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INDIVIDUAL DIFFERENCES IN BEHAVIOURAL REACTION TO A CHANGING ENVIRONMENT IN MICE AND RATS

by

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(With 5 Figures)
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Introduction

Wild house mice (*Mus musculus domesticus*) live in groups with a specific social organization called 'demes'. A group occupies a restricted territorial area and within this area a number of males possesses subterritories which they defend against intruders, but also against the other males in the group. Most females, and sometimes a top-dominant male, have more or less free access to the whole area (CROWCROFT, 1966). As a consequence the social environment of a male mouse is highly variable: at one moment it has to act as a dominant and defend its own subterritory, and the other moment it has to be submissive against the top-dominant or against other males when they trespass in their subterritories.

For successful functioning in such a system a highly developed socially adaptive ability is required (BARNETT, 1975; VAN ZEGEREN, 1980). However, from many physiological studies it appears that an individual differentiation exists with respect to the functioning in a social system. HENRY & STEPHENS (1977) showed a difference in the occurrence of hypertension between dominant and subordinate males in a mouse colony in which the dominants suffered from hypertension. In rats, which live in a social structure comparable to that of the house mouse, it was demonstrated that hypertension mostly occurred in those animals that took a position just below the top-dominant in the social hierarchy (the sub-dominants). But also top-dominants in a socially unstable situation, in which it was difficult for the top-dominant to maintain its position, developed hypertension (ALEXANDER, 1974; FOKKEMA, 1985).

MANUCK *et al.* (1983) demonstrated comparable results in cynomolgus monkeys. He 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 condition.

So, especially in socially unstable situations, a clear differentiation in the occurrence of stress pathologies is shown. Since a socially unstable situation is characterized by many changes in the social environment, it can be imagined that this differentiation is due to a fundamental difference between dominant/sub-dominant and subordinate animals in their reaction to a changing (social) environment. One difference between dominant and subordinate males is the level of aggression, as it is shown by the existing significant positive correlation between aggression and social position in a rat colony (FOKKEMA, 1985). Hence, it can be theorized that the supposed difference between dominant and subordinate males in their reaction to a changing environment may be better analysed from the comparison between aggressive and non-aggressive individuals. VAN OORTMERSSEN *et al.* (1985) demonstrated that aggressive and non-aggressive house mice indeed differ behaviourally in their reaction to changes in the social environment. When six males were released simultaneously in a new area, starting from familiar home cages, the aggressive males soon left their home cages, actively explored the new environment and furiously attacked every mouse they met. However, it was also often seen that they suddenly changed their behaviour into flight, possibly because they had lost contact with familiar ground. Non-aggressive males were much more cautious and after leaving their home cage they tended to return to it regularly. In this way they became gradually acquainted with the new surroundings and knew where to hide when attacked.

In order to investigate whether this differentiation between aggressive and non-aggressive individuals in a social situation reflects a more general and fundamental difference, we tested mice as well as rats in three experiments in a non-social situation. To measure the behaviour in such a situation a simple maze was used in which intra-, extramaze cues or the configuration of the maze could be changed.

Experiment 1

Introduction.

In a first experiment aggressive and non-aggressive male mice were tested on their reaction to a single change in a formerly invariable non-

social situation. Aggression is expressed as an attack latency score and this has shown to be a reliable indicator of aggressiveness (VAN ZEGEREN, 1980).

An invariable situation was realized by repeatedly letting the males run through a standard configuration of a Hebb-Williams type maze. After considerable training an extramaze or intramaze change was introduced and the reaction to such a change was measured.

Material and methods.

Subjects.

Males from a wild house mouse (*M. m. domesticus*) line were used in this study. This line is an outbred population descending from feral mice caught in the neighbourhood of Groningen in 1971 and since then maintained in our laboratory.

The mice were housed in plexiglass cages (17 × 11 × 13 cm) in a room with reversed light/dark cycle (dark from 12:30 p.m. to 12:30 a.m.). Food (standard pellets: Hope Farms AM 2) and water were available *ad libitum*. At weaning age (3-4 weeks) the litters were separated from their parents. At the age of sexual maturity (6-8 weeks) the animals were established in heterosexual pairs.

