SUMMARY This study investigated the behavior of hypertensive-prone and nonhypertensive-prone rat strains to see whether there are differences in behavioral reactivity to environmental stimulation. Of primary interest was general activity, because investigators have assumed it to be an index of reactivity to environmental stimulation and to be correlated with the elevation of blood pressure in spontaneously hypertensive rats (SHR) but not in normotensive Wistar-Kyoto (WKY) rats. Therefore, general activity was assessed in SHRs and WKYS as a function of walking and rearing in an open field (Experiments 1 and 2) and crossings in a shuttlebox test (Experiments 3, 4, and 5). Activity was assessed under a constant level of environmental stimulation in the open field (Experiment 1) and shuttlebox (Experiment 3) or under varying degrees of stimulation in the open field (Experiment 2) and shuttlebox (Experiments 4 and 5). In the open field and the shuttlebox, SHR activity was above WKY activity when the degree of environmental stimulation was constant. However, when stimulation was manipulated, the SHR activity level was similar for all intensity levels, while the WKY activity was inversely related to stimulus intensity. These results suggest that while the SHRs may generally be more active than WKYS, WKYS display a greater behavioral reactivity to environmental stimulation than SHRs. (Hypertension 6: 868-876, 1984)

KEY WORDS • behavior • reactivity • activity • spontaneously hypertensive rat • Wistar-Kyoto rat

The term "essential hypertension" is used to denote an elevation of arterial pressure for which no definitive physiological condition can be identified. Due to the unclear origin of this disorder, psychological factors, if indeed they exist, would be of etiological significance during the early developmental stages. An elevation of pressure resulting from exposure of genetically predisposed individuals to a stressful environment might be due to "hyper-reactivity" to environmental stimulation. While this is usually supported by the observation of large physiological responses in hypertensive humans and SHRs, no systematic effort has been made to either define the behavioral attributes of reactivity or determine what relevance, if any, it has to the pathogenesis of hypertension.

Initial attempts to approach this problem have consisted of documenting behavioral differences between hypertensive-prone and nonhypertensive-prone rat strains, with SHRs typically displaying a higher level of general activity than WKYS across a variety of tasks. That such behavioral differences are not associated with blood pressure levels per se is supported by several observations. First, the behavior of adult SHRs is very similar to young prehypertensive SHRs. Second, altering the salt intake of the Brookhaven strains influenced blood pressure but failed to produce substantial changes in behavior. Third, lowering the systolic blood pressure in SHRs by pharmacological intervention did not reduce locomotor activity, and, conversely, elevating the blood pressure in WKYS by means of a renal clamp did not alter locomotor activity in WKYS. Fourth, while F1 and F2 hybrid generations derived from cross-breeding SHRs and WKYS produced intermediate levels of blood pressure and locomotor activity, the two characteristics were not correlated. Therefore, to date, the evidence suggests that although the SHRs are more active than WKYS, this difference in activity cannot be correlated with a strain difference in blood pressure.

Although strain differences in activity are apparently unrelated to blood pressure per se, such tonic activity differences are often taken as an appropriate behavioral index of reactivity to environmental stimulation. We maintain, however, that the relationship of these behavioral differences to the issue of reactivity is ambiguous. On the one hand, tonic activity may be determined by the degree of environmental stimulation, which would suggest that hypertensive-prone organisms are more reactive to environmental stimulation. An alternative view suggests that such activity differ-
ences reflect phenotypic strain differences, which are independent of environmental stimulation. According to this view, such behavioral differences are due to "random fixation" during the process of selective breeding for blood pressure and are associated with but not causally related to blood pressure. From this perspective, these behavioral differences are only of interest insofar as they provide cues to biochemical and physiological differences between the strains that may be more directly relevant to the etiology of hypertension.

Unfortunately, the discrepancy in these views regarding the meaning of strain differences in tonic activity has not been adequately addressed in the literature and can only be assessed by more precisely defining the behavioral attributes associated with reactivity. Therefore, we assessed the activity of SHRs and WKYs under a variety of conditions to provide some data concerning the impact of environmental stimulation on the behavior of these strains, particularly as to whether the activity is related to the degree of environmental stimulation.

