

*BEHAVIORAL VARIABILITY IN SHR AND WKY RATS AS
A FUNCTION OF REARING ENVIRONMENT AND REINFORCEMENT CONTINGENCY*

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The spontaneously hypertensive rat (SHR) may model aspects of human attention deficit hyperactivity disorder (ADHD). For example, just as responses by children with ADHD tend to be variable, so too SHRs often respond more variably than do Wistar-Kyoto (WKY) control rats. The present study asked whether behavioral variability in the SHR strain is influenced by rearing environment, a question related to hypotheses concerning the etiology of human ADHD. Some rats from each strain were reared in an enriched environment (housed socially), and others were reared in an impoverished environment (housed in isolation). Four groups—enriched SHR, impoverished SHR, enriched WKY, and impoverished WKY—were studied under two reinforcement contingencies, one in which reinforcement was independent of response variability and the other in which reinforcement depended upon high variability. The main finding was that rearing environment did not influence response variability (enriched and impoverished subjects responded similarly throughout). However, rearing environment affected body weight (enriched subjects weighed more than impoverished subjects) and response rate (impoverished subjects generally responded faster than enriched subjects). In addition, SHRs tended to respond variably throughout the experiment, whereas WKYs were more sensitive to the variability contingencies. Thus, behavioral variability was affected by genetic strain and by reinforcement contingency but not by the environment in which the subjects were reared.

Key words: behavioral variability, response sequences, attention deficit hyperactivity disorder, body weight, response rate, environmental enrichment, deprivation, spontaneously hypertensive rats

The spontaneously hypertensive rat (SHR) may model some behavioral aspects of human attention deficit hyperactivity disorder (ADHD), a childhood disorder with symptoms including hyperactivity, impulsivity, and inability to sustain attention (American Psychiatric Association, 1987; Cierpial & McCarty, 1987; Cierpial et al., 1989; Sagvolden, Metzger, & Sagvolden, 1993; Sagvolden et al., 1992; Sagvolden, Pettersen, & Larsen, 1993; Tang, Gandelman, & Falk, 1982; Wultz & Sagvolden, 1992; Wultz, Sagvolden, Moser, & Moser, 1990). In support of this assertion, when SHR rats were compared with Wistar-Kyoto (WKY) rats (their normotensive genetic progenitor), the SHRs were more active and explored more (Hard et al., 1985; Hen-

dley et al., 1985; McCarty & Kopin, 1979; Moser, Moser, Wultz, & Sagvolden, 1988). SHRs were less reactive than WKYs to novel stimuli (e.g., a burst of white noise resulted in lower mean amplitude of startle response in SHRs), and SHRs showed a shorter duration of audiogenic immobility (freezing) (Delini-Stula & Hunn, 1985; Hard et al., 1985; Sutterer, McSparren, & Ingerman, 1988; however, see Knardahl, 1982; Rettig, Geyer, & Printz, 1986). Because of such findings, SHRs have been labeled as “fearless” or “anxiolytic” (Goto, Conceicao, Ribeiro, & Frussa-Filho, 1993), a description that may parallel the impulsive behavior of ADHD children labeled as “high risk takers.”

Learning deficits may provide another similarity between SHR rats and children with ADHD. Just as these children sometimes exhibit learning difficulties, SHRs required more trials than WKYs to learn to go to one arm of a T-maze (Low, Whitehorn, & Hendley, 1984) or to learn to repeat particular sequences of responses (Mook, Jeffrey, & Neuringer, 1993). Injection of amphetamine resulted in the SHR subjects learning sequences of responses as rapidly as control WKYs (Mook & Neuringer, 1994), again paralleling human ADHD, where administration

Supported in part by grants from Fundação de Amparo a Pesquisa do Estado de São Paulo and Conselho Nacional de Desenvolvimento Científico e Tecnológico to the first author and grants from the Medical Research Foundation of Oregon and National Science Foundation to the third author. We thank Gene Olson for his able assistance in caring for the animals.

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of amphetamine or methylphenidate often improves performance of repetition-demanding school tasks (Barkley, 1990; Gadow, 1986).

A third area of similarity involves behavioral variability. When food reinforcers were provided independently of variability, SHRs responded more variably than WKYs (Low *et al.*, 1984; Mook *et al.*, 1993). When high variability was required for reinforcement, both SHRs and WKYs satisfied the contingencies. The high baseline or operant-level variability in SHR rats may be related to reports that they sometimes learn more rapidly than control subjects in situations in which initial variability may be functional (e.g., in radial arm mazes or Morris water mazes) (Mook *et al.*, 1993; Widy-Tyszkiewicz, Scheel-Kruger, & Christensen, 1993; Wyss, Fisk, & Van Groen, 1992). Another way to look at these data is that SHRs tend to respond variably whether or not variability is explicitly reinforced; WKYs, on the other hand, increase their response variability only when such variability is necessary. Children with ADHD are also reported to exhibit generally greater variability across tasks than normal controls (Barkley, 1981, 1990; Zentall, 1984).

The present study extended previous research on behavioral variability in these rats by asking whether environmental rearing conditions would influence levels of variability and, in particular, whether an enriched rearing environment would result in the variability of SHR subjects approaching that of WKY control subjects. This question was motivated by three lines of research, one directed at human ADHD and two utilizing animal models. First, relatively high incidences of ADHD are reported in poor areas and in urban centers (Szatmari, Offord, & Boyle, 1989; Trites, 1979). These correlations have led to the suggestion that impoverished environments might contribute to ADHD. Many different factors may be confounded, of course, such as the finding that women in lower socioeconomic groups, in which environmental impoverishment might be found, tend also to manifest poor nutrition. An animal model may help to identify functional relationships.

