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Heritable variation for aggression as a reflection of individual coping strategies

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Abstract. Evidence is presented in rodents, that individual differences in aggression reflect heritable, fundamentally different, but equally valuable *alternative* strategies to cope with environmental demands. Generally, aggressive individuals show an active response to aversive situations. In a social setting, they react with flight or escape when defeated; in non-social situations, they react with active avoidance of controllable shocks and with sustained activity during an uncontrollable task. In contrast, non-aggressive individuals generally adopt a passive strategy. In social and non-social aversive situations, they react with immobility and withdrawal.

A main aspect of these two alternative strategies is that individuals with an active strategy easily develop routines (intrinsically determined behaviour), and consequently do not react (properly) to 'minor' changes in their environment, whereas in passively reacting animals it is just the other way around (extrinsically determined behaviour).

It has become clear that active and passive behavioural strategies represent two different, but equivalent, coping styles. The coping style of the aggressive males is aimed at the removal of themselves from the source of stress or at removal of the stress source itself (i.e. active manipulation). Non-aggressive individuals seem to aim at the reduction of the emotional impact of the stress (i.e. passive confrontation). The success of both coping styles depends upon the variability or stability of the environment. The fact that aggressive males develop routines may contribute to a fast execution of their anticipatory responses, which is necessary for an effective manipulation of events. However, this is only of advantage in predictable (stable) situations, but is maladaptive (e.g. expressed by the development of stress pathologies) when the animal is confronted with the unexpected (variable situations). The flexible behaviour of non-aggressive individuals, depending strongly upon external stimuli, will be of advantage under changing conditions.

Studies on wild house mice living under natural conditions show how active and passive coping functions in nature, and how the two types have been brought about by natural selection.

Key words. House mouse; rat; wild mice; aggression; individual differences; genetic variation; selection; Y-chromosome; behavioural strategies; routine formation; active coping; passive coping; natural population.

Introduction

The most commonly used definition of aggression is the delivery of noxious or potentially harmful stimuli to another animal to gain some advantage[48, 100]. The gain can be thought of as achieving and/or maintaining hierarchical ascendency and priority in the access to food, nesting material, shelter, mates and territory. Harm refers to any physical and emotional consequence to which a recipient shows an aversion[71]. As there are many types of aggression[47,65,70,99,100] and there are no general rules which specify the relationships between any two patterns of aggressive behaviour, each type has to be considered in its own context. In house mice and rats, the subjects we deal with in this paper, the main function of aggressive behaviour is clearly related to the establishment and defense of property, like territory and food[20,27], both under settled and under migratory conditions. The behaviour of rodents in a resident-intruder paradigm mimics this type of aggression[33] and is therefore commonly used to study aggression in a setting that conforms to what we believe happens in the field[64].

Despite the enormous interest in the causes and function of aggressive behaviour in a wide range of disciplines, such as ethology, ecology, psychology and physiology, relatively little attention has been devoted to individual differences in aggression and their significance. It is the aim of the present review to demonstrate that serious consideration must be given to the fact that individual differences in aggression reflect *alternative* modes of social interaction, and, even more generally, reflect fundamentally different but equally valuable strategies for coping with environmental demands.

Causes of individual differences in aggression

As for any other trait, differences in aggressiveness between individuals are caused by environmental differences, genetic differences and/or their interactions. Although several environmental factors, like parental influence, social isolation and group composition during adulthood, have been reported to play a significant role[34,35,57,72,85], other investigators have failed to find such effects[5,28,40,94]. More agreement exists about the presence of a genetically determined variation in aggression[43,56,79,84,88], despite the fact that interstudy comparisons are often thwarted by the various testing methods used[84]. One of the means to study the genetics of aggressive behaviour is artificial selection. In our laboratory we have successfully selected for attack latency in wild house mice, *Mus musculus domesticus*[90,91] (fig. 1), thereby demonstrating a significant genetic influence on phenotypic variation in this character. Attack latency is a reliable indicator of aggression, since there is a significantly negative correlation between attack latency and the number of attacks and accumulated attacking time, including chasing, biting and fighting[25,94]. Figure 1 shows the updated results of the bidirectional selection for short (SAL), and long attack latency (LAL), mice. However, although LAL males are reluctant to start aggression they nevertheless are able to fight back properly when they are attacked. The results show that, especially by selection for higher aggressiveness (SAL), a clearcut reaction can be achieved within a few generations.

There is evidence that, in natural populations of wild house mice, the very fast- and the non-attackers are particularly abundant (fig. 2). Thus, our artificial selection reflects the diversifying selection that takes place in nature[92]. The use of these selected lines therefore offered an optimal opportunity to study the origin and biological significance of individual differences in aggression and associated traits.

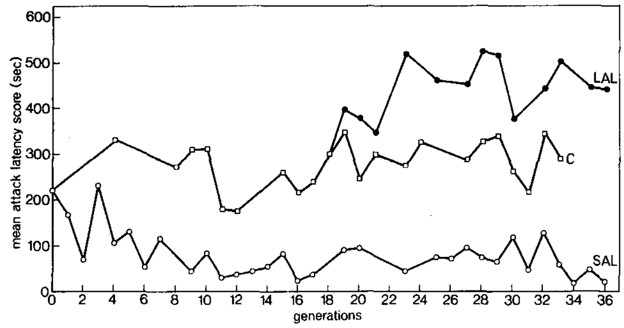

Figure 1. Selection for short vs long attack latency score, resulting in the SAL and LAL lines, respectively. Both lines were derived from a randomly bred control (C) population. After van Oortmerssen et al.[91]; brought up to date by previously unpublished results.

