.0 ± 2.8 and 21.8 ± 2.8 μ A respectively, MWU, $U=34.5$, $p<0.01$, Fig 1)

Avoidance conditioning The total number of avoidances during the 150 trials was higher in SAL than in LAL males (53.7 ± 4.3 and 36.4 ± 6.8 respectively), but just failed to reach statistical significance (MWU, $U=45.0$, $p=0.06$, one-tailed) However, the acquisition rate of conditioned avoidance responses (CARs) was different between the two groups (rANOVA, $F(4,92)=4.53$, $p<0.01$, one-tailed, Fig 2) On day 4 and 5 the two groups deviated significantly (MWU, day 4 $U=40.0$, $p<0.04$, day 5 $U=31.0$, $p=0.01$, one-tailed)

SAL mice made significantly more intertrial crossings (ITCs) than LAL males (120.1 ± 24.4 and 48.3 ± 10.4 ITCs per 5 sessions respectively, MWU, $U=22.5$, $p<0.01$) However, direct observations and inspection of the individual data suggested a subdivision within the LAL line One group ($n=8$) of the LAL males resembled the SAL individuals, this group explored the shuttlebox extensively and made a corresponding high number of ITCs. The other group ($n=8$) mainly showed immobility and made very few spontaneous crossings On an operational basis we defined the low-crossing LAL group (LC-LAL) as the individuals that made less ITCs than the least spontaneously crossing SAL male. The

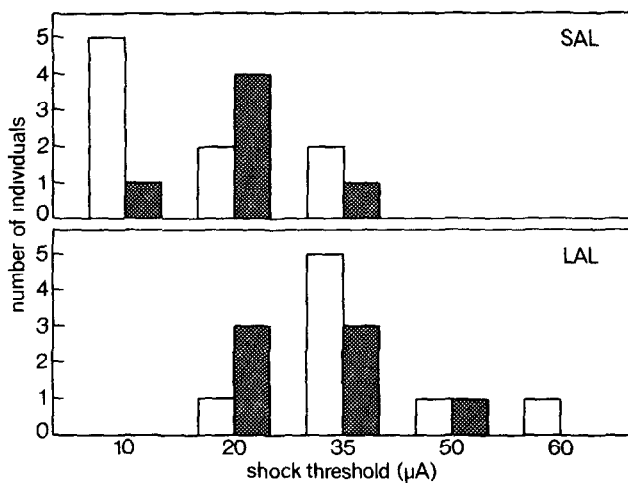


Fig 1. Individual shock thresholds in SAL and LAL male mice. The lowest shock intensity to which an individual reacts upon first (open bars) or second (shaded bars) presentation is given

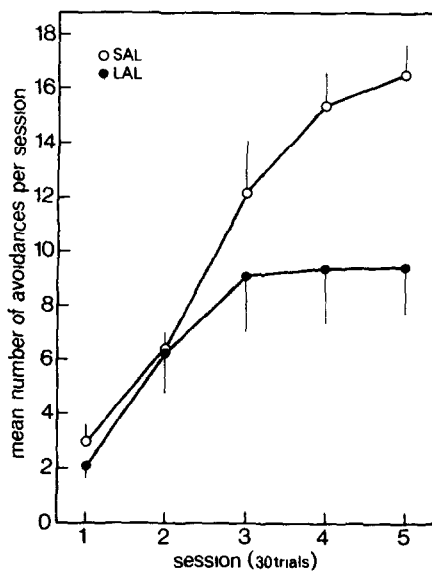


Fig 2 Avoidance performance in SAL and LAL mice. The curves represent the mean number of avoidances (\pm sem) during five avoidance sessions of 30 trials each

high-crossing LAL group (HC-LAL) consisted of animals that made as many or more ITCs than this SAL male. The average number of ITCs in the LC-LAL group was 17.4 ± 4.0 , in the HC-LAL group 79.1 ± 13.4 and in the SAL group 120.1 ± 24.4 ITCs per 5 sessions. The difference between the HC-LAL and the SAL group was not significant.

