

Visual discrimination learning in spontaneously hypertensive (SHR) and Wistar normotensive rats: computerized analysis of choice strategies

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Abstract. Spontaneously hypertensive rats (SHR) were found to learn a visual discrimination paradigm better than Wistar normotensive rats (NT). The present analysis of choice strategies used by rats was performed to detect possible correlates between patterns of responding and duration of learning. The following strategies were included into the analysis: perseveration and alternation of choice (response-set hypotheses), win-stay lose-shift and win-shift lose-stay (prediction hypotheses). A computer programme called "The Thinking Rat" was written to analyse rat strategies during the learning. The analysis was applied for two irrelevant dimensions of stimuli, i.e. position and orientation, and for colour as a relevant cue. SHR solved the task using different strategies than the NT rats. All subjects began by responding to position as a cue, but SHR gave up this strategy more quickly than NT rats did and responded earlier to colour. NT rats showed a strong preference to persevere in their choices with respect to stimulus position, whereas SHR used more frequently the prediction hypotheses with respect to colour. The analysis of performance and the analysis of choice strategies could indicate that the discrepancy in learning between SHR and NT rats may be caused by differences in attention.

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Key words: SHR, discrimination learning, attention, computerized analysis of behaviour

INTRODUCTION

We have earlier found that spontaneously hypertensive rats (SHR) perform better on a visual discrimination task, as compared with normotensive Wistar rats (NT). SHR committed fewer errors than NT rats when discriminating between black and white stimuli. The retention scores were also better in SHR than in the NT group. A most pronounced difference between the strains was observed in reversal learning, with SHR needing fewer trials to achieve the criterion than in acquisition, and NT rats learning slower in the reversal than in the acquisition stage (Łukaszewska and Niewiadomska 1995).

It is likely that these differences in performance were due to differences in strategies used by rats to solve the problem. Many investigators suggest that, in various behavioural tests, rat responses are not random, but are based on different strategies. For instance, when unstressed normal rodents are given two consecutive trials in a T-maze, they typically alternate choices (Dember and Earl 1957, Means et al. 1974), i.e., display a spontaneous alternation phenomenon. Rats readily acquire food-reinforced alternation (win-shift) responses (Means et al. 1971). Also, when given a choice, they typically enter a novel, previously unavailable alley rather than an alley in which they have obtained reinforcement (Means et al. 1974). In the radial-arm maze rats prefer to respond according to a win-shift rather than to a win-stay schedule (Gaffan and Davies 1981). Rats selected and used various strategies when trained to solve nonspatial visual discrimination problems in a swimming pool (Whishaw and Petric 1988).

Krechevsky (1932) noticed that in visual discrimination tests rats utilize some strategies in their choices trying to obtain the highest possible reinforcement. "Learning", according to Krechevsky (1938, p.532), "consists of changing from one systematic, generalized, purposive way of behaving to another and another until the problem is solved". When animals are given visual discrimination training in an apparatus similar to ours, the position of

stimuli is always an irrelevant cue. Rats learning visual discrimination tests are obviously guided by the position of the stimuli. Krechevsky (1938) reported that position habits are a common feature of rats, especially in the initial stage of discrimination learning. Other authors have also noted that rats are particularly prone to respond for long periods of time to an irrelevant position cue. Krechevsky (1938) proposed that task acquisition could be divided into a presolution and a solution phase. In the presolution phase, animals experiment with various "attempted solutions" from which an appropriate behavioural pattern is eventually selected. These systematic behaviour patterns were named by Krechevsky "hypotheses". Thus, in the presolution phase, rats were not actually learning a discrimination, but rather selected a strategy that could be used to solve the task.

Levine (1959) analysed a specific behaviour of rats in the visual discrimination test. He distinguished four different position related patterns of this behaviour: (1) position perseveration hypothesis, (2) position alternation hypothesis, (3) win-stay, lose-shift hypothesis, and (4) win-shift, lose-stay hypothesis. These four hypotheses were frequently observed in discrimination learning paradigms (Fellows 1967). Other theoretically plausible strategies have not been experimentally assessed.

The main difficulty in discriminational paradigms is the possibility that animals could respond toward an irrelevant cue or an irrelevant dimension of the stimuli presented. An irrelevant cue in discrimination learning is a cue which, if used to guide behaviour, cannot lead to the solution of the problem. It is important to present stimuli in a way that prevents the animal's preference of any incorrect behaviour. Satisfactory presentation of positive discriminative stimuli should ensure a chance level of performance from any of the wrong hypotheses and minimize the reinforcing effect of these hypotheses. This was done by Fellows (1967) by a set of sequences, which was used to establish the order of the stimuli presentation in this experiment.

During colour discrimination training we observed some differences between SHR and NT

strains in the way rats attempted to solve the test. The NT rats seem to reveal a stronger tendency than SHR to persevere in their responses directed by the position of the stimuli. Thus, we have analysed more formally strategies used by rats of both strains during discrimination learning. The purpose of this analysis was to find possible correlates between different patterns of response and differences observed in both strains, as well as in the number of errors and trials required to reach the criterion.