The experiments were divided into two sections, each of which describe a distinct strategy for studying behavior under varying environmental conditions. All of the experiments, however, have the following aspects in common. The rats were from a closed colony of SHRs and WKYs maintained at Syracuse University, were weaned at 21 days of age, housed in group cages as litters, and at 40 to 50 days of age were separated by sex. Young rats (25 to 35 days old) were taken from a group cage, tested, and then placed in another group cage until all selected subjects from a litter had been tested. Older subjects were taken from a group cage and placed in individual cages at least 2 days before being tested. When rats of similar age were used in different treatments, an effort was made to distribute members of a litter across experimental conditions and to employ a number of litters per treatment. Food and water were available ad libitum, and the light cycle was automatically controlled on a 12-hour on, 12-hour off, schedule, with the light cycle starting at 6 a.m.

Section I

In two experiments, open-field behavior of SHRs and WKYs was monitored. To observe any developmental and strain differences in these behaviors, the first experiment examined the activity and rearing behavior of males and females from each strain at three ages. Our procedure was modeled after that of Broadhurst in which there was a high level of ambient auditory and visual stimulation during the open-field test. In the second experiment, the intensity of environmental stimulation was manipulated to define operationally reactivity by the functional relationship between stimulus intensity and the frequency of such behaviors as walking, rearing, urination, and defecation.

Experiment 1

Methods

Rats. A total of 96 rats was given open-field testing. Eight male and eight female rats from the SHR and WKY strains were tested at either 30, 80, or 130 days of age.

Apparatus. Open-field testing was conducted in a circular arena made of clear Plexiglas that was 83 cm in diameter and 46 cm high. The wall was made opaque by lining the exterior of the plastic with Kraft paper. The arena was placed on a floor of gray tiles on which 19 radial segments of roughly equal size were marked. The arena was illuminated by a 500 W photoflood lamp in a reflector suspended 70 cm above the floor. The intensity of the light at the center of the open field, as measured by a Tektronix J16 photometer (Tektronix, Inc., Beavertown, Oregon) with a J6511 illuminance probe, was 715 ft candles. The top of the arena was covered with a double layer of white cheesecloth to provide a one-way visual screen through which the animal’s behavior could be observed. The room light was extinguished during testing. A speaker was mounted 70 cm above the floor at the center of the open field, and white noise was presented which measured 96 db at the floor of the open field. Duration of the test was controlled by a PDP-8e computer (Digital Equipment Corporation, Maynard, Massachusetts) which operated under the SKED software operating system (State Systems, Inc., Kalamazoo, Michigan).

Procedure. Each rat was observed in the open field for 2 minutes per day for 4 consecutive days. All testing was conducted between the hours of 1 p.m. and 3 p.m. Rats were carried from the colony to the open field in their home cage and then were transferred to the apparatus and placed in the center segment of the field. Observations began immediately when a timing circuit was activated that controlled the white noise and light. A crossing was defined by the passage of all four legs through a segment, and rearing was defined as extending the body while standing on only the hind paws. Two observers made independent counts of activity and rearing; differences in scores were averaged. Boli were removed, and the arena floor cleaned between subjects.

Results

The mean level of activity for each strain and sex over the three ages is presented in Figure 1. Differences in activity as a function of strain, sex, age, and days were examined by analysis of variance (ANOVA). As suggested by the data in Figure 1, SHRs displayed a significantly higher mean level of activity (54.3) than WKYs (15.7), p < 0.001, while the main effects of age and sex were not significant. There were, however, significant interactions between strain and age (p < 0.05), strain and sex (p < 0.01), and sex and age (p < 0.05). Analysis of simple effects revealed that the interaction between strain and sex was due to significantly higher activity in SHR females (56.9) than males (51.7), p < 0.001, while the difference between WKY males (17.2) and females (14.2) was
FIGURE 1. Mean open-field activity for three age groups of male and female spontaneously hypertensive rats (SHR) and Wistar-Kyoto (WKY) rats.

FIGURE 2. Mean open-field rearing for three age groups of male and female spontaneously hypertensive rats (SHR) and Wistar-Kyoto (WKY) rats.

not significant. For the strain by age interaction, an analysis of simple effects indicated that SHRs were significantly more active than WKYs at all ages (all Fs, \( p < 0.001 \)). The interaction was likely due to the fact that while SHRs displayed a peak activity at 80 days of age (57.9), WKYs were least active (13.5) at that same age. The sex-by-age interaction was due to decreasing activity with age in males and increasing activity with age in females. An analysis of simple effects of this interaction, however, indicated that the sex difference was only significant at 130 days of age (\( p < 0.01 \)).