Crossing experiments using these selected lines have revealed the influence of the Y-chromosome on attack latency[89,94] (and unpublished results), thus matching the findings of Maxson and collaborators[69], and of Carlier and Roubertoux[24]. This either means the involvement of more than one Y-chromosome, in concordance with the traditional idea that Y-chromosomes do not show genetic recombination with other parts of the genome, or it means that Y-chromosomes do indeed show recombination. Evidence is mounting that the latter is the case[51,73]. Attempts to bring the Y-chromosome of the SAL line onto the genetic background of the LAL line, by backcrossing, and vice versa, revealed the disappearance of the original Y-chromosomal effect in the F2 and F3 generations of backcrossing. This led to the conclusion that the genetic information on the Y-chromosome concerned with attack latency must be situated in the so-called PAR-region (pseudo autosomal region), which will be exchanged with the X-chromosomes when sperm cells

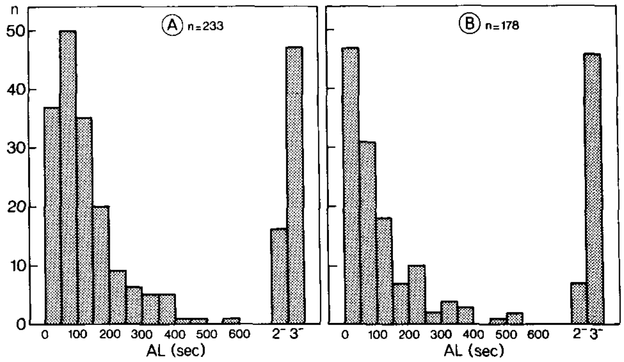

Figure 2. Attack latency score distributions of male house mice from two representative populations. Data are grouped in classes per 50 s, 2- and 3- indicate mice failing to attack in two or, respectively, all three of the tests conducted.

are formed in the F1-, and succeeding backcross, generations.

Classically, the androgens are considered to be the most important hormones in the control of aggression. This originates from the facts that in most species the male is more aggressive than the female, that castrating males reduces their aggressiveness, and that replacement therapy with moderate dosages of testosterone (T) restores the aggressiveness of castrates to normal levels[60]. Aggressive wild house mice do indeed show higher plasma T levels than non-aggressive ones[93], and the same holds true for aggressive and non-aggressive rats[77]. The crossing experiments between SAL and LAL mice also revealed that adult male plasma T levels are autosomally determined; high T levels being dominant over low T levels. A differential sensitivity to T between the lines is, however, already established before the age of 50 days[93]. It is this sensitivity that is influenced by the Y-chromosome, probably via processes related to the perinatally occurring sex-determining processes. One-day-old LAL mice, for example, possess significantly more Leydig cells than their SAL counterparts[29].

Besides the important pituitary-gonadal effects on aggression, there are also pituitary-adrenocortical effects. For instance, adrenalectomy reduces aggressiveness[19,44,62], whereas treatment of adrenalectomized mice with moderate dosages of either corticosterone or dexamethasone restores their aggressiveness. However, treatment with high dosages of corticosterone reduces the aggressiveness of intact mice[21,59]. Moreover, there seems to exist a direct relationship between ACTH levels and aggressiveness[17-19,62].

Another important factor that is positively correlated with aggressiveness is sympathetic tone and sympathetic reactivity[37,42,78]. For instance, Fokkema et al.[37] showed that more competitive rats had higher baseline levels of plasma noradrenaline than did less competitive rats. In addition, more competitive rats had a higher plasma catecholamine reactivity and a higher blood pressure reactivity[37]. It has also been demonstrated that the cardiac reactivity of more aggressive male rats is higher (tachycardia) than that of non-aggressive males (bradycardia)[16].

Despite the brevity of this outline it will be clear that the physiological parameters underlying aggression are also involved in many other behavioural characteristics; for instance, locomotor activity, exploratory activity and mental activity are all connected with an increased sympathetic tone[42]. A correlation between exploratory behaviour in a novel environment and cardiac response to an emotional stressor in an inhibitory avoidance situation has been demonstrated by Nyakas et al.[74]. Male rats that explored more showed less bradycardia as an emotional stress response; animals that explored less showed more bradycardia.

Moreover, Roman high- and low-avoidance rats, bidirectionally selected for two-way active shock avoidance performance[14], not only show differences in cardiac reactivity, but also show the same differences in aggression as the SAL- and LAL mice. Similar differences are found in many lines artificially selected for characteristics other than aggression, for example Maze-bright vs Maze-dull rats, Spontaneously Hypertensive vs the Wistar Kyoto rats[53], and the apomorphine sensitive vs apomorphine insensitive rats[26]. Therefore, it may be hypothesized that genetically determined individual differences in aggression, i.e., differences in response to confrontation with a male opponent, generally indicate how individuals meet threatening situations, i.e., reflect individual differences in coping styles.

Individual strategies in offense and defense

Aggression (offense) and flight/submission (defense) used to be considered as opposite poles of a single continuum[55,80]. It was suggested that those hormonal characteristics which predispose an animal to be highly aggressive should predispose it to be non-submissive, and vice-versa[60]. Later it was recognized that offense and defense can be manipulated separately, and although they may ordinarily vary in opposite ways, they are separable traits[2,61]. Surprisingly, there are few reports describing the behaviour of aggressive and non-aggressive individuals when attacked by a resident male upon intrusion of its territory. Moreover, the study of individual differences in defensive behaviour has been incorporated in only very few studies. Von Holst et al.[96] have described two distinct types of submissive tree shrews living in the cage of a resident male. One type actively tries to escape from the resident, whilst the other hardly responds to its threats and attacks. In addition, the differentiation in the physiological response of losers, during a confrontation between two conspecifics in an unfamiliar cage, suggests that some males predominantly respond to social interaction with a sympathetic adrenal-medullary pattern, whereas others respond with an increase in adrenocortical function. Thus, during defense animals may either be more sympathetically or more parasympathetically inclined. In addition, as shown before, the same distinction can be found in individual differences in offense. So it seems that some animals readily prepare for physical activity, and probably for an active involvement in social interactions as well, whereas others remain more passive.