At the age of 14 weeks the males were tested for their attack latency score (see VAN OORTMERSSEN & BAKKER, 1981). On the basis of this score two groups were selected, one with scores of more than 500 seconds and one with scores of less than 100 seconds. The slow-attacking (SA) group consisted of 23 males with a mean attack latency (AL) of 594.3 ± 5.7 seconds[1]). The fast-attacking (FA) group comprised 18 males with a mean attack latency of 55.0 ± 6.5 seconds.

Apparatus and testing procedure.

The maze used in this study was similar in design to the closed-field apparatus described by RABINOVITCH & ROSVOLD (1951). It was constructed of grey plexiglass and measured 18 × 18 × 7 cm. The maze was enclosed by transparent plexiglass in order to prevent the mice from jumping out. The configuration of the maze was constructed by means of (interchangeable) barriers of different length. Start- and goalbox consisted of plexiglass cages of 17 × 11 × 13 cm with an entrance alley.

Within three weeks after the AL test, the males were tested in the maze. Behavioural training and testing sessions were carried out between 13:00 and 16:00 hr, just after onset of the dark period during which the room was lit by two 15 Watt bulbs.

Previous to training the mice were brought at 85-90% of their ad libitum body weight. After this was accomplished the mice were subjected to maze running for three times a day; one trial per hour. In order to avoid disturbing the animals by handling the males were permitted to move freely from their home cage to the startbox. After this their home cage served as goalbox in which they received a food reward (Smith's chipito, ± 5 mg) provided that they entered it within the permitted time (see below). Subsequent to the three trials the mice were weighed and got their restricted diet.

Experimental design.

The configuration and error zones of the maze used in this experiment are shown in Fig. 1. The mice were trained to run without fail through this maze after which a change was

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[1]) All group values are expressed as mean ± sem.

introduced either extramaze or intramaze. The well structured environment was kept constant during the experiment. At the start of the training the mice had no experience with the maze. The time allowed for reaching the goalbox was maximally 10 minutes in the very first trial and maximally 3 minutes in all subsequent trials. The criterion for good performance was to fulfil a run errorless and within 15 seconds, or as there were some individuals which made every trial again the same (stereotyped) error, to fulfil 5 runs in which only that particular error was made, each within 15 seconds. Following the trial in which the criterion was attained a change was introduced. In experiment 1.a. extramaze cues were manipulated by turning the maze 90° with respect to the environment. In experiment 1.b. an intramaze cue was changed by sticking a piece of tape to the floor of the maze (see Fig. 1). The mice were tested only once in the changed situation, after which the original condition was reestablished and the final trial was carried out. In all trials the latency of reaching the goalbox and the number of errors were measured.

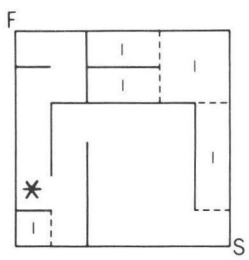

Fig. 1. Standard maze configuration with error zones, broken lines indicate error zone limits. An error is counted when the broken line has been passed with at least two paws. * indicates the position of the tape fragment in experiment 1.b. S = startbox. F = food reward in goalbox.

Results.

The results are summarized in Fig. 2. Through all training trials it took the SA-mice significantly more time to reach the goalbox than the FA-mice (Mann Whitney, $U = 108$, $p < 0.01$). The mean latency of the SA-group was 57.9 ± 7.0 s, during which on average 5.6 ± 0.7 errors were made, whereas that of the FA-group was 33.7 ± 5.8 s. Mean number of errors for the FA-group was 4.0 ± 0.5 which was not significantly different from the SA-group.