Marked differences in shuttle performance existed between the three groups (Fig 3), both in avoidance level (rANOVA, $F(2,22)=32.48$, $p<0.01$) and in acquisition rate (rANOVA, $F(4,88)=9.25$, $p<0.01$). Differences between the LC-LAL and the HC-LAL group were significant for the avoidance level ($F(1,14)=55.58$, $p<0.01$) and the acquisition rate of CARs ($F(4,56)=11.74$, $p<0.01$). This held also for the avoidance level ($F(1,15)=66.28$, $p<0.01$) and the rate of acquisition ($F(4,60)=17.75$, $p<0.01$) between the LC-LAL and the SAL group. Thus, shuttle performance was very poor in the LC-LAL group compared to the HC-LAL and the SAL groups, a difference that was highly significant from day 2 on (MWU, LC-LAL/HC-LAL day 2 $U=4.5$, day 3 $U=0.0$, day 4 $U=0.0$, day 5 $U=0.0$, LC-LAL/SAL day 2 $U=8.0$, day 3 $U=0.5$, day 4 $U=0.0$, day 5 $U=0.0$, $p<0.01$ for all cases). Between the HC-LAL and the SAL groups a significant difference in the rate of acquisition of CARs was found (rANOVA, $F(4,60)=2.50$, $p=0.05$).

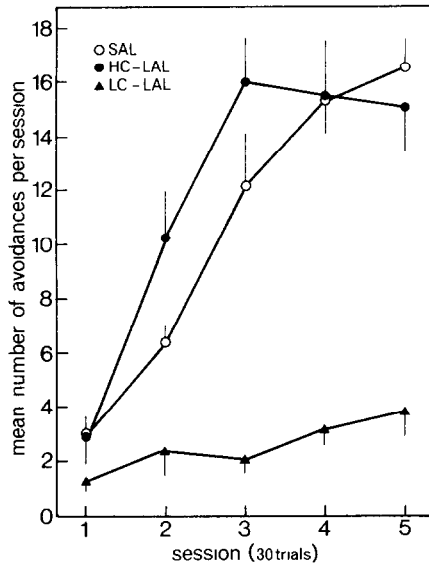


Fig 3 Avoidance performance in SAL and LAL mice. The curves represent the mean number of avoidances (\pm sem) during five avoidance sessions of 30 trials each in the homogeneous group of SAL males (all high-crossing), the high-crossing (HC-) LAL group and the low-crossing (LC-) LAL group.

The avoidance scores were also analyzed using the "avoidance criteria" as described by Driscoll and Bättig (1982). An animal is required to make four consecutive avoidances to be classified as an "avoider". All individuals of the HC-LAL and the SAL group were classified as avoiders, but only 2 of the LC-LAL group. The difference between the LC-LAL and the other groups was significant (LC-LAL/HC-LAL $\chi^2=9.60$, $p<0.01$, LC-LAL/SAL $\chi^2=10.43$, $p<0.01$). The mean number of trials to reach criterion for the two animals of the LC-LAL group was 149.0 ± 1.0 . The HC-LAL group required significantly fewer trials to reach the avoidance criterion than the SAL group (68.6 ± 6.1 and $105.6 \pm$

10.9 trials respectively, MWU, $U=13.0$, $p<0.05$)

Response latency was measured for avoidance and escape trials. Mean escape latencies were all approximately 8 s, so all mice escaped roughly within 1 s after US-onset (Fig. 4). Nevertheless, data analysis showed a significant difference in escape latencies between the three groups (rANOVA, $F(2,22)=6.27$, $p<0.01$), SAL males escaped more slowly than either HC-LAL or LC-LAL males ($F(1,15)=9.25$, $p<0.01$, $F(1,15)=7.24$, $p<0.02$ respectively). Avoidance latencies also differed between the three groups (rANOVA, $F(2,22)=9.99$, $p<0.01$). This overall difference was caused by significant differences between the LC-LAL and the HC-LAL group ($F(1,14)=5.27$, $p<0.04$) and between the LC-LAL and the SAL group ($F(1,15)=22.05$, $p<0.01$). Thus, it was remarkable that, although LC-LAL males were poor avoiders, whenever they did avoid, they were the fastest. Avoidance latencies generally showed a significant change over time ($F(4,88)=4.60$, $p<0.01$).