This implies that the individuals that are aggressive in their own territory will show much flight when defeated in the territory of another resident, whereas non-aggressive males will show more passive withdrawal when defeated. Substantial evidence exists that this is indeed the case. Fokkema[36] has demonstrated a significant positive correlation between the amount of aggressive behaviour an individual male rat shows in a victory test and the amount of active defense and flight behaviour it performs during defeat. In another study on male mice,

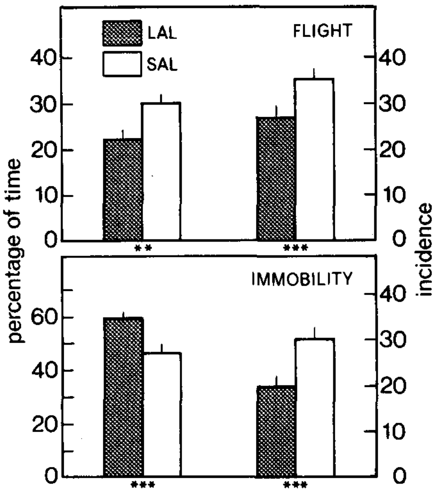

Figure 3. The amount of flight and immobility shown by non-aggressive (LAL) and aggressive (SAL) intruders when defeated by a trained fighter, expressed as mean (± SEM) percentage of observation time and mean (± SEM) frequency per observation period.

Benus[8] showed that SAL male mice were more engaged in flight behaviour than LAL males, whereas LAL intruders were significantly more immobile than SAL individuals (fig. 3). Moreover, the duration of an immobility bout is much longer (MWU-test, $p < 0.01$) in LAL (11.2 ± 1.3 s) than in SAL males (6.1 ± 0.6 s), which explains the relatively low incidence of immobility in the LAL mice. When offered an opportunity to actually escape from the territory of the resident, aggressive mice and rats use this opportunity more readily than non-aggressive individuals (fig. 4), which is most probably caused by the higher tendency of the aggressive males to initiate active behaviour.

These data are consistent with the existence of two fundamentally different types of responders to social interaction. These two types of individuals employ divergent strategies. One type tends to actively determine its social situation, and hence is aggressive in its own territory and predominantly flees and/or escapes when defeated, i.e., it adopts an active strategy; the other type passively endures social interaction and, thus, is non-aggressive and engages in immobility, i.e., it adopts a passive strategy.

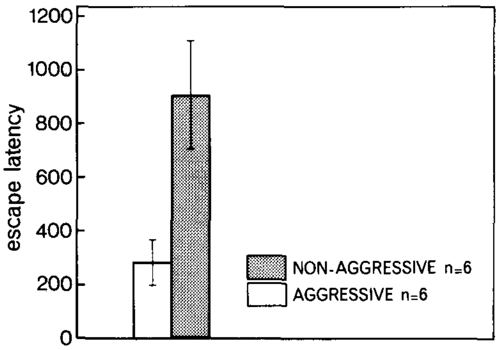

Figure 4. Differences between aggressive and non-aggressive male rats in escape latency (s) during a defeat confrontation with a dominant opponent.

Individual strategies in non-social aversive situations

The two types of responses to social interaction show a high similarity to fight-flight and to Selyean distress in combination with the conservation-withdrawal response, as described in the classical stress literature[22, 31, 46, 82]. In his fight-flight concept, Cannon[22] described a behavioural and neuroendocrine pattern by which an animal reacts to a threatening situation. He had shown an increased output of adrenaline coming from the adrenal of a cat exposed to a barking dog[23]. It was suggested that fear and rage responses, resulting in enhanced adrenal-medullary activity, helped the cat to cope with a threatening situation, since it created a state highly suited for either attack, or flight, or more generally overt action.

The Selyean distress response is described as an adrenocortical-driven part of a general adaptation syndrome (GAS). GAS is a general nonspecific reaction pattern with which an organism can combat damage caused by a variety of potential disease producers, such as toxins, cold, heat, X-rays, pain, and immobilization stress. It is characterized by adrenocortical enlargement, thymicolymphatic involution and intestinal ulcers. The syndrome is triphasic and the first stage is called the alarm response, or the initial appearance of marked, acute manifestations. Subsequently, these manifestations disappear, leading to a stage of resistance and, finally, a breakdown with complete loss of resistance evolves: the stage of exhaustion. Organisms go through the first two stages many times to adapt to the demands of the environment. Only prolonged or severe stress leads to stage three, which often results in death[83].

The term conservation-withdrawal was originally proposed by Engel and Schmale[31] to describe a triad of behavioural phenomena, namely relative immobility, quiescence and unresponsiveness to environmental input. They suggested that this response may be invoked either when input becomes excessive and beyond the organism's capacity to cope actively, or when available input becomes inadequate to meet needs. The biological goal of conservation-withdrawal is to conserve resources and to assure the autonomy of the organism until environmental conditions are once again more favourable. Reduced responsiveness does not necessarily imply a reduced awareness of the environment[31]. Henry and Stephens[46] state that conservation-withdrawal, which is characterized by restricted mobility, corresponds to the Selyean type of stress response, i.e. an increase in adrenocortical activity.