A differentiation between the two groups was already clear cut in the first training trial, which was the first experience of the mice with the maze. Compared to the FA-group with a mean latency of 125.9 ± 24.3 s the SA-group had a rather high latency of 219.6 ± 34.3 s (M.W., $U = 129$, $p < 0.025$). The number of errors in this first trial exhibited a similar picture. The FA-group entered on average 12.6 ± 2.3 error zones

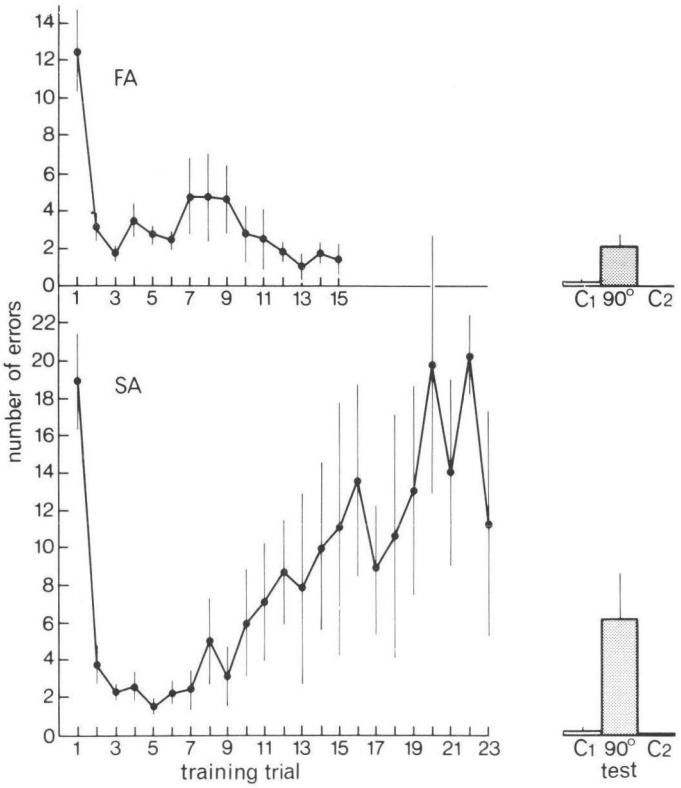

Fig. 2. Mean number of errors of a fast-attacking (FA) and slow-attacking (SA) group in the successive trials of a standard maze task and the reaction to the 90° turning of the maze, compared to the trial in which the criterion was attained (C1) and the trial in which the original situation was reestablished (C2).

and this differed significantly from the SA-group (M.W., $U = 143$, $p = 0.05$) which made 18.9 ± 2.5 errors on average (see also Fig. 2).

In the second trial both the FA-group and the SA-group have a much shorter running time and make far fewer errors compared to the first trial, but the decline in latency and in number of errors between the first and second trial is much larger in the SA-group than in the FA-group.

The final part of the performance curve again discriminates clearly between both groups (see Fig. 2). The FA-group shows a steady decline in latency and number or errors, whereas the SA-group after an initial decline exhibits a strong increase in both latency and number of errors. Not only the larger inter-individual variation is responsible for the fluc-

tuations in the curve of the SA-group compared to the FA-group, but also the larger intra-individual variation.

a) *Change in extramaze cues.*

The FA-males achieved the criterion in a mean number of 7.6 ± 1.0 trials which did not differ from the mean of 7.5 ± 0.9 trials for the SA-group. Whether the criterion was reached by an individual early in training of after more experience in the maze did not have any influence on its performance in the shifted position.

In the trial previous to the shift (trial C.1) there was as would be expected in view of the criterion no difference between the SA- and FA-group. The change in position of the maze caused an increase in latency and number of errors in both the SA- and the FA-group (see Fig. 2), but the increase in the SA-group was significantly larger (M.W., latency: $U = 68$; errors: $U = 70$, $p < 0.02$) than in the FA-group. After the maze had been returned to its original position (trial C.2) both groups returned to the level of trial C.1 although there was a slight but significant trend to execute the task somewhat faster in trial C.2 compared to trial C.1 (Wilcoxon matched-pairs, SA: $T = 23$, $p < 0.01$, FA: $T = 23$, $p < 0.025$).