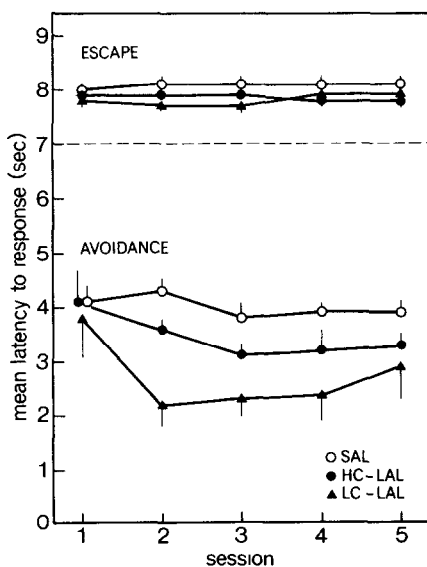


Fig. 4 Mean avoidance and escape latencies (\pm sem) per daily session of 30 trials in SAL, high-crossing (HC-) LAL and low-crossing (LC-) LAL mice. The CS-US interval is 7 seconds.

DISCUSSION

Male mice of lines that have bidirectionally been selected for attack latency achieve different performance levels in a two-way active shock avoidance task. On average the aggressive males were better active shock avoiders than the non-aggressive animals. It is unlikely that this difference is due to differences in learning abilities between SAL and LAL mice, though it is clear that the shuttle avoidance procedure is a complex

learning task, involving the presentation of several contingencies that may act separately and interact together to influence responding. However, it has been shown that none of the instrumental contingencies (CS termination, US termination and the avoidance contingency) differentially affect rat strains that differ in avoidance behaviour. Instead, the differences between strains are found to be a function of the classical contingency of CS-US pairings (Katzev and Mills, 1974). If the response that is required for good avoidance performance (like flight in an active task) is compatible with anticipatory responses that are classically elicited by contiguous CS-US pairings, avoidance performance will be facilitated. On the other hand, if the response requirement is incompatible with the classically elicited responses (for instance freezing when fleeing is required), avoidance learning will be difficult, and in some cases impossible. Freezing obviously interferes with the execution of an active avoidance response (Kriekhaus, 1965, Kriekhaus et al., 1965). Administration of amphetamine to poorly avoiding rats reduces freezing and enhances avoidance behaviour significantly. This improvement disappears when the drug is no longer administered (Barrett et al., 1973, Driscoll, 1986), indicating that poor avoidance performance is not caused by a learning deficit. The importance of the response compatibility has been stressed by Bolles (1970). He has suggested that the ease with which an animal can learn CARs depends upon the degree to which the situation evokes species-specific defence reactions, like running, jumping, or freezing. Accordingly, the difference in avoidance performance between our aggressive and non-aggressive male mice is most likely caused by a difference in the type of defensive response (active vs. passive) that is elicited rather than by a difference in learning abilities per se. This difference in response to the aversive situation is not only reflected in the level of avoidance performance, but probably also in the number of intertrial crossings. A difference in number of ITCs between superior and poor avoidance individuals has also been shown in numerous other studies (Broadhurst and Bignami, 1965, Coyle et al., 1974, Durcan et al., 1984b, Satinder, 1971). However, one has to consider the possibility that the number of ITCs reflects the general exploratory and/or motor activity of an individual and that a higher general activity may indirectly produce superior avoidance performance. This is unlikely to be the case, since no differences between high and low avoiding rat strains have been found in number of pre-session ITCs (Durcan et al., 1984b) nor in activity in a shuttlebox without administering shock (Coyle et al., 1974, Satinder and Hill, 1974). Furthermore, no differences between high and low avoidance strains have been found in activity cages (Durcan et al., 1984a). The ambulation scores of our SAL and LAL males in large living-cages are not significantly different (Benus et al., 1988). Therefore, it is likely that the number of ITCs during acquisition of a shuttle task does not reflect a general exploratory and/or motor activity, but reflects the mode of responding towards an aversive situation.