The previously described, behaviourally and physiologically active response of aggressive male rodents to social interaction very much resembles the fight-flight pattern, and the passive reaction of the non-aggressive animals seems to fit in with the conservation-withdrawal response. Although the classical view implied that the type of response elicited is largely situation-dependent, evidence has accumulated on an idiosyncrasy in the type of response to any challenging event[16, 39, 49]. What is the evidence that aggressive individuals generally show a fight-flight type of response and non-aggressive ones a conservation-withdrawal type of response? A very suitable experimental paradigm for testing whether individuals that differ in their response to social interactions also differ in their response to a non-social challenge is a two-way, active shock avoidance task. Although it is clear that the shuttle avoidance procedure is a complex learning task, involving the presentation of several contingencies, it has been shown that none of the instrumental contingencies 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[50].

If the response that is required for good avoidance performance (like fleeing 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 acquisition will be difficult, and in some cases, impossible. Therefore, animals with a general fight-flight type of response should be better active shock avoiders than individuals with a conservation-withdrawal type of response.

This prediction was confirmed in an experiment in which SAL and LAL male mice were subjected to five daily sessions of 30 trials each of two-way, active shock avoidance responding. The aggressive males were better shock avoiders than the non-aggressive individuals (fig. 5), and this difference could not be explained by differences in shock threshold, general exploratory and/or motor activity or sensory capacities of the animals[9]. It has also been demonstrated in rats that individuals show idiosyncrasies in their response patterns. For instance, Roman high-avoidance males are highly offensive in dyadic social confrontations, whereas the Roman low-avoidance rats hardly display any aggression. In addition, the spontaneously hypertensive rat (SHR) strain, which has been artificially selected for a physiological characteristic of the fight-flight response, i.e. a high sympathetic activity, is more aggressive in a resident-intruder paradigm than its normotensive Wistar Kyoto control strain[53], also showing a more rapid acquisition of the two-way, active shock avoidance response[52].

In an uncontrollable situation the idiosyncrasy in response patterns remains. In response to inescapable shocks, LAL male mice show a dramatic decrease in intertrial activity, whereas the activity of the SAL males is hardly altered (fig. 6). Even exposure to the shockbox without any shock being administered shows differences in the strategy adopted. The relatively high level of immobility in the non-aggressive males is indicative of the passive strategy with which they react to the exposure to a novel cage (a potentially threatening situation). The same reluctanct behaviour has been found in non-aggressive mice on entering a novel complex environment[91]. During the inescapable shock session SAL males keep on exploring the shockbox, possibly in a sustained attempt to escape from it, whereas LAL mice show an almost complete cessation of activity[10].

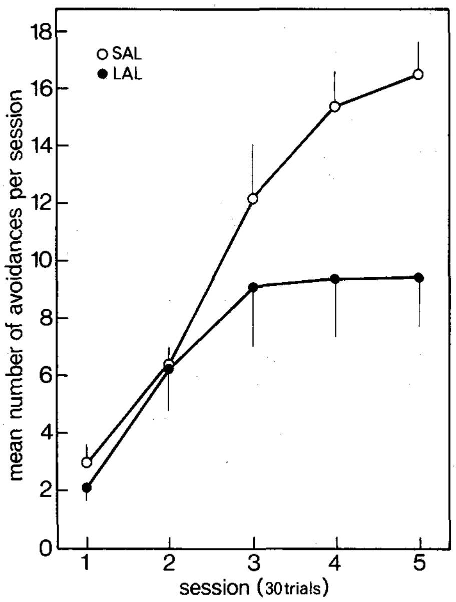

Figure 5. Avoidance performance in SAL and LAL mice. The curves represent the mean number of avoidances (± SEM) during five avoidance sessions of 30 trials each.

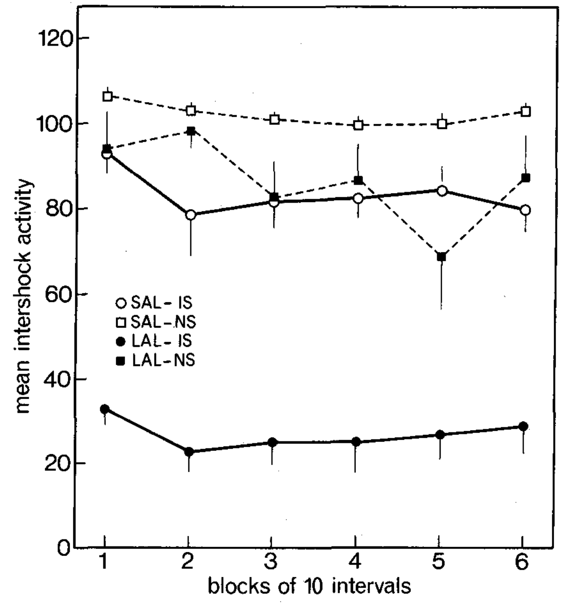

Figure 6. Mean intershock activity (± SEM) in SAL and LAL mice during blocks of 10 shock-intervals in an inescapable shock session (IS), and mean activity (+ SEM) in SAL and LAL mice in the shockbox without administering shock (NS).

The conclusion from the above-described data is that at one end of a continuum individual male rodents predominantly show an active behavioural strategy in any kind of aversive situation. On the other end of the continuum individuals predominantly show a passive behavioural strategy. If a strategy is defined as a series of behaviours, linked by the purpose of achieving a goal in a particular manner, then, in this case, the goal is to deal (that is, to cope effectively) with the demands set by the environment. The way aggressive individuals try to achieve this goal is to manipulate the circumstances or to remove themselves from a threatening situation (manipulators), whereas non-aggressive animals seem to adjust themselves to the situation and accept it as it is (adjustors). Therefore, it seems that the active and passive behavioural strategies of aggressive and non-aggressive individuals reflect different coping styles.