METHODS

Experimental procedure

Twenty male spontaneously hypertensive (SHR) Wistar-Kyoto and 20 normotensive Wistar rats served as subjects. The experiment was performed in two different age groups, in 3-month-old and 10-month-old, both SHR and NT rats. The visual discrimination paradigm involved two visual dimensions: the colour of stimuli (black vs. white) and their orientation (vertical vs. horizontal), and one directional dimension: the left or the right side of stimuli presentation in the testing apparatus. In each trial, a black vertical rectangle was paired with a white horizontal one, or a black horizontal rectangle was paired with a white vertical one. Orientation of the stimuli and their position were irrelevant cues, while colour of the rectangle was the relevant cue. The position and orientation of positive stimuli (i.e., of a black or of a white bar) varied randomly within sessions. Twelve trials were given per day until a criterion of 22 correct responses on two successive days was reached, so that no more than 1 error per day was committed. The experiment consisted of three stages: (1) acquisition (Ac), (2) retention (Rt) and (3) reversal (Rv). After completion of the visual discrimination, the rats were left undisturbed in their home cages for 60 days. The rats were then tested for the retention of the previously acquired training. The day after the criterion was reached in the retention test, the rats were subjected to reversal training, where the entire procedure was repeated but the stimuli values were reversed.

TABLE I

Position hypotheses				
Hypothesis	Strategy	Response	Outcome	Response
Position	win-stay	1	+	1
	lose stay	1	-	1
Position alternation	win-shift	1	+	2
	lose-shift	1	-	2
Win-stay, lose-shift	win-stay	1	+	1
	lose-shift	1	-	2
Win-shift, lose-stay	win-shift	1	+	2
	lose-stay	1	-	1

(according to Levine (1963))

The rat's response in every trial was noted as a left or right choice. Comparing the series of such responses with the pattern of stimuli (i.e., position of black and white colour and position of horizontal and vertical bar) and with the position of the reward in particular trials, we can find if rats use some hypotheses related to stimuli modalities.

We applied the sequences for the positioning of the positive stimuli as proposed by Fellows (1967). These sequences secure not more than 50% reinforcement in a session for any possible irrelevant hypothesis, and therefore induce rats to try another strategy until the proper one is found. The present analysis tested four hypotheses described by Levine (1963), shown in Table I. We searched for evidence of usage of these hypotheses within each class of stimuli, i.e. position (left, right), colour (black, white), and orientation (horizontal, vertical).

The "Thinking Rat" programme

The analysis of rats responses was performed after the completion of the behavioural task. The search for hypotheses possibly used by the animals was accomplished with a computer programme (an off line analysis) designed by us specifically for this purpose. The source programme is available to

those interested. The programming language used was Turbo-Basic and the programme was named by us the "Thinking Rat". Inputs to the programme were: sequence of the stimuli presented (i.e., position of black and white stimuli and position of horizontal and vertical stimuli), sequence of rat responses in consecutive trials, and designation of a colour associated with the reinforcement.

Every 12 trial session was examined with respect to 12 hypotheses (i.e., for each of three stimuli dimensions, four kinds of hypotheses were analysed: perseveration, alternation, win-stay lose-shift, and win-shift lose-stay) and every hypothesis was searched independently of the others.

According to the stimuli sequence used, the programme generated a sequence of theoretical responses compatible with the given hypothesis. Starting from the first trial, the response generated by the hypothesis was compared with the rat's actual response. If both responses were the same, the procedure was repeated for the next trial. If there was no match or the end of the session was reached the procedure was stopped. Six consecutive rat's choices identical with the theoretical sequence of choices according to the given hypothesis were necessary for a subject to be scored as testing the hypothesis. Thus, only six-trial or longer sequences of rat's responses were scored. The first nonmatching pair of theoretical responses and actual rat's response was checked in the same way and if not less than 6 consecutive pairs were identical, the next score was recorded. Consequently, for any hypothesis and any session 0, 1 or 2 sequences of rat's responses consisting of at least 6 consecutive ones compatible with the given hypothesis could be found.

Using the "Thinking Rat" programme we analysed in both strains the number of hypotheses observed, the length of the sequences tested for the particular hypothesis, the frequency of each hypothesis in the total number of hypotheses and changes of these factors during learning up to the criterion.

The possibility that irrelevant hypotheses used by rats could influence the effectiveness of discrimination learning seems very likely. Nevertheless, it is probably not proper to say that duration of

learning is simply a function of the number of irrelevant hypotheses tested. The relation between these factors could be obvious, e.g., because SHR learned quicker than NT rats, thus as a result, their number of hypotheses could be smaller than that of NT rats. To avoid this possibility, we introduced coefficients of learning strategies which are independent of the duration of the learning. For each rat the data were shown as the ratio of the sum of trials belonging to all sequences compatible with a particular set of hypotheses to the total number of trials. This was done independently for each dimension of discriminative stimuli. Thus, we obtained three coefficients: PH (position hypotheses), OH (orientation hypotheses), and CH (colour hypotheses). PH means the number of trials in sequences compatible with hypotheses of four different types (see Methods) in which position acts as relevant cue divided by the total number of trials; OH and CH were established in an analogous way. These coefficients were calculated for the whole period of learning, and in order to assess their changes during learning in three consecutive periods of the total time of learning. In each rat the time of learning up to the criterion in the particular stages of the experiment was divided into three equal periods. This procedure standardized the duration of learning in all rats, which allowed us to compare data between both strains.