b) *Change in intramaze cues.*

This experiment was carried out with 30 male mice; 14 SA-males and 16 FA-males. The results are even more salient than in the former experiment. In the FA-group there was no increase in number of errors or latency due to the tape stuck on the floor of the maze (see Fig. 3) whereas in the SA-group a strong increase in especially latency, but also in number of errors followed the change in intramaze cues. The latency increased from 4.9 ± 0.7 seconds to 36.2 ± 6.4 s and then diminished again to 6.9 ± 1.3 s. The FA-group exhibited in all three trials the same latency, 5.1 ± 0.7 s in trial C.1, 5.4 ± 1.0 s in the experimental trial and 3.6 ± 0.4 s in trial C.2, respectively. The difference between both groups in the trial with the change in intramaze cues was highly significant (M.W., $U = 32$, $p < 0.01$). The same held for the number of errors (M.W., $U = 27$, $p < 0.01$) which remained almost zero for the FA-group and showed an increase for the SA-group from 0.1 ± 0.1 to 3.9 ± 0.7 after which it returned to 0.1 ± 0.1. The difference between both types of males could easily be observed. The aggressive males ran blindly across the tape fragment or sniffed at it very shortly, whereas the non-aggressive males hesitated to cross the tape fragment.

Discussion.

It is concluded that also in a non-social situation aggressive and non-aggressive individuals differentiate in the way in which they react to a change in environment. Aggressive males perform very constantly in a standard maze configuration during training and show hardly any increase in latency to run and number of errors during these runs to reach the goalbox when a change, whether extramaze or intramaze is introduced. This is contrary to non-aggressive males whose performances are very variable during training and easily influenced (disturbed) by changes in the environment.

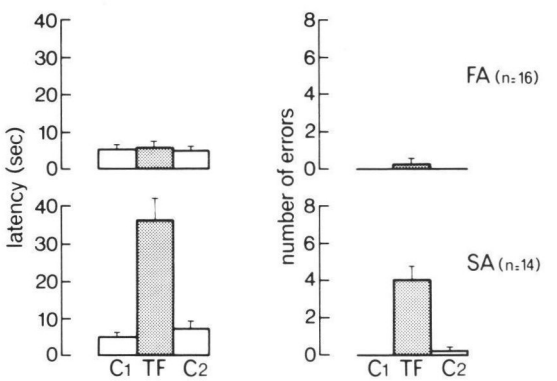

Fig. 3. Reaction of a fast-attacking (FA) and slow-attacking (SA) group to a tape fragment (TF) stuck to the floor of the maze, expressed in terms of latency and number of errors.

The difference in the performance curves between the FA- and SA-group does not refer to a difference in learning ability, but seems to reflect a difference in the amount of exploration between the two groups. In the first trial the goal of the maze running is unknown and consequently the behaviour of the males can only be considered as a reaction to a novel environment. In our interpretation the less aggressive animals show more exploration in a new environment than aggressive individuals which is in concordance with the findings of VAN OORTMERSSEN *et al.* (1985). Also the rising performance curve of the SA-group indicates that non-aggressive animals have a strong tendency to explore, even in a familiar environment. That the SA-animals actually acquire information about the environment which they use in subsequent behaviour is proven by the larger decrease in latency (between the first and second trial) com-

pared to the decline in the FA-group. The reason that the non-aggressive males do not sustain the short latencies can possibly be found in the fact that exploration itself can function as a reward (MONTGOMERY, 1954). Both the opportunity to explore and the access to information may be important determinants of behaviour (COWAN, 1983).

In solving a maze task rodents utilize extramaze cues as well as intramaze cues, but many studies point to a major role of extramaze cues and a minor concern of intramaze ones (OLTON & SAMUELSON, 1976; SUZUKI *et al.*, 1980; O'KEEFE, 1983), although it is known that odour trails are able to improve performance in a maze (DAVIS, 1970; MEANS *et al.*, 1971; OLTON & COLLISON, 1979). However, little is reported about individual differences in using extramaze or intramaze cues. But the very similar results in the experiments with either type of cues prove that the difference between aggressive and non-aggressive males is not caused by a differential use of extra- and intramaze cues. Another explanation for the disparity between aggressive and non-aggressive males seems more likely. 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 mice is fairly routine-like. During the repeated execution of the maze task they probably built up a routine and consequently do not react to changes in the environment. The non-aggressive individuals omit the upbuilding of a routine and seem to keep up with every detail of the environment and hence react to the extra- as well as intramaze changes.