A second line of research shows that when "debilitated" animals are placed in enriched environments, their behavior sometimes approximates that of control subjects. Such

studies have involved subjects whose debilities were produced by alcohol injections (Hannigan, Berman, & Zajac, 1993), brain lesions (Rose, Al-Khamees, Davey, & Attree, 1993; Rose, Davey, & Attree, 1993), toxic substances (Saari, Fong, Shivji, & Armstrong, 1990), and depletion of neurotransmitters (Pappas, Murtha, Park, & Condon, 1992; see also Renner & Rosenzweig, 1987). Might an enriched environment also result in SHR rats behaving like control WKYs?

A third line of research shows that when SHR infants are cross-fostered to WKY mothers, the infants' physiology and behavior sometimes approximate those of the WKY strain (e.g., Cierpial *et al.*, 1989; Cierpial, Murphy, & McCarty, 1990; McCarty & Fields-Okotcha, 1994). Although these cross-fostering results are consistent with an effect of rearing environment (WKY dams behave differently than SHR dams), here, too, other confounding factors might be responsible (e.g., differences in the dam's milk). Thus, once again, independent manipulation of the environmental milieu might help to identify important functional relationships.

In the present experiment, differences in rearing environments were established by housing "enriched" animals in large multi-compartment group cages (5 animals per cage) containing many different objects (e.g., tunnels, ladders, balls, etc.), with the cages located in a room visited continually by students and research personnel and containing many other rats. These subjects were frequently handled and placed in "play pens" where they could explore, interact with one another, and interact with a variety of objects. "Impoverished" subjects were housed alone, one animal per cage, in a quiet room separate from the main animal colony. These subjects were handled minimally (only when necessary for care and cleaning) and had no direct interactions with conspecifics or with novel objects. These housing procedures were similar to those commonly employed in studies that demonstrate physiological and behavioral effects of enriched versus impoverished rearing environments (Renner & Rosenzweig, 1987).

Four groups of animals were studied: enriched SHR, impoverished SHR, enriched WKY, and impoverished WKY. Because previous research had shown that sequence vari-

ability is affected by reinforcers contingent upon that variability, two reinforcement contingencies were compared: baseline, in which reinforcers were given without regard to behavioral variability, and vary, in which reinforcement depended upon relatively high levels of such variability. The main question was whether an enriched rearing environment would cause SHR behavior to approximate that of the WKY control subjects under both baseline and vary contingencies.

METHOD

The experiment was divided into two parts, separated by 4 months. In the interim, our laboratory was moved to a new building and the experimental rooms and animal colony therefore changed. Apparatus also differed somewhat, as will be described below. During the intervening 4 months, subjects were maintained with free access to food and water. The cages used to house the animals (enriched and impoverished) were the same throughout the experiment.

Subjects

Ten male spontaneously hypertensive rats and 10 male Wistar-Kyoto rats were obtained from Charles River Laboratories immediately after weaning at 21 days of age. Upon arrival in our laboratory, half of the SHRs and half of the WKYs were randomly selected and placed in an impoverished rearing environment, and the other half were placed in an enriched environment. Each impoverished rat (5 SHRs and 5 WKYs) was housed individually in a stainless steel cage (20 cm by 24 cm by 18 cm) with wire mesh floors, located in a room containing only these animals, and handled with gloves only as necessary for their care and the experimental procedures. The 5 enriched SHRs were housed together in a group cage (86 cm by 30 cm by 35 cm) containing sawdust for burrowing and a variety of "toys," including balls, hanging chains, copper tubes, marbles, and a running wheel. The 5 enriched WKYs were housed together in an identical group cage containing identical objects. Both group cages were located in a large animal colony visited throughout the day by researchers and students. Prior to and throughout Part 1 (to be described below), each enriched animal was handled at

least 4 days per week, received at least 15 min per day of human contact, and was placed several times per week in a wooden play box (61.25 cm by 81.25 cm by 28.75 cm) containing sawdust and a variety of objects such as plastic tubing, golf balls, and glass Petri dishes. Following the completion of Part 1, the enriched animals were maintained in their group home cages and provided with sawdust and toys, but they no longer received daily handling or experience in the play box. The impoverished animals continued to be housed in single-animal cages located in a separate room and were handled only as necessary throughout the experiment.

Until 3 months of age, all subjects were maintained with free access to food and water, at which time they were placed on a 21- to 22-hr food deprivation schedule, with food freely available for 2 hr per day. Impoverished animals were fed in their home cages, and enriched animals were fed as a group in feeding cages separate from their home cages in Part 1 and obtained food from hoppers attached to the outside of their home cages in Part 2. Water was continuously available in all home cages. A 12:12 hr light/dark cycle was maintained throughout, with experimental sessions occurring during the light phase, 5 to 7 days per week.

Apparatus

Part 1 of the experiment utilized 10 modified Gerbrands operant conditioning chambers (27 cm by 28 cm by 30 cm) with the ceiling and back and front walls made of clear Plexiglas and the side walls made of aluminum. The floor was made of wire bars 1 cm apart, above a removable tray containing kitty litter. The left wall contained three response keys and a square opening, 4.5 cm wide, below the middle key that were not used during this experiment. The right aluminum wall contained two response levers, left (L) and right (R), that were 5 cm wide, 9 cm apart center to center, and 6 cm above the floor. Between the levers was a pellet tray (3 cm in diameter) located 3 cm above the floor, into which 45-mg Noyes pellets were released by a Davis Scientific pellet dispenser located behind the wall. A small audio speaker provided auditory stimuli, and a 1.1-W lamp, located on the top of the ceiling, provided house-light. Each chamber was contained in a

sound- and light-attenuating cubicle (52 cm by 80 cm by 41 cm) with a one-way mirror on the door through which the animals could be observed.