Two other points need some consideration to be certain that the level of avoidance performance reflects the mode of responding towards challenging situations. The first point pertains to the difference in shock threshold between the aggressive and non-

aggressive mice. Our aggressive mice have a lower shock threshold than our non-aggressive mice. A lower threshold could imply a higher sensitivity to footshock and, therefore, a higher motivational level. It has been shown that an increase in motivational level (by increasing shock intensity) results in an improvement of avoidance performance (Seligman and Weiss, 1980). However, the similar escape latencies in both lines make a motivational difference as explanation for the difference in avoidance performance unlikely. The suggestion of Brush et al (1985) that higher sensitivity to electric shock results in poor avoidance performance, due to the fact that more fear (and hence more incompatible freezing responses) is elicited, is not applicable either, since the more sensitive (in terms of threshold) aggressive mice are much better avoiders than the non-aggressive individuals. The second point concerns the sensory capacities of the animals. In the present experiment the CS used was light. A mouse strain known for its defective vision, the C3H/HeJ strain (Sidman and Green, 1965) has a very low avoidance level when light is used as CS, but a very high avoidance level when a buzzer is used as CS (Duncan et al, 1971). So if non-aggressive mice have difficulties with visual discrimination then this may explain their low avoidance performance. Direct observations of the animals contradict this possibility, since LAL mice clearly respond to the CS by wincing.

Although on average the aggressive mice are better shock avoiders than the non-aggressive ones we cannot neglect the dichotomy within the non-aggressive line. Mice with a high spontaneous crossing frequency are much better avoiders than the rarely crossing mice. The final avoidance level of the HC-LAL individuals is similar to that of the SAL animals, which also have a high spontaneous crossing level. However, the HC-LAL group requires considerably fewer trials to reach the "avoidance criterion" as described by Driscoll and Battig (1982) than the SAL group. This is also expressed in the significant difference between the HC-LAL and the SAL group in acquisition rate of CARs. Furthermore, the escape and avoidance latencies are shorter in the HC-LAL than in the SAL group. This indicates that, in this case where for both groups the elicited response to aversive stimuli is compatible with the required response for good performance, the LAL males learn the task more readily than the SAL mice. This may be caused by a possible difference between these types of males in their responsiveness to stimuli introduced into a conditioning session, which can lead to slight differences in learning the classical and/or instrumental contingencies. Previous studies have shown that non-aggressive males are more responsive indeed to external stimuli than aggressive males (Benus, 1988, Benus et al, 1987).

How can the dichotomy within the non-aggressive line be explained? There are no indications that HC- and LC-LAL individuals differ with respect to learning ability, shock threshold or in visual abilities. Furthermore, none of the LAL mice attack male opponents within the time course of the test (600 s), neither in the standard test nor in a second test following the shuttle session. Accordingly, there are no indications that LC- and HC-LAL males differ with regard to their aggressive behaviour. The only differences seem to pertain to the level of avoidance performance and the extent of

exploratory behaviour during the shuttle sessions. This suggests that in non-aggressive male mice either type of defensive response, i.e. fight-flight or conservation-withdrawal, can be evoked by the aversive situation. This variability may be due to the fact that the non-aggressive mice derive from the 9th generation of selection, whereas the aggressive males, which all adopt an active strategy, have been selected for 31 generations. It is also possible that LAL mice generally have two options available to respond to aversive situations, and react either actively or passively. However, we surmise that LAL mice predominantly will assume a passive strategy, unless the external situation is easily and effectively controllable, or effective control is easily perceived. It is widely known that animals learn a one-way active shock avoidance task more readily than a two-way task (Anisman, 1973, Theios, 1963, Theios and Dunaway, 1964) and that the wide differences in two-way avoidance in RHA and RLA strains are minimized in one-way avoidance (due to an improvement in the RLA strain, Satinder and Petryshyn, 1974). In the less complex one-way task freezing can be rapidly suppressed since the running response is functionally effective in removing the organism from the dangerous situation (Bolles, 1970), and hence effective control of the external situation is easily perceived. If, for some unknown reason, the individuals of the HC-LAL group perceive the situation as more easily controllable than do the animals of the LC-LAL group, then it may be possible that the HC-LAL mice are able to adopt an active strategy. The prediction resulting from this suggestion is that in an uncontrollable situation, in which effective control is impossible, all non-aggressive mice will assume a passive behavioural strategy, whereas the aggressive males will maintain their active behavioural strategy. The experiment testing this prediction will be the subject of a next paper.

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