Experiment 2

Introduction.

In experiment 1 it was shown that aggressive male mice during training in a standard configuration of a maze and during the introduction of a change in the environment made fewer errors than non-aggressive individuals. It is suggested that the cause of this difference in performance can be found in the differential extent of routine-like behaviour. The hypothesis that the good performance of the aggressive males is due to their routine-like behaviour (and consequently their relative inattention to the surroundings) is tested in the next experiment. If the hypothesis is legitimate it must be expected that in a maze task which prevents the upbuilding *c.q.* use of a routine the aggressive mice will perform worse than the more attentive non-aggressive animals. We created

such a situation by means of presenting aggressive and non-aggressive males every day a different configuration of a Hebb-Williams type maze.

Materials and methods.

Subjects.

Origin and housing conditions of the mice were the same as in experiment 1. Once again two groups of males were selected on the basis of their attack latency score. The fast-attacking group had a mean AL of 76.8 ± 18.6 s while the slow-attacking group had on average an AL of 591.0 ± 9.0 s. Both groups consisted of 10 individuals.

Apparatus and testing procedure.

The maze used in this experiment was the same one used in the first experiment. The various configurations could be created by use of interchangeable barriers of different length. The testing procedure was exactly the same as in experiment 1.

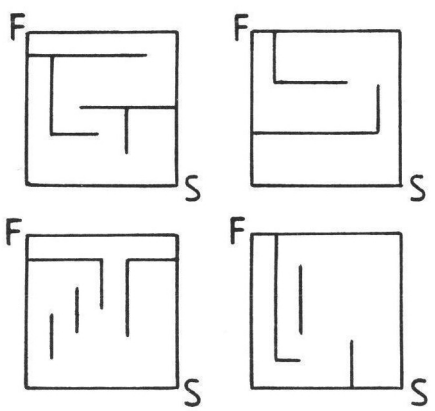

Fig. 4. Some examples of configurations of the Rabinovitch & Rosvold procedure. S = startbox. F = food reward in goalbox.

Experimental design.

The configuration used in this experiment and the matching error zones are described by RABINOVITCH & ROSVOLD (1951). A few examples are shown in Fig. 4. Prior to testing the mice were taught where to find the goalbox (diagonally facing the startbox). At the same time the mice got adapted to the maze and established the habit of eating the food reward. This was accomplished in 4 practice problems (A, B, C, F in RABINOVITCH & ROSVOLD, 1951), in 3 trials per practice problem. Then the actual testing started. On twelve consecutive days the mice were tested in the twelve different test problems, each three trials a day. The time permitted per trial was maximally 3 min after which the mouse was removed from the maze. In all trials the latency of reaching the goalbox and the number of errors were measured.

Results.

The FA-group produced almost twice as many errors as the SA-group, on average 22.9 ± 3.4 and 12.6 ± 0.8 errors per test problem, respectively. This is a significant difference (M.W., $U = 9$, $p < 0.01$). The individual trials of the test problems show a similar disparity (see Fig. 5). Both in the first, second and third trial a significant difference existed between aggressive and non-aggressive males (M.W., $U = 17$, $U = 18.5$ and $U = 10$, $p < 0.01$, respectively). The decrease in number of errors between the successive trials within a test problem due to learning effects was equivalent in both groups.

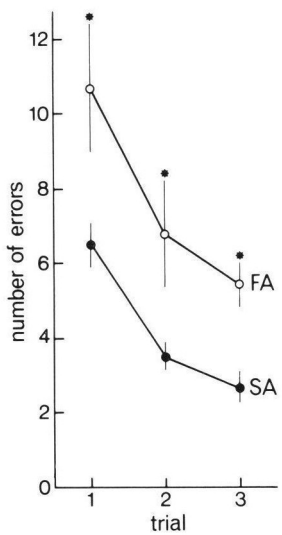

Fig. 5. Mean number of errors per trial made in 12 different maze configurations by a fast-attacking (FA) and a slow-attacking (SA) group.