Part 2 utilized five modified Gerbrands operant conditioning chambers (27 cm by 28 cm by 30 cm) that were somewhat different from those in Part 1, with ceiling and back and front walls constructed of Plexiglas and side walls made of aluminum. The right side wall contained three response levers, with only the middle and right levers used in the present experiment and the leftmost lever locked in place. The two operative levers will again be referred to as L and R, respectively. The levers were located 9 cm above the floor and 9 cm apart. A pellet tray was located in the center of this wall, 1.5 cm above the floor, into which were dispensed 45-mg Noyes food pellets from a Gerbrands pellet dispenser. A 1.1-W lamp located on the top of the ceiling provided houselight, and a speaker, located behind the wall containing the levers, provided auditory stimuli. Each chamber was housed in a sound- and light-attenuating box containing a viewing lens to permit observation. In both parts, each chamber was connected to an Apple® Macintosh computer through a Metaresearch Benchtop® interface, and programs were written in True Basic.

Procedure

There were five experimental conditions, with each session lasting 45 min or until 200 trials were completed, whichever occurred first. (We also measured a number of other aspects of behavior, e.g., neophobia, number of pellet presentations before first eating, time to shaping, and acquisition of repeated patterns, to be described in a different forum.) A trial, initiated by illumination of the houselight, consisted of four lever-press responses on the L or R lever. Each of the first three responses was followed by a 0.05-s darkening of the chamber, which served as feedback for effective responses, and the fourth response was followed by an end-of-trial (EOT) signal provided by a 1-s period of dark. Trials without reinforcement ended with only the EOT; trials with reinforcement ended with the EOT followed by a food pellet. Providing an EOT after all trials, those with reinforcement and those without, resulted in a tendency to pause after the fourth

response in a trial rather than responding continuously across trials. Two other differences distinguished trials with reinforcement from those without. First, for trials with reinforcement, the EOT included a beeping tone (3000 Hz in 0.05-s bursts), whereas no sound was provided at the end of trials containing no reinforcement. Second, for trials without reinforcement, the EOT was reset by responses, to insure a period of no responding between trials. For trials containing reinforcement, responses were naturally interrupted by a period of eating; therefore, the prepellet EOT was not reset by responses (they were rare) (i.e., a pellet was presented at the end of the EOT lasting exactly 1 s). Due to a programming error in Part 2, only responses on the R lever reset the EOT for trials that did not end with reinforcement, with responses on the L lever during this period having no effect. Because few responses occurred during EOTs by this stage of the experiment, the programming error appeared to have had little or no effect.

Part 1

Prior to Part 1, each rat was placed in the experimental chamber for two 45-min sessions with 20 Noyes pellets in the food hopper at the beginning of each session. Broad categories of behavior were recorded by hand, as were the number of pellets eaten. Successive approximations to the lever-press response were then reinforced with food pellets, and the animals were given five training sessions during which every response resulted in a food pellet. In most cases, shaping of responses on one lever resulted in responding on both levers. In a few cases in which responses were made only to one lever, presses of that lever were put on extinction for short periods until the subject responded on both levers (this occurred within the five training sessions). No group differences were observed in any behavioral measure taken during these preliminary training phases, including time to learn to press the levers. In the first of the two experimental phases, a pellet was contingent on four responses without regard to which lever was pressed (i.e., a fixed-ratio [FR] 4 contingency). Any combination of four responses across the two levers resulted in reinforcement (e.g., LLLL, LRLR, RRRR, or LRRR, etc.). In the second phase,

a vary contingency required that the current sequence of four responses had to differ from each of the previous four sequences for reinforcement (i.e., a lag 4 variability contingency; Neuringer, 1991, 1992; Neuringer & Huntley, 1992; Page & Neuringer, 1985). For example, if an animal had just responded with LLRR, reinforcement was provided only if none of the previous four trials contained that same pattern of responses (e.g., if the four previous sequences had been LLLL, RRLR, RRLR and LLRL). If the current sequence repeated any one of the previous four sequences, the trial ended without reinforcement. Seven sessions were provided under each of the two phases, previous research in our laboratory having indicated that this would suffice for the vary and FR 4 contingencies to yield behavioral differences.

Part 2

Part 2 repeated the same FR 4 and vary contingencies used in Part 1. Because a 4-month period intervened between Parts 1 and 2, during which tail markings of the group-housed animals faded sufficiently to make a few of their identities uncertain (group identities remained certain) and because the apparatuses differed, the results were analyzed separately for the two parts. Part 2 concluded with a yoke procedure to control for reinforcement frequency. Reinforcement had been more frequent under the FR 4 contingencies than under vary. Therefore, during the yoke phase of Part 2, reinforcement was provided independently of variability, as in the FR 4 phases, but the frequency of reinforcement was yoked to that in vary: Reinforcement did not depend on any particular sequence of left and right responses; instead, whether or not a sequence ended with food was determined by whether the subject had received food during an analogous trial in a vary session (Page & Neuringer, 1985). The last three sessions of the vary condition were used to schedule reinforcements under yoke, with the three sessions cycling. For example, reinforcement during the first, second, and third yoke sessions replicated the same pattern of trials with and without reinforcement during the 15th, 14th, and 13th vary sessions, respectively; reinforcement during the fourth yoke session replicated the 15th vary session, and so on. In brief,

frequencies and distributions of reinforcements were identical in vary and yoke, and four responses per trial were required in both phases, but sequences of L and R responses were required to vary during the vary phase but were permitted and not required to vary during yoke. Fifteen sessions were provided under the FR 4 and yoke contingencies, this number greater than in Part 1 to insure that differences would be maintained over a longer period of testing. Because all subjects quickly reached high and relatively stable levels of sequence variability under vary, this condition was terminated after 10 sessions.