Individual strategies in response to changes

Many physiological studies indicate that the active behavioural strategy of aggressive individuals is not very successful under challenging social circumstances. For instance, Henry and Stephens[46] have shown that in a complex mouse colony, in which it is difficult for the dominants to control all the alleys and boxes of the colony simultaneously, the dominants suffer from hypertension, whereas the subordinates are normotensive. In rats it has been demonstrated that hypertension mostly occurs in those animals that take a position just below the top-dominant in the social hierarchy (the sub-dominants). Even the top-dominants, in a socially unstable situation in which it is difficult for them to maintain their position, develop hypertension[3,36]. Manuck et al.[68] have demonstrated similar results in cynomolgus monkeys. They have housed males in either periodically reorganized, or stable, social groups. Dominant males which were assigned to the reorganized (unstable) groups developed significantly larger coronary artery atherosclerosis than did subordinate males from the unstable group or dominant males from the stable social situation. Although these data are based on findings in dominant and subordinate animals, it can still be concluded that aggressive and non-aggressive individuals show a clear differentiation in the occurrence of stress pathologies under socially unstable situations, since a significant correlation between the level of aggression and social status exists[15,36,75,91].

Since a socially unstable situation is characterized by many changes in the environment, it can be imagined that aggressive and non-aggressive individuals differ in their response to a changing (social) environment. To test this idea relatively simple experimental designs can be used. For example, LAL and SAL mice have been trained to run without error through a maze with an invariable configuration, after which a minor change in extra- or intramaze cues was introduced and the reaction to that change was measured. Both types of mice learned equally quickly how to solve this maze task, which indicates that differences in learning abilities between the two lines do not determine differences in performance levels. However, once the mice had learned how to reach the goalbox a major difference arose between the two types of males. Whereas the aggressive mice invariably fulfilled the task very fast and without error, the non-aggressive mice started to explore the maze extensively and hence made a lot of errors[12].

The reaction to a change (the change was only introduced when both types of males had reached the criterion of accomplishing the maze task three successive times without making an error) also differed very much between the aggressive and non-aggressive mice. Aggressive individuals hardly responded to either a change in extramaze cues (turning the maze 90° with respect to the environment), or to a change in intramaze cues (sticking a piece of tape to the floor of the maze). In contrast, the behaviour of the non-aggressive animals was easily influenced (disturbed) by either change in the environment[12] (fig. 7). In rats, a significant negative correlation was also found between aggression score and increase in the number of errors in response to a change in extramaze cues, indicating that the more aggressive males were less affected in their performance by this change[12]. In view of the rather constant execution of the maze task by the aggressive males and their relative insensitivity to a change in the environment, one can postulate that the behaviour of the aggressive individuals is routinized (which is *not* the same as stereotyped). During the repeated execution of the maze task they probably develop a routine and consequently do not react to changes in the environment. The non-aggressive animals do not develop routines and keep on reacting to every detail of the environment, both the extra-, as well as the intramaze changes.

What happens when the animals are prevented from developing or using a routine? This has been tested by presenting SAL and LAL mice every day (after three trials) with a different maze configuration, so that a con-

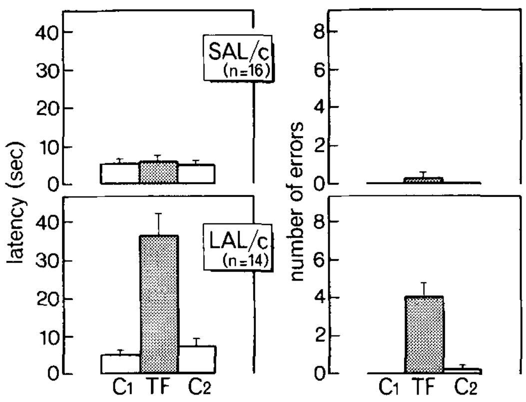

Figure 7. Reaction of aggressive (SAL) and non-aggressive (LAL) mice to a tape fragment (TF) stuck to the floor of a maze, expressed in terms of latency and number of errors.

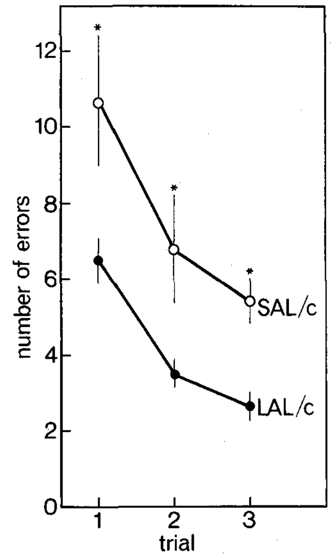

Figure 8. Mean number of errors per trial in 12 different maze configurations in aggressive (SAL) and non-aggressive (LAL) mice.

tinuously changing environment is created. Without the possibility of finding their way to the goalbox in a routine-like fashion the aggressive male mice made significantly more errors than the non-aggressive males (fig. 8), which were better able to reconstruct the way to the goalbox every time, probably owing to their higher attentiveness to details in the surroundings. In rats the significant positive correlation between aggression score and mean number of errors over all test problems also indicates that the more aggressive animals perform worse in a continuously changing environment than the less aggressive individuals[12].