With regard to changes in activity over days, there was a significant decrease in activity over days in the 30-day-old (\( p < 0.05 \)) and 130-day-old (\( p < 0.05 \)) WKY groups. In contrast, in the SHR groups, the decline in activity over days increased with age. Specifically, although there was no decline over days in the 30-day-old SHRs, activity did decline in the 80- (\( p < 0.05 \)) and 130- (\( p < 0.01 \)) day-old groups.

The mean rearing scores for male and female SHRs and WKYs at the three ages are presented in Figure 2. An ANOVA of these data indicated a significantly higher level of rearing in SHRs (7.1) than in WKYs (1.6), \( p < 0.001 \). In addition, there was a significant strain-by-sex interaction (\( p < 0.01 \)), which was due to a significantly higher level of rearing in female SHRs (8.3) than male SHRs (6.0), \( p < 0.001 \), while it did not differ in male (1.8) and female WKYs (1.1A).

There was a significant decline in rearing over days (\( p < 0.001 \), which interacted with strain, sex, and age as separate interactions as well as in combination (\( p < 0.05 \)). Because the days factor was common to all significant interactions, simple effects analyses were calculated to determine which groups showed a significant decline in rearing over days: male WKYs at 30 days of age; female WKYs at 30 and 130 days of age; and all SHR groups.

Experiment 2

To date, open-field behaviors of SHRs and WKYs have been examined under minimal or intense stimulus conditions (Experiment 1), although there has been no attempt to establish a relationship between stimulus intensity and behavior in the same procedure. Therefore, in the second experiment, measures of open-field behavior of SHRs and WKYs were observed under stimulus conditions that varied in intensity. It was hypothesized that examination of behavior as a function of environmental stimulation would provide a better operational definition of behavioral reactivity than the strain difference in tonic activity level that has been typically reported.

Methods

Rats. Sixty males 60 to 65 days of age from both SHR and WKY strains were employed.

Procedure. The degree of environmental stimulation was manipulated by varying the intensity of either the auditory or visual component of a compound stimulus presented during open-field testing. Values for the low, moderate, and high auditory stimuli were 75, 85, and 95 db; these stimuli were calibrated by a Simpson Model 220 Soundlevel Meter (Simpson Electric, Elgin, Illinois), with the microphone placed in a vertical position at the center segment of the open field. During testing with either of these three auditory intensities, the visual stimulus was 2 ft candles. Thus, the behavior of 10 rats from each strain was observed during the presentation of a low-intensity visual stimulus and one of three auditory intensities. Another 30 rats from each strain received open-field testing in which the intensity of the auditory component was constant (75 db) while the visual stimulation was either 2, 120, or 715 ft candles. The AC power to a 500 W bulb was varied by means of a variable transformer to produce a variation in intensity. This, of course, produced a spectral shift that was particularly evident at the low-intensity setting. The apparatus, duration of the test, and scoring were identical to those described for the first experiment. After each rat was tested, the occurrence of urination was noted, and the number of boli were counted.
Results

The mean ambulation scores for SHRs and WKYs over the range of visual and auditory stimuli are presented in Figure 3. For the auditory manipulation, SHRs were significantly more active (46.3) than WKYs (18.6), \( p < 0.001 \). In addition, there was a significant strain-by-intensity interaction \( (p < 0.05) \). A simple effects analysis of this interaction revealed that SHRs were significantly more active than WKYs at all three intensities \( (p < 0.01) \). Most important, while SHRs displayed a similar level of activity at all three intensities, the ambulation of WKYs was inversely related to stimulus intensity \( (p < 0.01) \). When the visual intensity was varied, only the strain difference was significant \( (p < 0.001) \), with SHRs \( (43.5) \) ambulating more than WKYs \( (13.6) \) across all levels of stimulus intensity.

The mean rearings for SHRs and WKYs across the stimulus conditions are presented in Figure 4. For the auditory manipulation, the mean rearing score for the SHRs \( (5.2) \) was significantly higher than that found for WKYs \( (2.1) \), \( p < 0.001 \). For the visual stimulus conditions, there was a significant difference between SHRs \( (4.8) \) and WKYs \( (0.9) \), \( p < 0.001 \), as well as a significant strain by intensity interaction, \( p < 0.05 \). A simple effects analysis of this interaction indicated that SHRs reared more than WKYs at all three intensities \( (p < 0.01) \). In addition, while WKYs displayed similar rearing frequency at all stimulus intensities, SHRs reared more with increasing intensity of illumination, \( p < 0.05 \).