Statistics

All data reported in this paper were evaluated with a repeated-measures analysis of variance (ANOVA), followed by analyses of simple effects, where appropriate. Data expressed as proportions were normalized using the arc sin transformation.

RESULTS

Changes of learning strategies coefficients with the progress of learning

The mean values obtained for the three coefficients of learning strategies are given in Figs. 1, 2 and 3. These

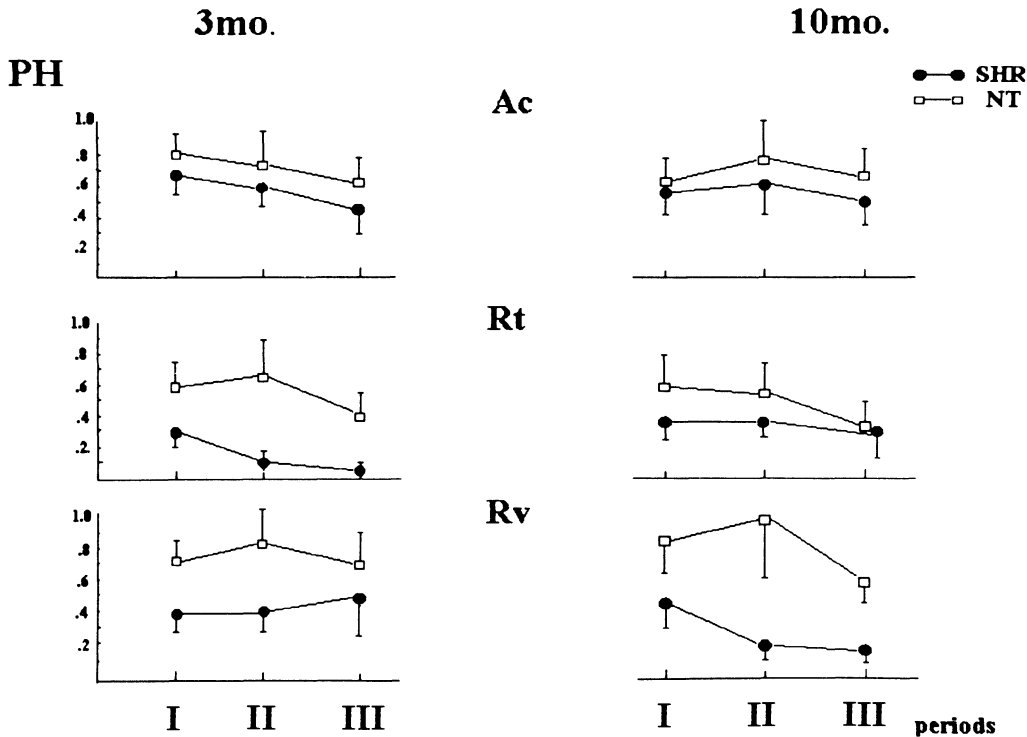


Fig. 1. Mean values of PH coefficient in younger (3 mo., left panel) and older (10 mo., right panel) SHR and NT rats across three consecutive periods of learning in acquisition (Ac), retention (Rt) and reversal (Rv) of visual discrimination.

data were analysed in three-way ANOVAs (Strain x Stage x Period) performed independently for each coefficient and independently for both age groups.

THE POSITION HYPOTHESES - PH COEFFICIENT

Figure 1 shows the mean values of PH coefficient obtained for younger and older groups of SHR and NT rats across consecutive periods of learning in stages Ac, Rt and Rv.

There were large differences in the mean value of PH between SHR and NT rats, both in younger ($F(1,16)=20.36$, $P<0.001$) and older groups ($F(1,16)=21.02$, $P<0.001$). The SHR did not show as strong a preference for position hypotheses as the NT rats. The occurrence of position hypotheses was different in acquisition, retention and reversal ($F(2,32)=9.23$, $P<0.001$ for the younger and $F(2,32)=4.05$, $P<0.03$ for the older group) and was also different in the three periods of learning in particular stages ($F(2,32)=12.28$, $P<0.001$ and $F(2,32)=15.60$, $P<0.001$ for the younger and the older group, respectively).

The within-subjects analysis showed a slight, though significant, Strain x Stage interaction, both in the younger ($F(2,32)=3.38$, $P<0.03$) and the older group ($F(2,32)=3.65$, $P<0.03$). The significant interaction was mainly due to the fact that the frequency of position hypotheses was the highest in the Ac stage for the SHR, and in the Rv stage for the NT rats. Since there was no significant interaction of Strain x Period in the younger group we can assume that the PH coefficient changed across the consecutive periods of learning in the same way in SHR and NT rats. In the older group the course of changes of PH coefficient was different in SHR and NT rats (significant interaction of Strain x Period, $F(2,32)=7.57$, $P<0.002$). Analysis of the period effect revealed that the greatest strain difference was in Rv. In this stage the value of PH in SHR ($F(2,144)=24.2$, $P<0.001$) rapidly decreased from the first to the second period and remained at the same level in the third period, whereas in the NT rats ($F(2,144)=20.7$, $P<0.001$) PH was the highest in the second period of Rv learning and began to decrease in the third period (Fig.1).