Under more stable living conditions, aggressive individuals are also more routinized in their behaviour than are non-aggressive ones. This has been demonstrated in a Y-maze in which male mice lived for a week and in which only one of the two arms gave access to the food compartments. The number of errors made in response to reversal of the arm that was blocked was taken as an indicator for the degree of routine formation. SAL males made significantly more errors, and hence were more routinized in their performance than LAL mice, which adjusted their locomotion pattern to the new situation relatively easily. During the training period of one week the SAL males apparently developed a strongly anchored locomotion pattern, which was difficult to alter when the change was introduced[11].

The social (in this case aggressive) behaviour of SAL mice has also been shown to be more routinized and less dependent upon environmental stimuli than that of LAL males (males of the LAL line which were willing to attack an intruder were used here). Males were given different amounts of experience with male opponents, after which their own females were introduced as opponents. The more extended the experience with male intruders was, the more SAL males subsequently attacked their own females. In contrast, LAL mice appropriately changed their behaviour towards the females (fig. 9). Thus the attacking behaviour of SAL mice becomes routinized, whereas that of LAL males remains flexible.

Very generally, it can be concluded that the behaviour of aggressive males is more routinized and less dependent upon actual environmental stimuli than the behaviour of non-aggressive individuals. The consequence is that aggressive males either do not react properly to a change in the environment or take a long time to do so, whereas non-aggressive animals readily adjust their behaviour to a new situation. The foundation of this difference in the extent of developing routines may be sought in the organization of behaviour. Fentress[32] has suggested that integrative behaviour systems commonly display two fundamental principles of operation: interaction and self-organization. The basic idea of such a system, which Fentress demonstrates with grooming behaviour in mice, is that it can be activated by a variety of factors normally defined as extrinsic to the system (e.g., irritating substances), but once activated the system generates patterns of activity that are to a large extent independent of extrinsic factors (e.g., rapid and stereotyped phases of a grooming sequence are difficult to disrupt by peripheral stimulation such as a click or mild electric shock[32]). The balance between intrinsic and extrinsic determinants must be considered from a dynamic point of view[33]. A shift in balance towards more interaction with the environment is characterized by a relatively broad range of influences to which the system is responsive, and a loose organization of behavioural outputs that are easily disrupted (e.g. the behaviour of non-aggressive individuals: a mainly extrinsic behavioural organization). A shift in the other direction results in performance that is less dependent on afferent information and is less easily disrupted by extrinsic factors (e.g., the behaviour of aggressive individuals: a mainly intrinsic behavioural organization); the sequential structure of the system outputs generally increases[32].

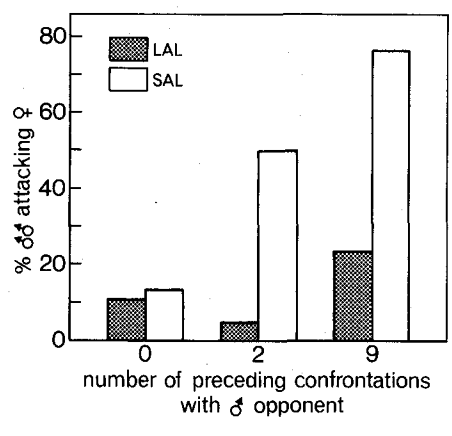

Figure 9. Percentage of LAL and SAL residents that attack their females in relation to the number of preceding confrontations with male opponents.

How fundamental this difference in intrinsic/extrinsic behavioural organization between aggressive and non-aggressive individuals is has been demonstrated in an experiment on re-entrainment to a reversed light-dark (LD) cycle. The circadian activity pattern of an individual is determined on the one side by the pacemaker, an intrinsic factor, and on the other side by the LD cycle, an extrinsic factor. Inversion of the LD cycle causes a gradual adjustment of the activity pattern to the new cycle. The significantly faster rate of re-entrainment in the non-aggressive male mice suggests that their sensitivity to the actual LD cycle (the extrinsic factor) is greater than that of the aggressive mice, which seem to be more dependent upon their endogenous clocks (the intrinsic factor)[13].

Alternative coping styles?

It has been suggested that the active and passive behavioural strategies of aggressive and non-aggressive individuals, respectively, reflect alternative coping styles. Coping can be defined as the mechanism an individual utilizes to meet a significant threat to its stability and to enable it to function effectively, i.e., to maintain control[95]. However, a passive (behavioural withdrawal) response to aversive events has generally been related to a loss or absence of control, both in non-social[67], and social[46], situations. How can this be reconciled with our postulate? The notion that passivity is indicative of a loss of control is based particularly on the marked behavioural effects that are caused by exposure to inescapable shocks, an instrumentally uncontrollable situation, which have been confirmed in a variety of species[67]. The greater passivity of animals exposed to uncontrollable events in comparison to animals exposed to controllable events led to the conclusion that behavioural passivity ensued from experiencing an absence or loss of control. Because of the similarity of the behavioural response of animals exposed to uncontrollable non-social events and that of subordinate animals it has been taken for granted that subordinate animals experience an absence of control. However, a number of objections against this notion can be made.

In the first place, exposure to inescapable shock does not reliably produce behavioural passivity[4,7,10,41,66,81]. Also the data presented have shown that exposure to inescapable shocks does not necessarily result in behavioural passivity, but that individual males show idiosyncratic characteristics in their response patterns that go beyond the instrumental controllability or uncontrollability of a situation (active shock avoidance, inescapable shocks).