The separate test problems differed in the extent to which they discriminated between the aggressive and non-aggressive group. Nine test problems discriminated clearly between both groups, while three test problems (tests 3, 6 and 12) did not discriminate between FA- and SA-males. In all nine discriminating configurations the SA-group made significantly less errors than the FA-group. So the FA-males always performed worse than or at the utmost equally to the SA-group. Hence the relationship between aggression and number of errors shown in this experiment is not caused by certain specific configurations, but must be viewed as a rather general phenomenon.

Discussion.

By testing the animals every three trials in a different configuration it is hardly possible for them to find their way in the maze in a routine-like fashion. Every day the way to the goalbox must be reconstructed by means of environmental stimuli whether intramaze (the locations of the various partitions, the angles between alleys and the distances between choice points) or extramaze (beacons in the surroundings of the maze). The expectation that in such a situation the aggressive males will perform worse than the non-aggressive males is clearly confirmed. Without the possibility to find their way in a routine-like fashion the aggressive animals make more errors compared to the non-aggressive ones. This shows that the non-aggressive males rely to a lesser extent on a routine and are better able to reconstruct the way in the maze, possibly on account of their higher attentiveness to details of the surroundings.

The difference in routine-like behaviour between aggressive and non-aggressive males can be viewed as the extent to which their behaviour is intrinsically organized or is controlled by external factors. FENTRESS (1976) 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 for 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 substance) 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, FENTRESS, 1976). The balance between intrinsic and extrinsic determinants must be considered from a dynamic point of view (FENTRESS, 1980) as the relative importance of central and peripheral factors can differ from one context to another (mice with denervated faces show considerable distortions of normal grooming patterns when tested in their home cage but show normal grooming patterns when tested in a small novel environment).

Thus behaviour is controlled by both intrinsic and extrinsic factors, but the relative contribution of these factors does not remain constant, but varies for instance from one context to another. It is then possible that the shifting priorities between intrinsic and extrinsic behavioural control exhibit individual differences. In our case this means that aggressive males soon shift to intrinsically organized behaviour, whereas

non-aggressive individuals tend to stay dependent on and be influenced by extrinsic factors.

The data obtained in this study are in full agreement with the view of a differential intrinsic/extrinsic behavioural control. In experiment 1 the long latency in the first trial, the fluctuating performance during training, the easily induced disturbance and in experiment 2 the good performance in a continuously changing environment can be explained by a mainly extrinsic behavioural control of the less aggressive individuals. The rather constant execution of the standard maze task by the more aggressive animals, their relative insensitivity to minor changes and their relative incapacity to find the way in a more continuously changing maze refer to a mainly intrinsic control of their behaviour.

Experiment 3

Introduction.

In the previous experiments it is shown that aggressive and non-aggressive male mice behaviourally differ in their reaction to a change in the environment. The question arises whether this phenomenon found in mice is a general one, that is, whether it also holds for other species. This question is answered in the next experiment in which the previously described experiments 1.a. and 2 are repeated with laboratory rats (*Rattus norvegicus*) which live in a social structure comparable to that of the house mouse.

Material and methods.

Subjects.

Males from the Tryon Maze Dull-S3 rats (originating from Cpb TNO, Zeist, The Netherlands and bred in our laboratory) were used.

After weaning (at the age of one month) standard groups of 8 males per cage were formed. Two weeks before the aggression test a male was paired with a female and was allowed to establish a territory in a cage of 84 × 60 × 50 cm. The cages were located in a room with a reversed dark/light cycle (dark from 9:00 hr till 21:00 hr).

At the age of 5-7 months the males were tested for their aggression score (see KOOLHAAS *et al.*, 1980) in a resident-intruder situation.

In all situations food and water were available ad libitum.

Apparatus and testing procedure.

The maze was similar in design to the maze used in the former mice experiments. However, it was constructed of wood and measured 60 × 60 × 25 cm. The maze was covered with wire-mesh in order to prevent the rats from walking across the walls to the goalbox. Start- and goalbox measured 20 × 45 × 25 cm.

Directly following the aggression test the males were tested in the maze. Behavioural training and testing sessions were carried out between 9:00 and 12:00 hr, just after onset

of the dark period. Previous to each training or testing session (6-12 trials a day) the rats were deprived of food for 17 hours.