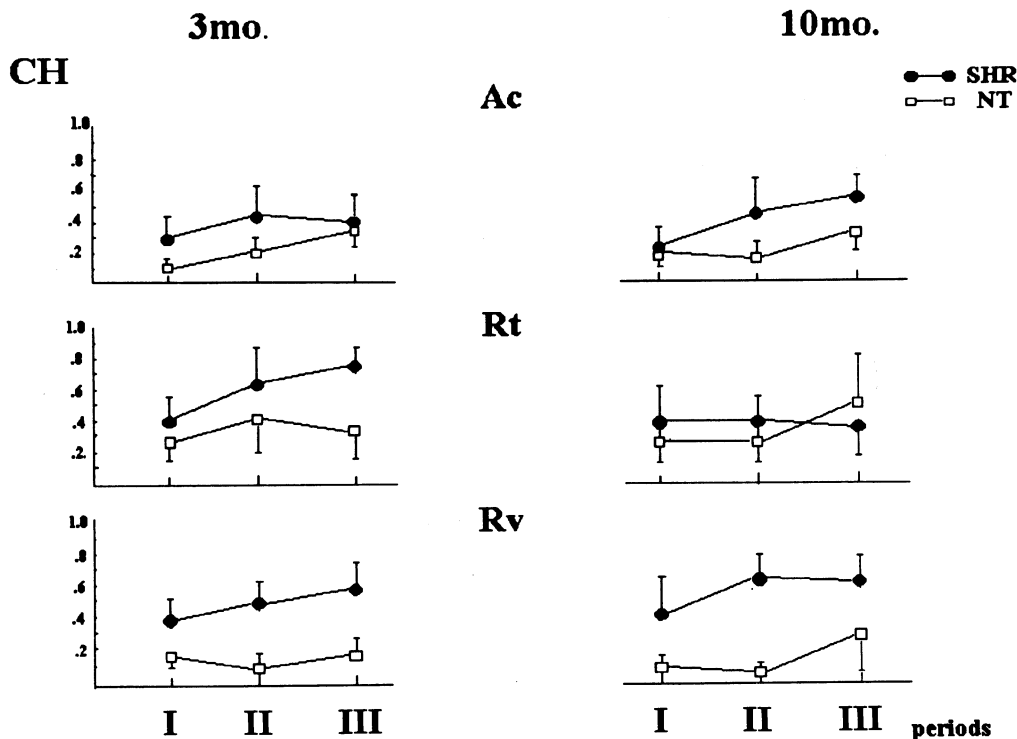


Fig. 2. Mean values of CH coefficient in younger (3 mo., left panel) and older (10 mo., right panel) SHR and NT rats across three consecutive periods of learning in acquisition (Ac), retention (Rt) and reversal (Rv) of visual discrimination.

THE COLOUR HYPOTHESES - CH COEFFICIENT

The results of colour hypotheses analysis are shown in Fig. 2. The overall ANOVA on CH coefficient in younger and older SHR and NT rats showed no significant effect of stage, but there was a significant effect of strain ($F(1,16)=9.25$, $P<0.008$ and $F(1,16)=15.97$, $P<0.001$ for younger and older rats, respectively) and period ($F(2,32)=6.98$, $P<0.003$ for the younger and $F(2,32)=21.9$, $P<0.001$ for the older group).

In the younger group no one interaction was significant. This means that, although in general SHR applied colour hypotheses more frequently than did NT rats, the strategies based on the colour dimension changed similarly in both strains during consecutive periods of learning in acquisition, retention and reversal stages. In contrast, the ANOVA performed on the older group demonstrated a significant Strain \times Period interaction ($F(2,32)=5.02$, $P<0.01$). This interaction was due to the fact that the mean values of the CH coefficient in SHR were the lowest in the first period, then rapidly increased and

became similar in the second and third period (excluding the Rt stage), whereas in NT rats CH values did not change between the two initial periods and did not grow until the last period of learning. In fact, the greatest strain difference in the frequency of colour hypotheses was observed in the second period of learning (Fig. 2) in reversal ($F(1,144)=15.3$, $P<0.001$; analysis of strain effect). Examination of Fig. 2 reveals that the character of differences between the SHR and NT rats was similar in Ac and Rv, but more expressed in the Rv stage.