There is a second, more fundamental objection to the coupling between behavioural passivity and loss of control. Control is commonly defined as the execution of an active response that alters the occurrence of the aversive event[76,97]. Indeed, the instrumental effect of pressing a lever or shuttling to the adjacent compartment in response to a conditioned stimulus in a shock avoidance task is indisputable, but it is not very often realized that passivity also may have instrumental effects. From an instrumental point of view a passive strategy is based on the possibility that the subject may remain undetected and/or undisturbed and that the source of threat will leave the area itself[87]. The instrumental effect of a passive strategy can clearly be shown in a social situation. We have seen that when confronted with a physically stronger resident male, non-aggressive mice predominantly freeze, whereas aggressive mice mostly flee (fig. 3). However, because of their immobility non-aggressive mice are less often attacked than the fleeing, aggressive mice, as is indicated by the smaller number of fights, which are all initiated by the resident (fig. 10). The instrumental effect, namely to avoid attacks, is (now that the opponents are confined to a cage) more efficiently achieved by adopting a passive strategy than by reacting actively and hence, in this situation, a passive strategy leads to a greater degree of control. But also in a more complex social setting a passive strategy can be successful. By adopting a passive strategy the subordinate animal does not defy the dominant one, and instead of competing, it accepts the situation. This strategy is clearly effective, since the animals live relatively undisturbed[15,54] and continue to gain access to desired goals, such as food, and, occasionally, females[45].

Summarizing, it can be stated that the difference between aggressive and non-aggressive individuals in behavioural response to aversive environmental events cannot be interpreted in terms of control and loss of control. Both the active and the passive strategy may lead to control, and thus represent different coping strategies. In this respect, the distinction Folkman and Lazarus[38] have made between two main modes of coping is of interest. They distinguish problem-focused (P-) and emotion-focused (E-) coping. P-coping entails direct action on the self or on the environment to remove the source of stress, whereas E-coping is aimed at the reduction of the emotional impact of the stress, and functions primarily through psychological processes. Thus, an individual is

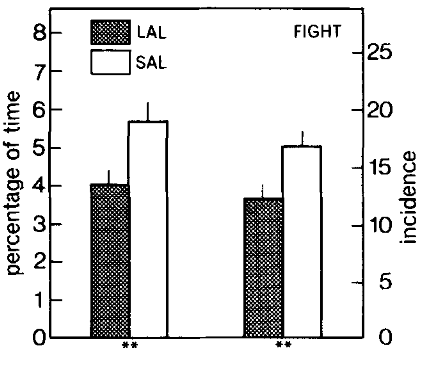

Figure 10. The amount of fighting between a trained fighter and a LAL intruder and between a trained fighter and a SAL intruder, expressed as mean (± SEM) percentage of observation time and mean (± SEM) frequency per observation period.

not only presumed to be coping if its behaviour consists of responses to environmental factors that help it to master the situation, but coping can also include psychological processes that contribute to successful adaptation to the aversive situation[58, 63]. The data presented in this paper indicate that the behaviour of the aggressive rodents is aimed at the removal of themselves from the source of stress or at removal of the source of stress itself, which is suggestive of a P-coping style. It is more difficult to assess the non-aggressive individuals as E-copers, due to the lack of an objective criterion. However, a relationship between behavioural passivity and attenuation of emotional distress has often been suggested[45, 95]. It seems clear, at least, that the behaviour of the non-aggressive males is aimed at an adjustment to the environment rather than at taking action to manipulate the situation. Therefore, it is plausible that the difference between aggressive and non-aggressive individuals can be characterized in terms of alternative coping styles.

The success of the two coping styles is likely to depend upon the variability or stability of the environment, in the context of the differences in organization of behaviour between aggressive and non-aggressive individuals. The exact relationship between coping style and flexibility/rigidity in behaviour remains unclear at present, although there are indications that the neostriatal dopaminergic system is involved in both characteristics[8]. However, a common dimension may be anticipation. Anticipation is closely related to predictability of events. In general, it has been stated that predictability, like controllability, is of fundamental value to an organism[6]. It has not only been shown that animals prefer, for instance, predictable shock conditions over unpredictable ones[6], but it has also been demonstrated that predictability of shock results in less gastric ulceration than does the absence of a warning signal[98]. Many authors find the predictable shock is less aversive for an organism, while many others find the predictable shock is more aversive than unpredictable shock. To explain this discrepancy, Weinberg and Levine[97] relate instrumental control to the concept of predictability. They state that many investigators studying predictability have, in fact, introduced control as a variable into their design. The data suggest that only in situations where animals have some control over shock, may signalled shock be less aversive.

In this respect the 'preparatory response' hypothesis is interesting. This hypothesis suggests that a signal allows the animal to respond in such a way that the shock is made less aversive, for instance by making preparatory postural adjustments during inescapable shocks and thus actually reducing the amount of shock received. In an avoidance condition such preparatory or anticipatory responses will allow the animal to manipulate the aversive event effectively. In fact, a well established active avoidance response is an anticipatory action. This suggests that in the aggressive male mice, with their high propensity to manipulate situations actively, the performance of anticipatory responses is more important than in the emotion-focused coping, non-aggressive mice. Anticipation may be defined as knowledge about the relation of an action to the goal[30]. Routinized behaviour, that starts as an action controlled by knowledge about its relation to the goal, but later on is simply triggered by the stimuli in whose presence it has been repeatedly performed, may contribute to a fast execution of anticipatory responses and hence to effective manipulation of aversive events. The more reluctant behaviour of the non-aggressive mice does not benefit from the formation of a routine. If they are to be able to adjust themselves to a situation, more flexible behaviour – which largely depends upon detailed external information – is indispensible. In conclusion, the differences in routine formation and environmental dependence between the aggressive and non-aggressive mice are consistent with the idea that their respective coping strategies are suited to different environmental conditions.