Data Analyses

The main dependent variable was U value, a measure of overall sequence variability, calculated as follows:

$$U = -\sum[(P) * \log_2(P)]/\log_2(16),$$

where P is the the relative frequency of each sequence and the summation is across the 16 possible sequences. $U = 1.0$ indicates that all sequences occurred equally (high variability), $U = 0.0$ indicates that only one sequence occurred during the session (low variability), and intermediate values indicate more or less variation according to their approximation to 1.0 (Page & Neuringer, 1985).

Separate analyses of variance (ANOVA) were performed for the two parts of the experiment, with the data provided by arithmetic averages from each subject over the last three sessions of each condition. There were two between-subjects variables, rearing condition (enriched vs. impoverished) and genetic strain (SHR vs. WKY), and one within-subject variable, reinforcement contingency (FR 4 vs. vary in Part 1; FR 4 vs. vary vs. yoke in Part 2). Newman-Keuls tests were used for pairwise comparisons, and statistical significance was indicated by $p < .05$.

RESULTS

Response variability is discussed first. Figure 1 shows the U values for each subject in each of the four groups across each session of Part 1, and Figure 2 shows similar data for Part 2. For ease of comparison, Figure 3 shows group averages over the last three sessions of each phase, these being the data used for the statistical analyses. Enrichment and

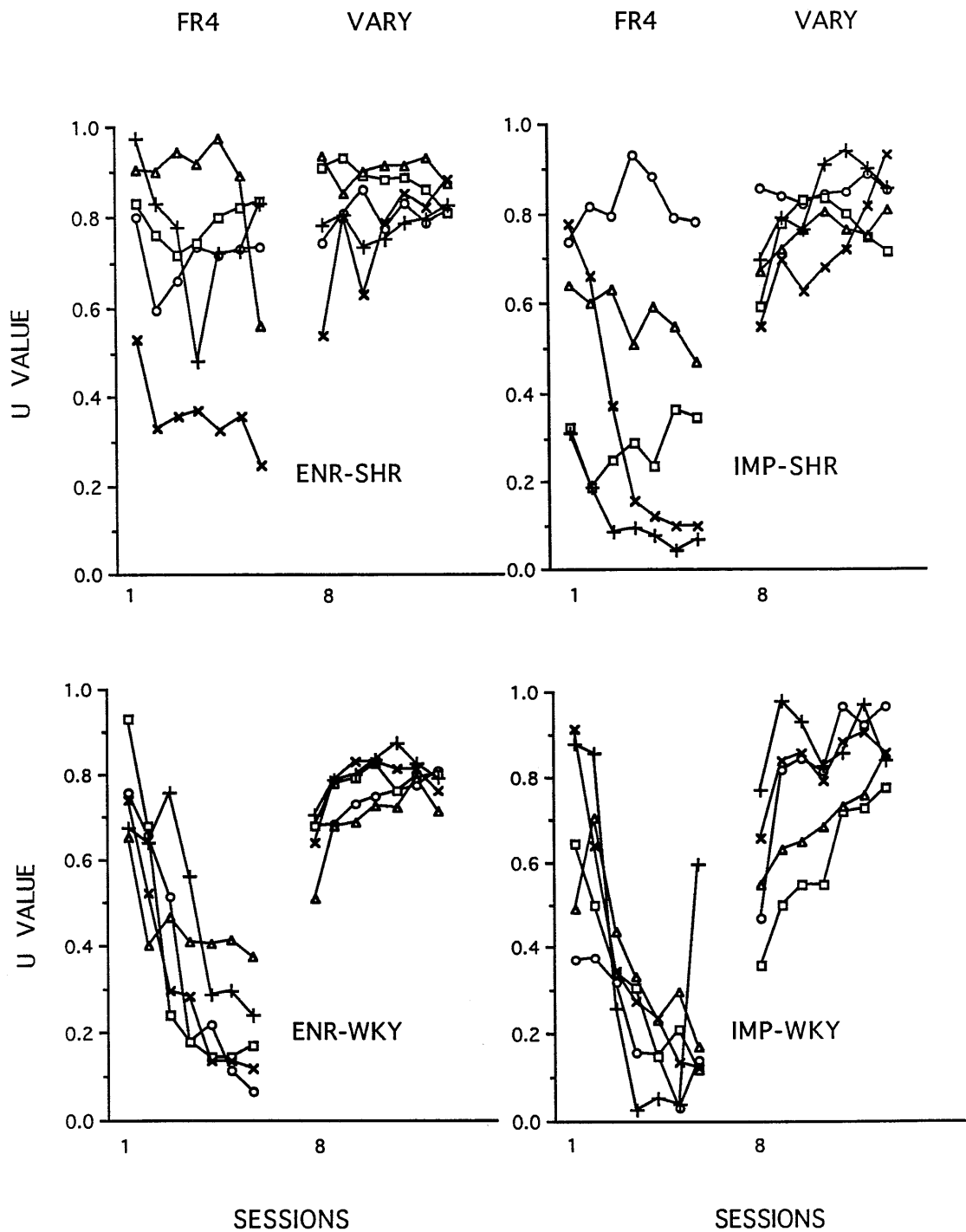


Fig. 1. U values, a measure of sequence variability, for each session in Part 1. High U s indicate high levels of sequence variability. Under FR 4 contingencies, reinforcers were provided independently of sequence variations. Under vary contingencies, reinforcers depended upon high levels of variations. The 5 subjects in each of the four groups (enriched SHR, impoverished SHR, enriched WKY, and impoverished WKY) are shown individually.