THE ORIENTATION HYPOTHESES - OH COEFFICIENT

Figure 3 presents the mean values of the OH coefficient in both age groups of SHR and NT rats. These values did not differ between strains, stages of the experiment or across periods of learning except in the younger group in Rt. This was confirmed in the analyses of variance which detected a significant influence of the Stage factor ($F(2,32)=11.21$, $P<0.001$) and significant interaction of Strain \times Stage ($F(2,32)=8.49$, $P<0.001$) and Stage \times Period

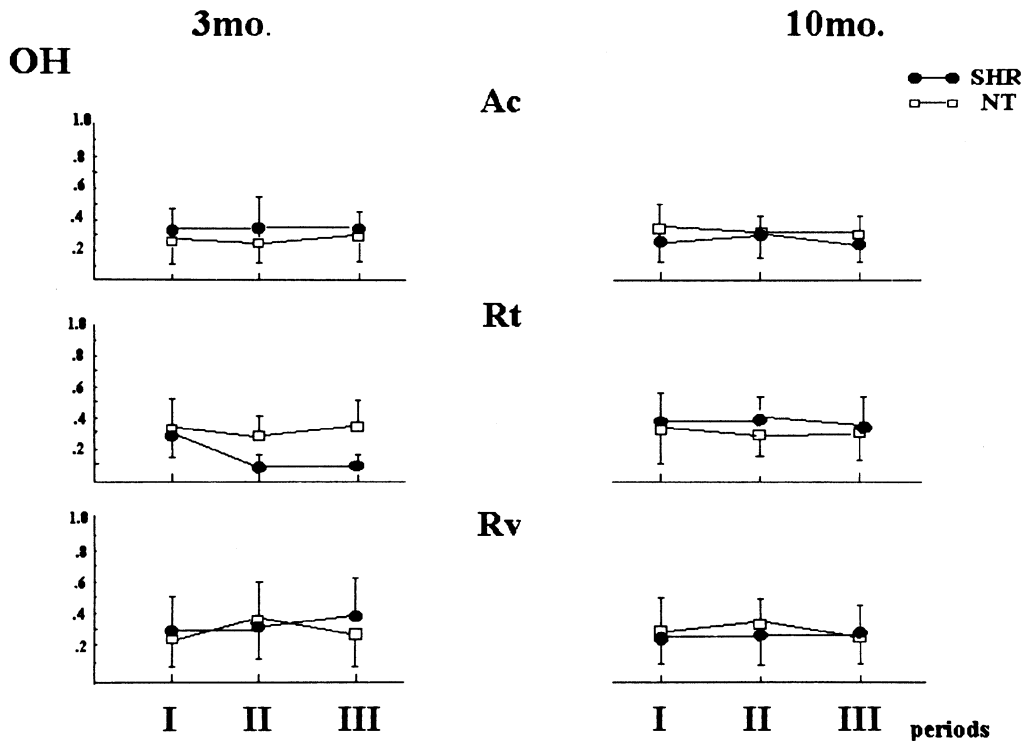


Fig. 3. Mean values of OH coefficient in younger (3 mo., left panel) and older (10 mo., right panel) SHR and NT rats across three consecutive periods of learning in acquisition (Ac), retention (Rt) and reversal (Rv) of visual discrimination.

($F(2,32)=2.92$, $P<0.027$) only in the younger group. This difference was due to the fact that orientation hypotheses were observed only marginally in younger SHR during the last two periods of Rt stage.

Frequency of different type of hypotheses in total number of hypotheses

Analysis of learning strategies coefficients for particular stimuli dimensions detected many significant differences in the number of hypotheses applied by SHR and NT rats across the periods of discriminative training. We also examined whether there were differences between strains in the preference for a distinctive type of hypotheses shown by Levine (see Table I). Figure 4 shows the mean values of PH and CH coefficients for both age groups of SHR and NT rats in acquisition, retention and reversal separately for perseveration together with alternation hypotheses and win-stay, lose-shift together with win-shift, lose-stay hypotheses. Among these four types of hypotheses may be distinguished the "response-set" hypotheses (persever-

ation and alternation) which are independent of the outcome of the rat's choice and the "prediction" hypotheses (win-stay, lose-shift and win-shift, lose-stay) in which the rat's choice is determined by the outcome of the choice in preceding trials (Levine 1963). It is certain, however, that the response-set hypotheses are based on reference memory (or habits), but in prediction hypotheses working memory is involved (Sutherland and Mackintosh 1971, Squire 1987, Squire et al. 1993). This important difference prompted us to express our data independently for these two categories of hypotheses. Thus, the PH coefficient which concerns a position dimension for response-set hypotheses is expressed as the number of trials in sequences compatible with perseveration plus alternation hypotheses *versus* the total number of trials to the criterion value. Similarly, for the prediction hypotheses the coefficient is expressed as the number of trials in sequences compatible with win-stay, lose-shift plus win-shift, lose-stay hypotheses *versus* total number of trials. The CH coefficient was calculated similarly for the colour dimension. The search for concomitant differences between strain for orientation