Active and passive copers in natural populations

A knowledge of the behavioural profiles of aggressive males and non-aggressive males provides an important contribution to a better understanding of the functional significance of both types of individuals in a natural population. Since variation for attack latency is largely genetic in origin[90] (fig. 1), and selection for attack latency generally coincides with selection for coping style and organization of behaviour (data presented on SAL and LAL mice)[8], the bimodal shape of the variation for attack latency in wild house mouse populations[94] (fig. 2) suggests that both the aggressive and non-aggressive individuals, i.e., active and passive copers, are favoured by natural selection. Subsequent research has led to a model for the organization of a house mouse population, and has proposed a selection in favour of the aggressive individuals within a settled deme (i.e., a closed colony), and a selection in favour of the non-aggressive mice under migrational conditions[92].

The active, routinized behavioural strategy of the aggressive mice and the passive, flexible strategy of the non-aggressive animals explain how this is achieved. When introduced into an unfamiliar environment, aggressive male mice, which are easily triggered to attack owing to their active attempt to manipulate situations and to routine formation, pay little attention to the new environment, and are intensively engaged in fighting and chasing all mice they detect. This 'biting off more than one can chew' phenomenon results in great fatigue, a sudden awareness of the unfamiliar surroundings and, therefore, flight[91]. In this situation the behaviour is clearly maladaptive, since it results in a low chance for the aggressive mice of establishing new territories. However, the more passive, non-aggressive individuals gradually explore a new environment, hide when attacked and, finally, are very well able to establish a territory[91]. Once they have settled they are likely to maintain their territory, because intruders usually do not attack territory holders[1,86] and, even if an incidentally trespassing male does attack, the non-aggressive male will fight back effectively and be able to expel the intruder[34].

Within a deme, however, the non-aggressive mice will not be able to establish a territory. In the first place, they are reluctant to initiate aggressive interactions and, in the second place, all mice are living in a familiar environment, which is an advantage to the socially active, routinized, aggressive males. Hence, within a deme the most actively reacting and routine-like males will have the best chances to establish and maintain a territory. On the other hand, under migratory conditions there will be a selection in favour of the non-aggressive mice. They are the ones that are able to establish a new deme. They will be able to reproduce until the most aggressive individuals among their progeny begin to take over territories. A gradual selection in favour of high aggressiveness will be the result. Thus, at least in wild house mice, the existence of active and passive copers has very probably been brought about by natural selection.

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The behavior of the homozygous and heterozygous sub-types of rats which are genetically-selected for diabetes insipidus: A comparison with Long Evans and Wistar stocks

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Abstract. Several aspects of spontaneous and conditioned behavior (food and water intake, locomotion and emotionality, passive and active avoidance acquisition and retention) of standard (albino and pigmented) rats, and rats heterozygous (HEDI) and homozygous (HODI) for diabetes insipidus, are reviewed. As would be expected, HODI rats have been repeatedly found to consume far more fluid than either HEDI or control rats. Pigmented rats appear to be more active than albinos. HODI rats exhibit less marked emotional responses than do control rats, among which the pigmented ones exhibit the highest emotionality. Light aversion is more evident in albino than in pigmented rats. No differences are found among HEDI, HODI and normal Long Evans rats. It is quite difficult to provide a clear-cut statement concerning inter-strain differences in passive avoidance behavior, possibly because of the variety of techniques employed. In any case, HODI rats do not perform worse than normal controls do. In one-way active avoidance paradigms, pigmented rats perform better than albinos, and the performance of HODI rats does not differ from that of controls. In two-way avoidance paradigms, albinos appear to outperform pigmented rats. Once again, there are no obvious differences between HODI and control animals.

In addition to indicating that HODI rats may actually be less emotional than the other groups of rats reviewed here, the studies described once again fail to confirm the previously alleged functions of vasopressin in memory consolidation.

Key words. Homozygous and heterozygous for diabetes insipidus rats behaviors; emotionality; feeding and drinking; locomotion and exploration; passive and active avoidance; Brattleboro rats.

Introduction

Most behavioral research is currently being carried out on inbred or outbred rats obtained from commercial or institutional sources. Broadly speaking, these animals can be divided into albino and pigmented rats, and this chromatic classification already entails important behavioral differences. Indeed, it is widely accepted that the albino locus has quite a number of effects on spontaneous and conditioned behavior. It may be possible that these differences are not exclusively related to the visual system[72, 78] but to other biological features as well. These may include the activity and induction of hepatic microsomal enzymes[41, 42], footshock-induced analgesia[69], sympatho-medullary activity during footshock stress[48], hormonal responses (prolactin, growth hormone, corticosterone) to morphine or stressors[43], kainic acid neurotoxicity[63], brain 5-hydroxytriptamine metabolism[59], ethanol preference[44], and drug and sleep sensitive behavior[37], to mention but a few. On the other hand, there are also significant differences between groups of albino rats, such as differences in the taste reactivity to NaCl shown by Fischer 344 and Wistar rats[33], in parental behavior in virgin female Wistar and Sprague-Dawley rats[40], as well as intra-strain differences in amphetamine-induced rotational behavior of Sprague-Dawley rats from different sources[32].

At present, those engaged in behavioral research are becoming more and more aware of the differences that exist between the several strains of *Rattus norvegicus*, and various strains and stocks are being increasingly selected and bred for specific characteristics. In fact, the genetic background of rats can be manipulated to such an extent that it fits specific research needs[28, 54]. For example, much interest has been aroused by the inter-strain differences which exist between normal Long Evans and homozygous diabetes insipidus rats (HODI) of the Brat-