Table 1 presents the various measurements of urination and defecation of the two strains. While only two of the 60 SHRs defecated in the open field, 28 of the 60 WKYs did so, which is significantly different \((% = 30.1, df = 1, p < 0.001)\). In addition, a higher percentage of WKYs \((83\%)\) than SHRs \((52\%)\) urinated during testing \((x^2 = 13.7, df = 1, p < 0.001)\).

Discussion

The results from the first experiment clearly indicate some important differences in the behavioral attributes of SHRs and WKYs. First, in the type of stimulating environment employed, SHRs were considerably more active than WKYs. This difference was reflected not only in a higher rate of ambulation but also in a considerably higher incidence of rearing. Although the following characteristics were not quantified, there was a consistent difference in the nature of mobility in the open field in these two strains. Whereas SHRs ran around the arena, frequently reared toward the stimulation, and crossed through the center segments, WKYs literally crawled. Their characteristic response was to lie on the floor with legs splayed and slowly crawl. As indexed in the second experiment, WKYs displayed a much higher incidence of defecation and urination under these conditions.

Second, the results from the second experiment in which stimulus intensity was manipulated suggest that the appropriate characterization of SHR would be hyperactive, rather than hyperreactive. This characterization is based on the observation that although the am-
TABLE 1. Percentage of SHRs and WKYs Urinating and Defecating in the Open Field under Low, Medium, and High Auditory or Visual Stimulation

<table>
<thead>
<tr>
<th>Open field activity</th>
<th>Auditory intensity (db)</th>
<th>Visual intensity (ft. candles)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Urination</td>
<td>75 85 95</td>
<td>2 120 715</td>
</tr>
<tr>
<td>SHR</td>
<td>90 70 60</td>
<td>10 40 40</td>
</tr>
<tr>
<td>WKY</td>
<td>90 80 90</td>
<td>90 70 80</td>
</tr>
<tr>
<td>Defecation</td>
<td>0 10 0</td>
<td>0 20 0</td>
</tr>
<tr>
<td>SHR</td>
<td>30 40 50</td>
<td>40 60 60</td>
</tr>
<tr>
<td>WKY</td>
<td>0.7 1.3 1.0</td>
<td>1.2 1.9 2.4</td>
</tr>
</tbody>
</table>

bulation of SHRs was higher than that of WKYs, it was constant across varying stimulus conditions, whereas the ambulation of WKYs was an inverse function of stimulus intensity. With respect to rearing, however, SHRs did display increased rearing as a function of the intensity of visual stimulation.

Section II

The following three experiments compliment the results of Experiment 2 in identifying behavioral attributes that reflect differences in reactivity to environmental stimulation. The strategy, however, was altered in two ways. First, a shuttlebox was employed in order to monitor activity over a long period of time. Second, in contrast to previous open-field studies in which there was a constant ambient level of stimulation, stimulation was presented on a response-contingent basis when activity occurred.

Experiment 3

Because there is little information regarding the activity of SHRs and WKYs over longer time periods, the first experiment established the basic pattern of activity of each strain in this apparatus. Based on the results of Experiment 1, it was expected that SHRs would display a higher level of activity than WKYs in this procedure.

Methods

Rats. Ten males and 10 females 25 to 35 days old from both SHR and WKY strains were employed.

Apparatus. All rats were individually tested in one shuttlebox, a BRS/LVE mouse shuttlebox (Beltsville, Maryland), enclosed in a ventilated chamber for attenuating extraneous auditory and visual stimuli. The shuttlebox was modified in two ways. First, the door that separated the two compartments was enlarged to an opening from the floor 5.3 cm high and 5.8 cm wide. Second, every other grid was removed to allow bolus to fall to a tray below the grid. Therefore, the floor consisted of 10 grid bars in each compartment. The shuttlebox was interfaced to the computer that controlled the experimental sequence and data collection, as previously described.