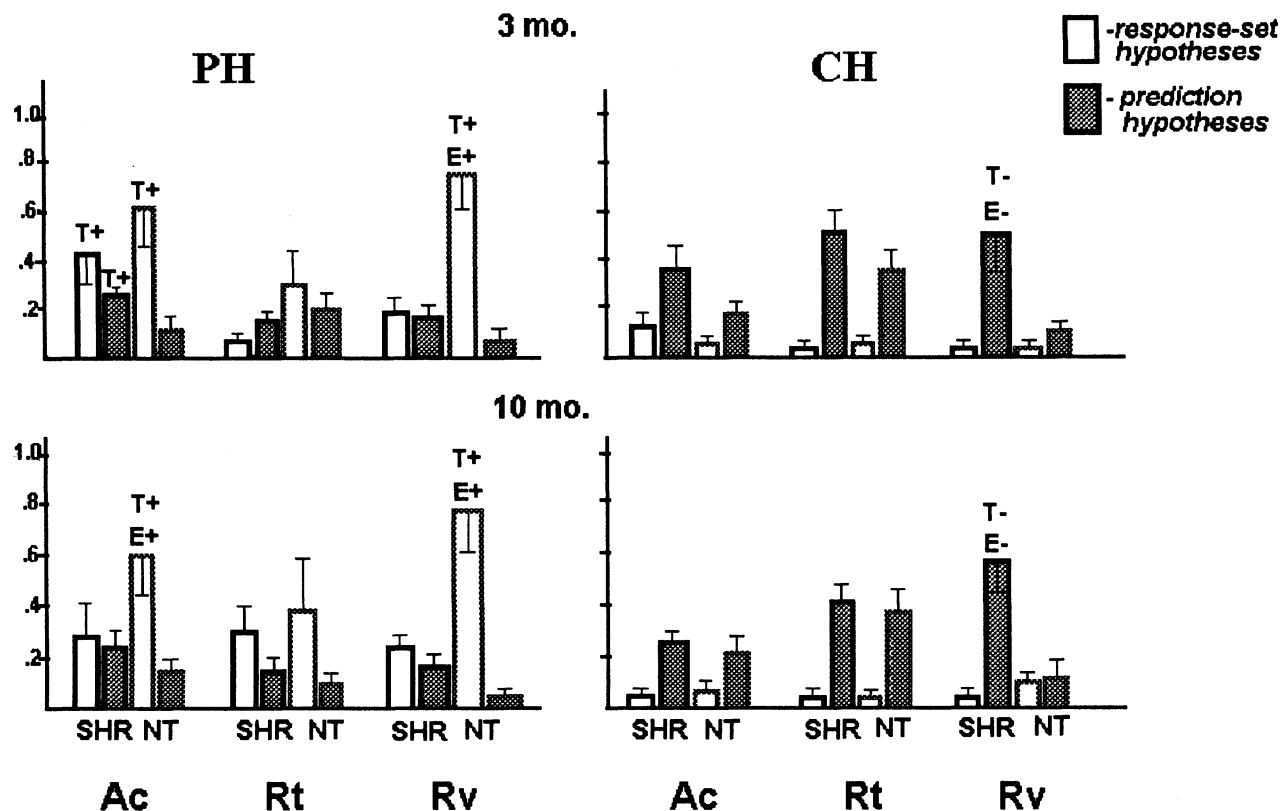


Fig. 4. Frequency of different types of hypotheses. Mean values of PH (left panel) and CH (right panel) coefficients in SHR and NT rats of both age-groups are shown separately for response-set (open bars) and prediction (shaded bars) hypotheses in the acquisition (Ac), retention (Rt) and reversal (Rv) of visual discrimination. The notations above the bars indicate significant positive (+) or negative (-) correlation between number of trials (T) or errors (E) and PH or CH coefficient.

modality has yielded no significant results. Thus, the data for the OH coefficient were excluded from Fig. 4.

The three-way ANOVAs Strain \times Stage \times Age performed independently for the response-set and prediction hypotheses and independently for the position and the colour dimension resulted in many significant differences.

PH COEFFICIENT

Figure 4 (left panel) shows that the PH coefficient for response-set hypotheses was lower in SHR than in NT rats ($F(1,32)=67.3$, $P<0.001$). The values of PH were also significantly different in the particular stages of the experiment ($F(2,64)=20.03$, $P<0.001$). The significant interaction of Strain \times Stage ($F(2,64)=16.82$, $P<0.001$) indicates that in

different experimental stages rats of both strains used response-set hypotheses in a different way. This was due to the fact that the frequency of response-set hypotheses with regard to the position dimension for SHR was the highest in the Ac stage, while for NT rats this frequency was highest in the Rv stage. Analysis of Stage effect revealed that in SHR the PH coefficient differed significantly between Ac, Rt and Rv stages only in the younger group ($F(2,64)=13.8$, $P<0.001$). In the NT rats differences of PH values were significant between Ac, Rt and Rv both in the younger ($F(2,64)=19.1$, $P<0.001$) and the older group ($F(2,64)=8.5$, $P<0.001$). There were no overall significant differences in PH between the younger and older animals.

The PH coefficient for prediction hypotheses was higher in SHR than in NT rats ($F(1,32)=32.01$,

$P < 0.001$) and was also different ($F(2,64) = 4.80$, $P < 0.025$) in the particular stages of the experiment in both strains. There was no significant influence of the age factor and no significant interactions.

CH COEFFICIENT

Figure 4 (right panel) shows that with regard to the colour dimension response-set hypotheses were very rare and the CH coefficient for this category of hypotheses was similar in SHR and NT rats ($F(1,32) = 0.87$, NS). The influence of the age factor was also insignificant, however the CH values differed significantly in the particular stages of the experiment ($F(2,64) = 10.35$, $P < 0.001$). The within-subjects analysis demonstrated a significant interaction of Age \times Stage ($F(2,64) = 12.44$, $P < 0.001$). This was due to the fact that in younger rats CH was significantly higher in Ac than in Rt and Rv, whereas in the older group CH was the highest in Rv (Fig.4).