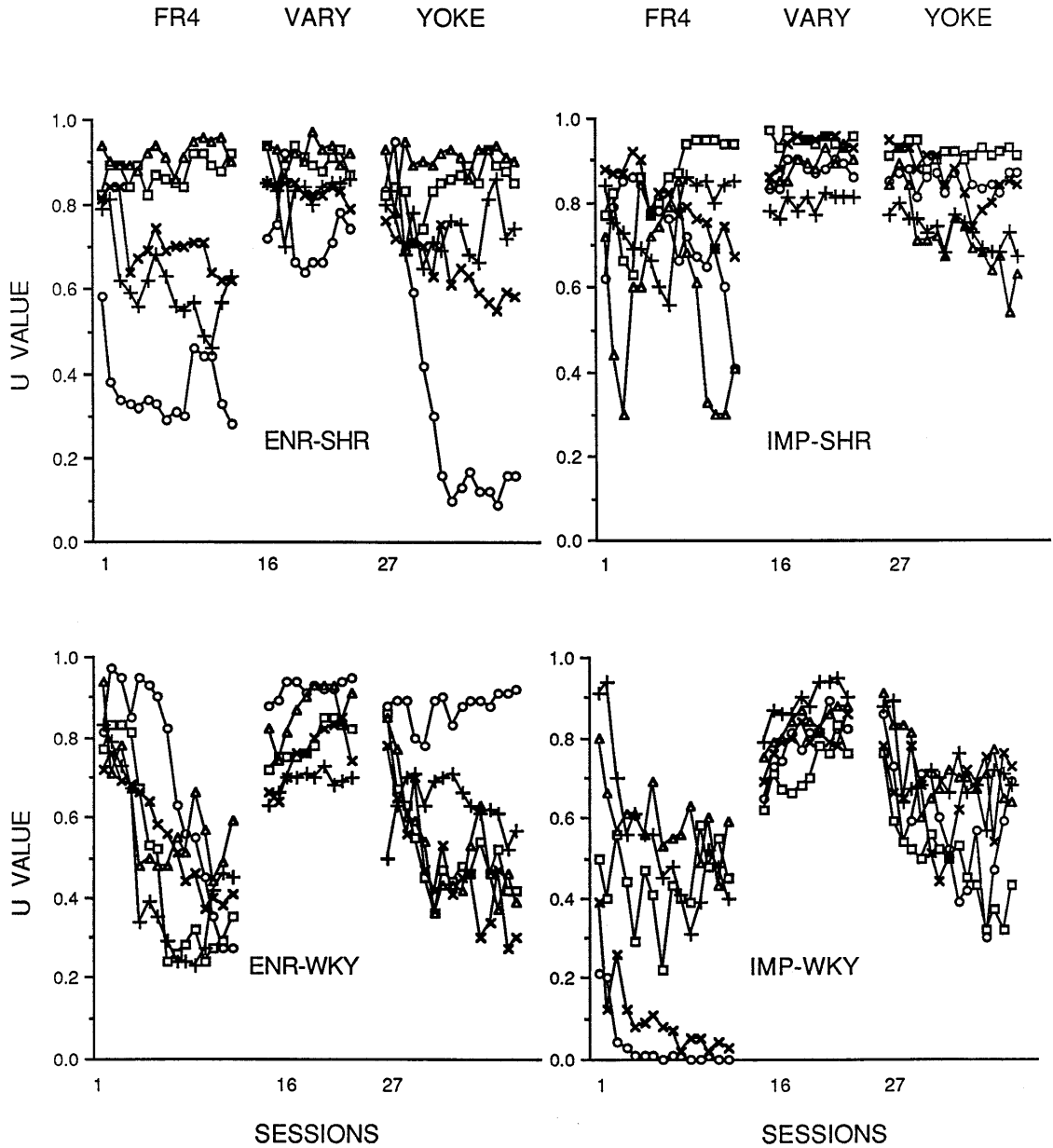


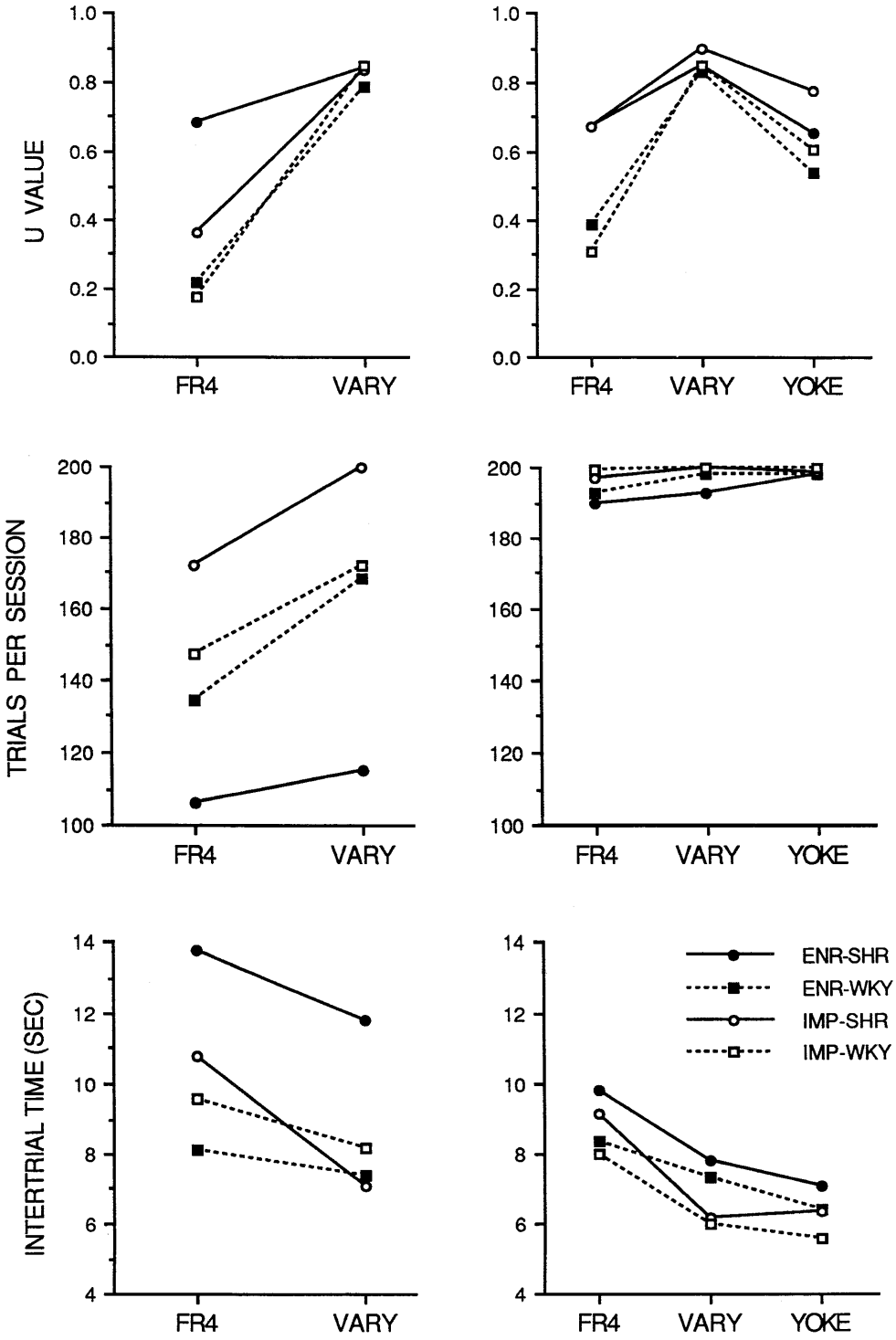
Fig. 2. *U* values for each session in Part 2. Under FR 4 contingencies, reinforcers were provided independently of sequence variations. Under vary contingencies, reinforcers depended upon high levels of variations. Under yoke contingencies, frequencies of reinforcement were matched to those in the vary condition, with the reinforcers presented independently of sequence variability.

impoverishment conditions resulted in no statistically significant effects on response variability in either part of the experiment, $F(1, 16) = 3.078$ and $F(1, 16) = 0.255$ in Parts 1 and 2, respectively. On the other hand, although there was considerable variance with-

in each group, strain exerted statistically significant main effects on response variability, $F(1, 16) = 14.587$ and $F(1, 16) = 7.826$ in Parts 1 and 2, as did reinforcement contingencies, $F(1, 16) = 93.037$ and $F(2, 32) = 26.510$ in Parts 1 and 2. Of most importance,

PART I

PART II



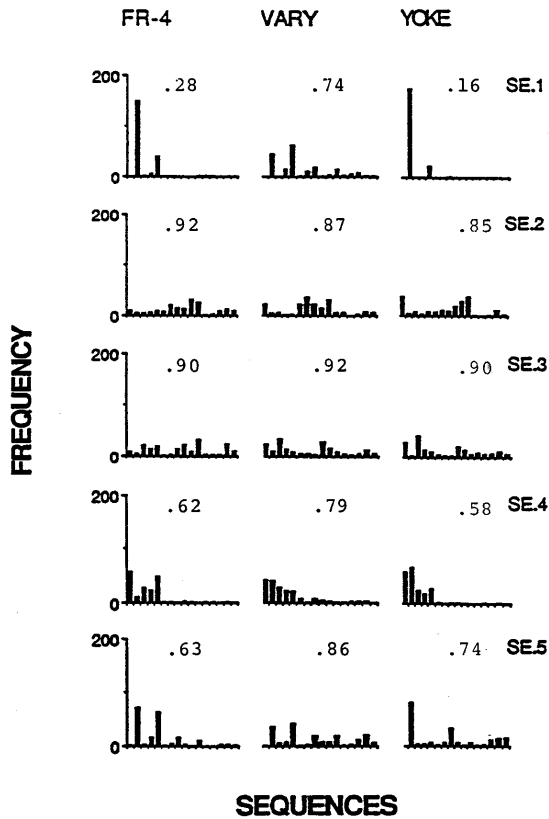


Fig. 4. Frequency of occurrence of each of the 16 possible sequences during the final sessions of FR 4, vary, and yoke contingencies of Part 2. Data shown are from each individual subject in the enriched SHR group, with *U* values provided above each graph. The 16 possible sequences were ordered from left to right along the abscissa so that the leftmost sequences have the fewest alternations and the rightmost sequences have the most alternations, that is, LLLL, RRRR (no alternations); LLLR, LLRR, LRRR, RLLL, RLLL, RRRL (one alternation); LLRL, LLLL, LRRR, RLLR, RLRR, RRLR (two alternations); and LRLR, RLRL (three alternations).

significant interactions were obtained between genetic strain and reinforcement contingency in both parts of the experiment, $F(1, 16) = 10.634$ and $F(2, 32) = 4.784$ in Parts 1 and 2. Additional analyses (Newman-Keuls) of these interactions showed that the *U* values

from the SHR groups were significantly higher than those from the WKYs under FR 4 contingencies in both parts of the experiment; this difference approached statistical significance ($p < .08$) under the yoke contingencies of Part 2, with SHRs responding more variably than WKYs; and SHR and WKY *U* values did not differ under the vary contingencies in either part. In other words, when food pellets were contingent upon variability (vary), both SHRs and WKYs responded variably, but when pellets were presented independently of variability (FR 4 and yoke), the SHRs responded, on average, with higher levels of variability than did the WKYs.