Procedure. All rats were tested between 8 a.m. and 3 p.m. Each one was selected from a litter, placed in an individual cage for transport to the shuttlebox, and placed in the chamber for 1 hour. During the session, no visual stimulation was present in the chamber, and the ambient auditory level was 73 db. Activity as indexed by crossing from one chamber to the next was recorded in 5-minute blocks. Between tests, the bolus were counted and removed, and the tray and grid cleaned.

Results

The frequency of activity of SHRs and WKYs during a 1-hour session is presented in Figure 5. The data...
were averaged for males and females because the analysis revealed that neither sex nor the interaction with sex were significant. The ANOVA did reveal a significant decline in activity over the session (p < 0.001), and a significant strain-by-time interaction (p < 0.01). Simple effects analysis of this interaction indicated that while the WKYs were significantly more active than SHRs during the first 15 minutes of the session, they were significantly less active than SHRs during the last 30 minutes of the session. Therefore, despite the similarity of total activity for the two strains (56.3 for SHRs and 56.2 for WKYs), there was a distinct difference in the pattern of activity. SHRs displayed a slightly higher rate of activity over a longer period of time and showed a higher defecation frequency (5.8) than WKYs (1.2), p < 0.001.

Experiment 4
To examine the influence of environmental stimulation on the pattern of shuttlebox activity in these strains, two additional experiments were conducted. In the first, the basic no-stimulus condition from Experiment 3 was replicated, and two additional groups were included in which crossing from one compartment to the next resulted in the presentation of a stimulus. Based on the results of Experiment 2, it was expected that the additional stimulation would have a greater influence on the activity of WKYs than SHRs.

Methods
Rats. Thirty males and 30 females 25 to 35 days old from both strains were employed.

Apparatus and Procedure. The apparatus was the same as that used in Experiment 3. Within each strain, the 30 male and 30 female rats were randomly divided into three groups of 10 males and 10 females per group. One group from each strain was identical to the no-stimulus condition in Experiment 3. In the other two groups, movement from one chamber to the other was followed by a 1-second presentation of a visual stimulus in either the entered chamber (to-stimulus group) or the exited chamber (from-stimulus group). The lights were mounted on the end wall of each chamber and produced 1.2 ft candles of illumination.

Results
Activity of the SHRs and WKYs over time is presented in Figure 6. As in the previous experiment, the analysis revealed no significant effect of sex or interaction with sex, therefore, the data for males and females were averaged within each strain. There was a significant decline in activity over time (p < 0.01), which is consistent with the results of Experiment 3. Most important, there was a significant strain-by-stimulus interaction (p < 0.05). Further, simple effects analyses of this interaction indicated that while the activity was equivalent in the three SHR groups, the activity of the two WKY groups that received stimulation was significantly lower than that observed in the control group (p < 0.001). Therefore, the activity level of WKYs was significantly influenced by additional environmental stimulation, while the behavior of SHRs was constant regardless of the presence or absence of stimulation.

The frequency of defecation for the SHRs and WKYs under the three stimulus conditions is presented in Figure 7. While there was no significant difference for the stimulus conditions or sex, there was a significantly greater frequency of defecation among SHRs (6.8) than WKYs (3.1), p < 0.001, which was similar to the results of Experiment 3.

Experiment 5
In this experiment, the activity level was compared between a control group (no-stimulus condition) and a group that received intense response-contingent stimulation upon crossing from one chamber to the other. This experiment was, therefore, a replication of the previous experiment with more intense stimulation, which was expected to amplify the effect found previously.

Methods
Subjects. Thirty males and 30 females 25 to 35 days old from both strains were employed. Within each strain, rats were divided into two groups of 30 that consisted of an equal number of males and females.
Procedure. After being randomly assigned to a group, each rat was given a 1-hour session in the shuttlebox. In the control group, stimulation in the chamber was minimal (as described in Experiments 3 and 4). In the stimulation group, in contrast, movement from one chamber to the other produced a 1-second compound stimulus that consisted of illumination of two lights, one at the end of each chamber (2.5 ft candles), and a 2800 Hz, 100 db auditory pulse from a Sonalert (Mal- lory Electronics) in the shuttlebox ceiling.