Figure 4 also shows that the frequency of prediction hypotheses, as judged from CH values, was higher in SHR than in NT rats ($F(1,32) = 37.84$, $P < 0.001$). The main effect of the Stage factor was significant ($F(2,64) = 7.21$, $P < 0.005$), while the influence of the Age factor was insignificant. The only significant interaction was that of Strain \times Stage ($F(2,64) = 8.06$, $P < 0.001$). Analysis of Stage effect revealed that in SHR the frequency of colour prediction hypotheses was the highest in Rv (Fig.4) and significantly different than in Ac and Rt ($F(2,64) = 6.9$, $P < 0.005$), whereas in NT rats the frequency of these hypotheses was the lowest in Rv (Fig.4) and different than in Ac and Rt in both age groups ($F(2,64) = 4.4$, $P < 0.025$ for the younger and $F(2,64) = 4.1$, $P < 0.025$ for the older group).

Relationship between patterns of response and duration of visual discrimination learning

To find a possible correlation between different patterns of responding and duration of learning in SHR and NT rats, a linear regression analysis was

performed. The values of PH and CH coefficients were correlated with the number of errors and trials required to reach the criterion in all stages of the experiment. This was done separately for response-set and prediction hypotheses and separately for both age groups (Fig.4).

In SHR of both age groups the analysis detected a significant negative correlation between the CH values of the prediction hypotheses and the number of trials ($r = -0.79$, $P < 0.01$ for younger and $r = -0.89$, $P < 0.01$ for older group) and errors to the criterion ($r = -0.77$, $P < 0.02$ for younger and $r = -0.85$, $P < 0.01$ for older rats) only in the reversal learning. With regard to position dimension, a significant positive correlation was observed between PH coefficient values of response-set hypotheses and the number of trials ($r = 0.79$, $P < 0.01$) and between PH coefficient values of prediction hypotheses and the number of trials ($r = 0.65$, $P < 0.02$) only in younger SHR in the acquisition stage.

In NT rats PH values for response-set hypotheses were positively correlated to a significant degree with the number of trials ($r = 0.75$, $P < 0.02$ for younger and $r = 0.81$, $P < 0.02$ for older rats) and errors ($r = 0.78$, $P < 0.01$ only for older rats) in acquisition and with the number of trials ($r = 0.80$, $P < 0.01$ for younger and $r = 0.82$, $P < 0.01$ for older rats) and errors ($r = 0.72$, $P < 0.02$ and $r = 0.76$, $P < 0.01$ for younger and older rats, respectively) in the reversal learning.

DISCUSSION

In the present study the rats response strategy was examined as a factor which may affect performance of spontaneously hypertensive and control Wistar normotensive rats in visual discrimination learning. The results of the analysis demonstrated that SHR solved the task by using different response strategies than the NT rats. The SHR did not show so strong a preference for hypotheses in which position acts as a relevant cue as the NT rats, and this difference, present in all experimental stages, was particularly strong in reversal learning (Fig.1). On the contrary, SHR used hypotheses in which colour

acts as a relevant cue more frequently as compared with the NT rats, and again the biggest difference was observed in the reversal learning (Fig.2). As to the position modality, the frequency of hypotheses observed in SHR was the highest in acquisition, while for NT rats in reversal. Moreover, during the particular stages of learning the course of changes in the frequency of position hypotheses observed was different in SHR and NT rats. This difference was most clear in reversal and for younger rats also in retention. In SHR the tendency to be guided by the positional cues decreased from the first to the second period of learning, whereas in NT rats the frequency of position hypotheses increased in this time and was the highest in the second period of learning. This indicates that, although the rats of both strains began by responding to position as a cue, SHR gave up this strategy more quickly as compared with the NT rats and responded earlier to colour dimension.

The NT rats showed strong perseverance in their choices for the position of stimuli. This was particularly evident in reversal learning, whereas in SHR the frequency of different types of position hypotheses was similar. These findings may suggest that SHR adopt different strategies more rapidly than NT rats, or rapidly switch between strategies when the test situation is changing. With respect to colour dimension, which was the relevant cue, a significant between-strain difference was observed only for prediction hypotheses in reversal. SHR applied these strategies in 53% of reversal learning trials, whereas NT rats only in 11% (means for both age groups). It must be noticed that in SHR during reversal we observed mainly the colour win-stay hypothesis. Of course, with respect to the relevant cue of stimuli, the outcome of usage of the win-stay, but not of the win-shift, hypothesis is identical with the correct performance. In addition, for relevant colour, sequences detected as compatible with win-stay, lose-shift hypothesis are almost identical (except the first element of sequence) with those detected as perseveration hypothesis. Thus, we can only say that in reversal the frequency of all types of colour hypotheses in SHR was higher than in NT

rats, but we are unable to differentiate between response-set and prediction hypotheses.