The rats were put in the startbox and removed from the goalbox by hand. The food reward per trial consisted of two Sumelpo-pellets of 52 mg. Immediately after the training or testing session the rats were allowed to eat for 5 hours after which they were deprived till the next session 17 hours later.

Experimental design.

Change in extramaze cues.

The configuration and error zones of the maze were the same as in experiment 1.a (see Fig. 1). In 12 trials a day the rats were trained to run through the maze until they showed no more decrease in mean latency during 4 consecutive days. The time allowed for reaching the goalbox was maximally 3 min. After reaching criterion the maze was turned 90° with respect to extramaze cues and the rats were tested 4 times in the changed position.

In all trials the latency of reaching the goalbox and the number of errors were measured.

Rabinovitch & Rosvold procedure.

The configurations, error zones and procedure were exactly the same as in experiment 2 with the exception that the rats in contrast to the mice were tested in two different test problems per day over 6 consecutive days (that is 1 trial per half hour in stead of 1 trial per hour).

Results.

Change in extramaze cues.

The aggression score, expressed as the percentage of time spent on aggressive behaviour in a 10 min test, of the males in a first group ($n = 10$) varied from 9.6% to 47.9%. A second group ($n = 10$) had aggression scores of 0.1% to 32.9%. Only a correlation coefficient between aggression score and performance during the test can be given since extreme groups are not selected.

A significant negative correlation is found between the aggression score and the increase in number of errors made in the shifted position compared to the original (standard) position. The same holds for latency. This indicates that the more aggressive males are less affected in their performance by the change in position of the maze. The Spearman rank coefficients for the correlation between aggression score and increase in number of errors and increase in latency are -0.70 ($p = 0.02$) and -0.64 ($p < 0.05$), respectively. Similar results are obtained in the second group. The Spearman rank coefficient for the correlation between aggression and increase in latency in the shifted position amounts to -0.87 ($p < 0.01$).

Rabinovitch & Rosvold procedure.

The ten rats used in this experiment varied in aggression score from 2.4% to 43.3%. The significant positive correlation between aggression score and mean number of errors over all test problems ($r_s = 0.78$, $p < 0.01$) indicates that the more aggressive animals perform worse in the continuously changing environment than the less aggressive rats. The number of errors made per test problem ranged from 12.3 to 31.1 with a mean of 22.7 errors.

Discussion.

As is stated before for mice, the differentiation in aggression reflects a differentiation in behavioural reaction to a changing environment. The more aggressive animals react to a lesser extent to a change in a formerly constant environment, while the less aggressive individuals perform better in a continuously changing environment. The identical results obtained in this rat experiment indicate that the relation between aggression and behavioural reaction to a changing environment has more general validity. The underlying mechanism by which the relation may be explained is that of the organization of behavioural control which (like FENTRESS (1976) already expressed) is based upon two fundamental principles, namely interaction and self-organization. The behaviour of aggressive individuals is then more determined by self-organization whereas the behaviour of non-aggressive males is more dependent on interaction with external cues.

Discussion

Many studies reveal a relation between aggression and other behavioural components. LAGERSPETZ (1964) selected for high (TA-strain) and low (TNA-strain) aggression in mice, but she also found that the TA-strain was more active in the open field and defecated less in aggressive encounters than the TNA-strain. BRAIN & NOWELL (1969) found a significant correlation between aggression and ambulation in the open field in mice. Two strains of Hull's selected rats on low and high emotional reactivity turn out to be differentiately aggressive; the low emotional reactive strain being more aggressive than the high emotional reactive strain (ANNEN & FUJITA, 1983). The Roman high and low avoidance rat strains (selected for active avoidance in a shuttle box) not only show to be differentially active in the open field (RHA being more active than RLA,

BIGNAMI, 1965), but also are differentially aggressive (RHA being more aggressive than RLA, KOOLHAAS, unpubl. obs.).

Most of these differences between aggressive and non-aggressive animals are explained in terms of emotionality. However, in the view of the present experiments it is likely that this differentiation in emotionality once again reflects a differentiation in the extent of intrinsic versus extrinsic behavioural control and thus in the way in which an animal reacts to changes in its environment. Hence, aggression is correlated with a more general tendency to react in a specific (rather routine-like) way to changes in the environment. So far, the causal relationship between the two is unclear.