Results

Total activity for the four groups is presented in Figure 8. An analysis of total activity scores revealed that although there was no significant effect of strain or sex, there was a significant strain-by-stimulus condition interaction ($p < 0.01$). Simple analysis of this interaction showed that while the activity of the SHR groups did not differ between the control and stimulating conditions, the total activity of WKYs receiving response-contingent stimulation was significantly lower (34.3) than the activity of the control group (62), $p < 0.001$. Mean number of boli was significantly higher in the SHR groups (4.5) than in the WKY groups (2.6), $p < 0.01$.

General Discussion

A rather consistent finding in the present experiments was that although SHRs were generally more active than WKYs, their behavior was fairly constant in a given environmental condition. In contrast, the overall level of activity in WKYs varied a great deal as a function of the environmental stimulation, which suggests that WKYs, not SHRs, are hyperreactive to stimulation. This conclusion is based on the following data. First, in the open-field test procedure, the behavior of the WKYs was characteristic of a more emotional animal. Specifically, WKYs displayed a low level of activity and rearing coupled with a high rate of defecation, while SHRs displayed a considerably higher level of open-field activity consistent with previous reports. In addition to the behaviors that we measured, there were some qualitative differences worth noting. The general nature of the activity of the two strains was considerably different, namely, SHRs ran around the arena, reared, and crossed through the middle, while WKYs assumed a flat position on the floor, literally crawled at a slow rate, frequently stopped, displayed jaw quivering, and defecated. Although this is speculative, these behaviors certainly suggest an animal that is reacting emotionally to environmental stimulation.

Second, variation of the environmental stimulation in the open field (Experiment 2) influenced the activity of WKYs, while SHRs displayed similar levels of activity across various conditions. This type of test more clearly differentiates a tonic level of activity from phasic changes that would appear to be a more appropriate behavioral index of reactivity to stimulation. The results are consistent with those of other reports demonstrating that aversive stimuli affect the behavior of WKYs more than that of SHRs. For example, less suppression of activity in SHRs than WKYs by aversive stimuli has been reported for drinking behavior, lever pressing on a schedule of reinforcement for food, and general activity. In addition, Schaefer et al. found that the presentation of a novel tone prior to the introduction of shock greatly reduced responding in WKYs, while it had little influence on the rate of responding among SHRs. These observations cannot be attributed to a strain difference in the strength of appetitive responding behavior, because comparable results have been found for both appetitive and nonappetitive tasks. Therefore, a variety of data suggests that it is difficult to suppress activity in SHRs, whereas activity in WKYs is more easily influenced by environmental stimulation.

Third, the strain difference regarding the influence of environmental stimulation was further illustrated by the studies of shuttlebox activity (Experiments 3, 4, 5). In contrast to the open field in which stimulation was always present, in the shuttlebox stimulation was response-contingent, so that it only occurred following ambulation from one chamber to the other. The results were consistent with our findings for the open field, namely, the activity level of SHRs remained constant under all conditions examined while the activity of WKYs was reduced when movement produced either a mild (Experiment 4) or intense (Experiment 5) stimulus.

Another interesting aspect of these data concerned the pattern of activity in SHRs and WKYs when no stimulus was presented (Experiment 3). At the onset of the session, activity was higher in WKYs; but later in the session it declined to below that of SHRs. This strain-by-time interaction for activity reflects differential habituation and is very similar to the finding of Rosecrans and Adams in SHRs and Wistar rats during running wheel activity over 4 days. Although these two test procedures differed considerably in the period of sampling activity (1 hour vs 4 days), the same pattern of habituation emerged. A similar difference in
activity during the initial exposure to a novel environment has also been reported for the Brookhaven strains. Specifically, the activity as indexed by crossings in a shuttlebox was higher in salt-resistant rats than salt-sensitive rats for the first 10 minutes of the session prior to the beginning of avoidance training. However, the differential pattern of activity over time, which was observed in our Experiment 3 and by Rosecrans and Adams, does not appear to hold for all situations. For example, Myers et al. examined the activity of SHRs and WKYs in an automated activity chamber over the same time period that we employed (1 hour) and found SHRs to be more active than WKYs over the entire session.