An interesting finding was the existence of some correlations between the way rats solved the task and the duration of learning. In SHR the frequency of colour prediction hypotheses correlated negatively with the number of errors and duration of learning in reversal, when SHR reached the criterion value much earlier than NT rats. In NT rats the frequency of response-set hypotheses directed by position, as an irrelevant cue, correlated positively with the number of errors and the duration of learning both in acquisition and reversal, the stages in which performance of NT rats was significantly less accurate than that of SHR. In younger SHR a significant positive correlation between the number of trials (but not the number of errors) and frequency of response-set hypotheses was detected. These correlations found for SHR and NT rats show that a higher frequency of position hypotheses accompanies lower efficiency of learning, while a higher frequency of colour hypotheses coincides with enhanced efficiency of learning. These observed relations agree well with between-strain differences in the duration of learning and differences in the strategies.

The search for differences in orientation hypotheses yielded no impressive results. Differences, if present at all, were only negligible (Fig. 3). When searching for sequences of rat responses compatible with the given hypotheses, sequences which occurred by chance were also detected. It is reasonable to assume that when only by-chance-sequences are detected (false-positive), the mean value of OH should not be influenced by factors of the experiment. As mean values of OH in the present study did not differ between strains, stages and periods of learning, it is conceivable that in fact rats may not use orientation hypotheses.

The age effect on learning strategies in SHR and NT rats was not so clear as on the performance parameters. From the analysis of hypotheses it is concluded that differences in learning efficacy between younger and older NT rats in acquisition and retention and SHR in retention (behavioural data, Łukaszewska

and Niewiadomska 1995) cannot be attributed entirely to differences in choice strategies used by rats from distinctive age groups.

There is no question that many factors determine the course of learning. Each of these factors may act differently in SHR and NT rats during visual discrimination. The results of performance analysis together with results of analysis of strategies could indicate that the discrepancy in learning between SHR and NT rats may be, at least partly, caused by differences in attentional processes. We presume that SHR are characterized by greater selectivity of attention and/or greater ability to switch attention over cues present in the given environment than NT rats. This was supported by the findings that SHR started to respond to the visual cues earlier than NT rats, and during the presolution period switched more frequently between different types of hypotheses. The NT rats, on the other hand, used for a long time only the position perseveration hypothesis. Spatial cues have a high priority for rats and are automatically attended to, whereas visual cues are not so preferred by rats and need probably more attention to be selected (Mackintosh 1965). The higher selectivity of attention could be also helpful in tests of high difficulty, as the present task was, when the stimuli are not easy to differentiate (Wise and Bower 1988).

The postulated changes in attention of SHR could facilitate both acquisition of new information and also modification of acquired memory in reversal. Sutherland and Mackintosh (1965, 1971) explain many phenomena of visual discrimination learning, among them the effect of overtraining on reversal, in terms of a selective attention theory. In reversal, the performance of rats exposed to further overtraining trials after reaching the criterion in acquisition was better than that of non-overtrained rats (Reid 1953, Harlow 1959,). Mackintosh (1965) postulated that overtraining can lead to faster reversal learning because attention to the relevant dimension of stimuli has been strengthened and rats must only reestablish their choice response. Moreover, many investigators have shown that overtraining facilitates reversal of visual discrimi-

nation because it shortens the period of position responses in the middle of reversal (Mackintosh 1965). Along with these fundamental assumptions we postulated that SHR behaved in reversal similarly to overtrained rats. They learned quicker in reversal than in acquisition, and the results of analysis of strategies also seem to support this supposition. The frequency of position hypotheses in SHR decreased with duration of the reversal and was lower in the middle than in the initial period of learning, while in NT rats the frequency of position hypotheses was the highest in the middle of reversal. Accordingly, such analogies between behaviour of overtrained rats and SHR in reversal could indicate that attentional processes in SHR are changed as compared with those of NT rats. However, the present results do not resolve the question as to whether changes in attentional processes in SHR are unique to visual cues or are associated with a polymodal set of intero- and exteroceptive stimuli.

It should be carefully noted that our analysis used to assess rat patterns of responding had some limitations which were the consequence of theoretical assumptions. It detected not only true sequences generated by rats using any hypothesis, but in some percentage, also sequences which are by chance compatible with any hypothesis. In this case, the absolute number of hypotheses detected could be higher than the number of hypotheses actually used by rats. Instead, such parameters as variability of learning coefficients and the course of changes of these coefficients could reflect true changes in frequency of usage of hypotheses. As we mentioned above, the limitations of the "Thinking Rat" analysis are exemplified in the results for the OH coefficient. Values of PH and CH coefficients displayed greater variability and their course of changes seems logically connected with the changes in performance. Therefore, it is probably justified to presume that SHR and NT rats used different choice strategies to solve the task and this could be, in part, the reason for the differences observed between strains in the effectiveness of learning. We believe that the "Thinking Rat" analysis of choice strategies, despite its shortcomings, adds

some useful information on learning processes in stimuli discrimination paradigms.

ACKNOWLEDGEMENTS

This research was supported by grants from the State Committee for Scientific Research, 0752/P2/92/03 and statutable to the Nencki Institute.

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Received 17 November 1994, accepted 24 February 1995