Analyses of particular sequences support these conclusions. Figures 4, 5, 6, and 7 show frequencies of each of the 16 possible sequences for each animal in each of the four groups. To save space, we show data from the final sessions of each of the three conditions in Part 2 (i.e., the final session of FR 4, vary, and yoke, respectively). These figures show, first, that under vary contingencies, the distribution of sequences was relatively flat for all subjects, indicating high sequence variability. Second, for many SHR subjects (SE 2, SE 3, SI 3, and SI 5), distributions under the FR 4 and yoke contingencies were also quite flat. Thus, SHRs tended to behave variably even under baseline conditions. Third, for the remaining subjects, the distributions were generally more peaked under FR 4 and yoke than under vary, indicating that sequence variability decreased when the contingencies did not require variability. This characterized all of the WKY subjects, both enriched and impoverished, as seen in Figures 6 and 7. Fourth, under FR 4 and yoke, the distribution of sequences tended to be asymmetric, with the high peak tending to be to the left, showing that subjects favored sequences with few alternations.

Although rearing conditions did not influence behavioral variability, other effects of rearing were observed. Table 1 shows group

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Fig. 3. *U* values (top row), number of trials per session (with 200 being maximum, middle row), and median intertrial times (bottom row) under FR 4 and vary contingencies of Part 1 (left column) and FR 4, vary, and yoke contingencies of Part 2 (right column). Data are arithmetic means across the final three sessions under each contingency and across the 5 subjects in each group. Note that lines connect the points in these graphs in order to enhance visual clarity and that the lines do not imply that FR 4, yoke, and vary data lie along a single quantitative continuum.

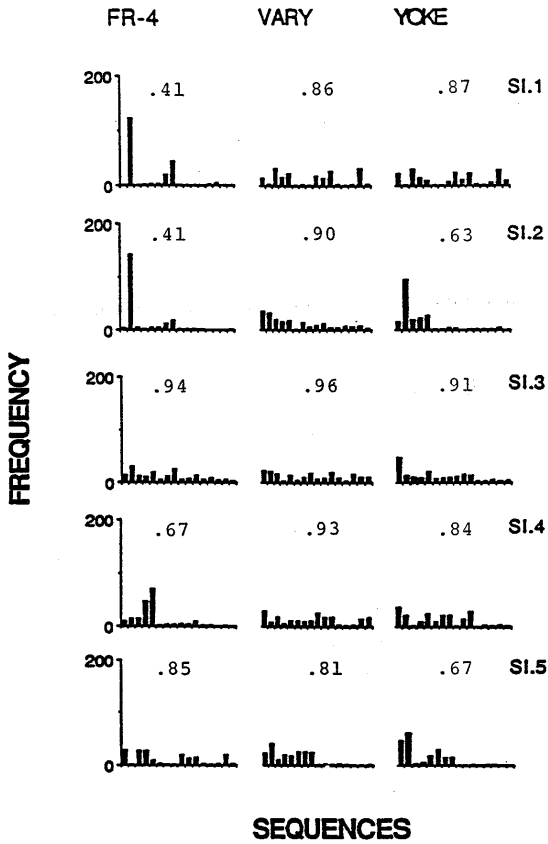


Fig. 5. Frequency of occurrence of each of the 16 possible sequences during the final sessions of FR 4, vary, and yoke contingencies of Part 2 for individual subjects in the impoverished SHR group. See Figure 4 for order of the sequences along the abscissa.

average body weights at the completion of each part of the experiment. At the end of Part 1, the enriched rats weighed significantly more than their impoverished counterparts, $F(1, 16) = 24.685$, and SHRs weighed significantly more than WKYs, $F(1, 16) = 6.242$. Although body weights were not recorded at the outset of the experiment, the subjects were randomly assigned to enriched and impoverished conditions; therefore, it is likely that rearing environment was responsible for some of the observed weight differences. By the end of Part 2, this pattern had changed somewhat. Although there was again a main effect of rearing environment, with enriched subjects weighing more than impoverished subjects, $F(1, 16) = 37.252$, a significant Environment \times Strain interaction was now observed, $F(1, 16) = 13.638$. Analysis of this in-

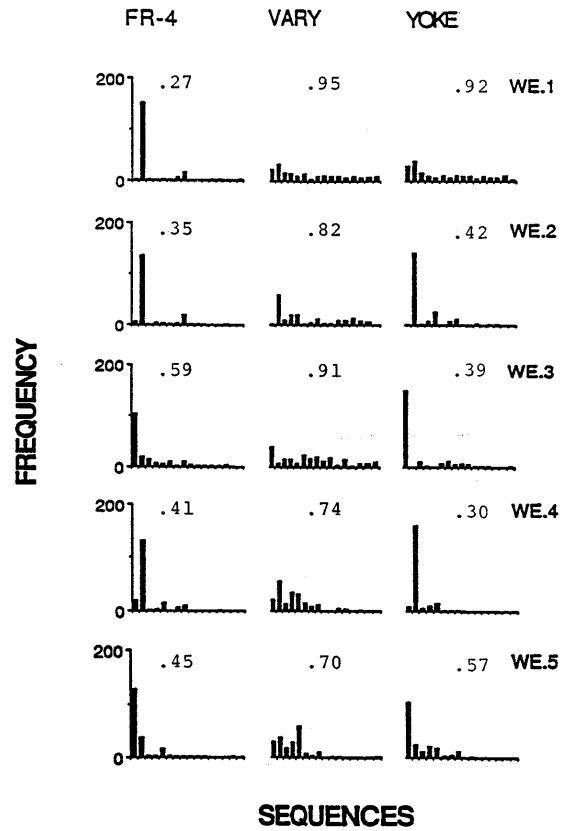


Fig. 6. Frequency of occurrence of each of the 16 possible sequences during the final sessions of FR 4, vary, and yoke contingencies of Part 2 for individual subjects in the enriched WKY group. See Figure 4 for order of the sequences along the abscissa.