These findings are consistent with our previous findings concerning performance in an active avoidance task. Specifically, during a pretest when a compound light-tone signal was presented 10 times prior to pairing it with shock, WKYs more frequently crossed to the other chamber and terminated stimulation than SHRs; this finding was observed in both old and young WKYs. Evidence that latency to respond during the pretest is an appropriate index of reactivity was provided by the manipulation of the intensity of the auditory signal (Experiment 2). We think that these findings, in toto, reflect a general strain difference in the tendency to approach or withdraw from environmental stimulation. Knardahl and Sagvolden, for example, found that when a novel object was placed in an open field, SHRs showed considerable exploration of the object while WKYs spent less time doing so. This is consistent with an informal observation in our colony regarding behaviors elicited by opening the cage: SHRs will generally approach the front of the cage, rear, and look around, while WKYs huddle at the back of the cage or cling to the back wall.

In summary, we propose that this series of experiments is consistent with a number of other reports in the literature suggesting that the WKY strain is behaviorally reactive to environmental stimulation and not the SHR. In contrast, SHRs in most situations are more active than WKYs, which can be taken as a reflection of reduced emotionality in the SHR strain. One possible characterization of SHRs would be hyperactive rather than hyperreactive. Such a conclusion would be premature, because few comparisons of activity have been made with strains other than the WKY. When such comparisons have been made, the activity level of SHRs tends to be comparable to other strains, while the activity level of WKYs is typically found to be considerably lower in the open-field. For example, Schaefer et al. found similar levels of open-field activity in SHRs and Wistars, while the WKYs were significantly below both strains. In addition, in a recent paper, McCarty and Kirby found comparable levels of open-field activity and rearing in SHRs and in both of the New Zealand strains, while WKYs were significantly below any strain examined. The highest activity level was recorded in the Brown Norway strain. Therefore, these comparisons indicate that SHRs do not necessarily display an unusually high level of activity, but rather that WKYs display an unusually low level of activity.

There are, however, some inconsistencies that need to be addressed. First, in our series of experiments, defecation, which was employed as a measure of emotionality, was not consistent in all of our experiments. Whereas SHRs had a low rate of defecation in our open-field studies, they had a higher rate than WKYs in the shuttlebox. Unfortunately, in the shuttlebox the total count was taken at the end of a 1-hour session; therefore, it is not possible to determine during which period of time the high rate occurred. However, while defecation differences are frequently employed to assess emotionality, we did not find this measure sensitive to the manipulation of stimulation (Experiment 7), as was general activity. In addition, not only did we find an inconsistency in our data, these results also differ from those reporting no difference in defecation between SHRs and WKYs in the open field. Therefore, because the defecation measure has been so inconsistent over various experiments, it is difficult to determine the relationship between this measure and the concept of reactivity.

Second, while it has been consistently reported that SHRs and WKYs differ in baseline activity, their response to environmental stimulation may depend upon the intensity of the stimulation. Although we have found reduced activity in WKYs in a variety of situations when environmental stimulation was presented, there is some evidence that high intensity levels of stimulation tend to increase activity in SHRs. For example, McCarty and Kopin consistently found that inescapable footshocks elicited greater increases in activity measures in SHRs than in WKYs. Knardahl and Sagvolden also found that, while SHRs and WKYs did not differ in shuttle activity when no shock was present, the introduction of shock increased the activity in only SHRs. These data suggest either a threshold difference or a distinction between the effects of conditioned vs unconditioned stimuli on the behavior of these strains. Unfortunately, there are insufficient data to determine the validity of either interpretation in accounting for the differential influence of stressful stimuli on activity.

Third, the notion that WKYs are behaviorally more reactive to stimulation than SHRs stands in contrast to a wide variety of data showing enhanced physiological reactivity in SHRs over that found in WKYs. Specifically, in response to an aversive stimulus, SHRs compared to WKYs show larger increases in heart rate, blood pressure, pituitary-adrenal response to ether stress, and release of plasma catecholamines.

In summary, while behaviorally SHRs appear to be less emotional than WKYs, they do display more vigorous physiological disruption by aversive stimuli than WKYs. This fundamental discrepancy in the two aspects of functioning that are generally used to assess the effects of stressful environmental stimulation makes it difficult to state clearly the relationship between aversive stimulation, behavioral predispositions of an organism, and the pathogenesis of hypertension.
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Is the hypertensive rat really hyperreactive?
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Hypertension. 1984;6:868-876
doi: 10.1161/01.HYP.6.6.868

Hypertension is published by the American Heart Association, 7272 Greenville Avenue, Dallas, TX 75231
Copyright © 1984 American Heart Association, Inc. All rights reserved.
Print ISSN: 0194-911X. Online ISSN: 1524-4563

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