The differentiation in reaction to a changing environment may have important consequences for the functioning of the animals in a social setting. It is already stated that aggressive male mice in a new environment (for instance under emigratory conditions) exhaust themselves by attacking and chasing every other mouse (VAN OORTMERSSEN *et al.*, 1985). One might say that they react very routine-like to the presence of other males. The consequence of this blind attacking behaviour is that finally not the aggressive, but the non-aggressive males succeed in establishing territories in the new area. Thus the differentiation in behavioural reaction to a new situation is reflected in the successfulness of functioning in this situation.

Also in a more settled situation, a stable colony of rats, aggressive and non-aggressive males differ in their reaction to the other members of the colony. The main behavioural strategy of aggressive males is characterized by threatening postures, approach and flight behaviour (KOOLHAAS *et al.*, 1985). If aggressive rats react in a routine-like way to the presence of other males this implies that they will not only attack and threaten subordinate and subdominant males, but also the top-dominant. The result of this is that the aggressive males in a colony are more often attacked and threatened by the top-dominant than the non-aggressive males. The non-aggressive males avoid confrontations with the top-dominant and live relatively undisturbed (KOOLHAAS *et al.*, 1985). The more frequent attacks and threatening postures have their impact on the physiology and the occurrence of hypertension which points to a malfunctioning of the more aggressive (subdominant) males (FOKKEMA, 1985).

Concluding we can say that non-aggressive individuals seem to be more attentative to their environment (due to their extrinsic behavioural control). In a situation which asks for adaptation to changes this seems

to result in a more successful functioning; the non-aggressive males are the ones that exploit new areas and in a colony they can live relatively undisturbed and mostly without developing stress pathologies.

Future research will focus on a more exact characterization of the extent of routine-like behaviour of aggressive and non-aggressive individuals and on the relative contribution of genetic and ontogenetic factors in the development of this differentiation in behavioural control.

Summary

Aggressive and non-aggressive male mice differ in their reaction to a changing social environment. In order to investigate if this differentiation holds also for non-social situations male mice are trained in a standard maze task, whereafter a change (extramaze and intramaze, respectively) is introduced. The results indicate that aggressive males fulfil their task fairly routine-like and do not react to a change which is in contrast to the non-aggressive individuals.

In a second experiment a more continuously changing situation is created by testing the animals every 3 trials in a different maze configuration. In this situation in which a routine cannot be developed *c.q.* used, the aggressive males performed worse than the non-aggressive animals. It is suggested that the behaviour of aggressive males is mainly controlled by intrinsic factors whereas the behaviour of non-aggressive males is more dependent on external factors.

Similar results are obtained when repeating the experiments with rats. This indicates that the relation between aggression and behavioural reaction to a changing environment has more general validity. The possibly underlying mechanism is discussed as well as the consequences for the functioning of the animals in a social setting.

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Zusammenfassung

In einer sich verändernden sozialen Umgebung zeigen aggressive und nicht aggressive Mäuse verschiedenartige Reaktionen. In der vorliegenden Arbeit ging es darum zu untersuchen ob diese divergenten Reaktionen auch in nicht sozialen Situationen auftreten. Zu diesem Zweck wurden männliche Mäuse in einem Standard-Labyrinth trainiert. Nach der Gewöhnung wurde eine Veränderung im Labyrinth oder dessen Umgebung angebracht. Aus den Befunden dieser Testes wurde der Schluss gezogen, dass das Verhalten aggressiver Mäuse, im Gegensatz zu dem Verhalten nicht aggressiver Mäuse, stark durch Routine, nicht jedoch durch Veränderungen der Umgebung bestimmt wird.

Eine nicht kontinuierlich verändernde Umgebung wurde in einem folgenden Experiment verwendet, wobei der Labyrinthaufbau nach jeweils drei Durchgängen variiert wurde. In dieser das Erlernen bzw. Ausführen von routinemässigem Verhalten unterbin-