teraction showed a relatively small difference in weights between the two SHR groups, $F(1, 16) = 2.905$, not significant, but a large and statistically significant weight difference between the two WKY groups, $F(1, 16) = 47.986$. The impoverished SHRs again weighed significantly more than the impoverished WKYs, $F(1, 16) = 7.318$, but the enriched SHRs now weighed significantly less than their WKY counterparts, $F(1, 16) = 6.338$.

Rearing conditions also influenced the number of trials completed per session (middle graphs of Figure 3). The enriched animals completed fewer trials than the impoverished ones in Part 1, $F(1, 16) = 20.430$. Also significant in Part 1 was the interaction between strain and rearing conditions, $F(1, 16) = 13.290$, with impoverished SHRs re-

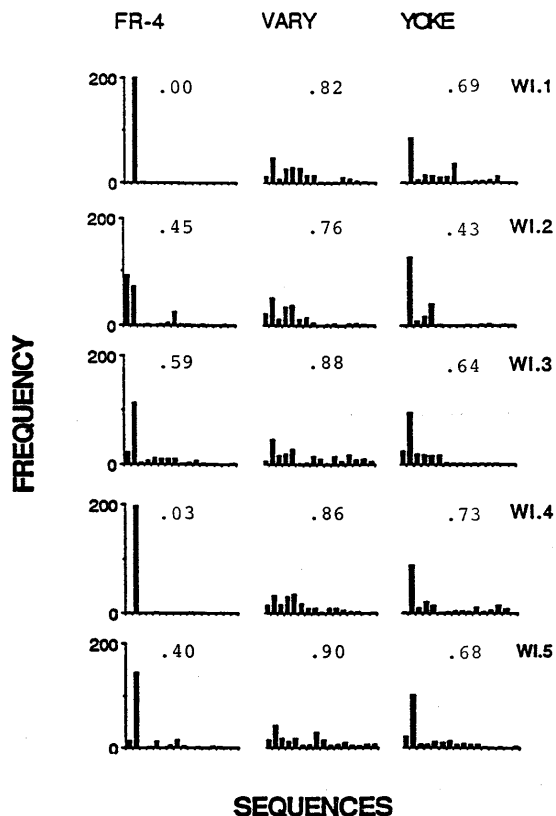


Fig. 7. Frequency of occurrence of each of the 16 possible sequences during the final sessions of FR 4, vary, and yoke contingencies of Part 2 for individual subjects in the impoverished WKY group. See Figure 4 for order of the sequences along the abscissa.

sponding more than their enriched counterparts, but no difference between the WKY groups. None of the differences were significant in Part 2 because, as can be seen, all groups approached the limit of 200 trials per session; thus, there may have been a ceiling effect.

Because trials per session approached the imposed limit, we also evaluated within-session intertrial times (ITT) or intertrial latencies (Figure 3, bottom). Session median ITTs were calculated by ranking the times between

starts of successive trials, with all trials in the session included. There was a statistically significant interaction between strain and rearing condition in Part 1, $F(1, 16) = 40.933$, and a significant main effect of rearing condition in Part 2, $F(1, 16) = 10.783$. Enriched SHRs responded more slowly (longer ITTs) than their impoverished counterparts throughout the experiment. The same effect was seen for the WKYs in Part 2, but the enriched WKYs responded faster than impoverished WKYs in Part 1. Comparing the two strains, SHRs responded more slowly than WKYs, $F(1, 16) = 31.632$ and $F(1, 16) = 8.188$ in Parts 1 and 2. The increase in response speed across the two phases of Part 1, $F(1, 16) = 21.245$, and three phases of Part 2, $F(2, 32) = 157.55$, may have been related to changes in the subjects' ages, body weights, and conditioning experiences across the experiment. ITTs and U values for individual animals are provided in Appendixes A and B.

DISCUSSION

The main question was whether an enriched rearing environment would cause the SHR strain of rats to behave like control WKYs. Other studies have shown that when animals are adversely affected by various types of brain lesions or drugs, an enriched environment may result in behavior that approximates that of control subjects (e.g., Rose, Al-Khamees, Davey, & Attree, 1993; Rose, Davey, & Attree, 1993). We asked whether the same might be true for genetically mediated differences, and in particular whether response-sequence variability in SHR rats would be influenced by enriched versus impoverished rearing environments. The main result was negative: Rearing conditions did not affect behavioral variability in either SHRs or control WKYs.

Negative results are always difficult to interpret. Absence of differences could be due to unidentified factors or to poor experimen-

Table 1
Mean (and SD) body weights (g) of the four groups at the end of Parts 1 and 2.

	Enriched SHR	Impoverished SHR	Enriched WKY	Impoverished WKY
Part 1	330.6 (20.5)	302.6 (13.8)	319.2 (15.1)	280.2 (7.2)
Part 2	401.4 (29.8)	379.6 (14.7)	433.6 (16.1)	345.0 (16.5)

tation, and negative findings tend to be dismissed as uninformative. However, in the present case, rearing environment (the main independent variable) influenced two other measures, namely body weight and response latency. Animals raised under enriched conditions weighed more than those raised under impoverished conditions and tended to respond more slowly. Furthermore, behavioral variability (the main dependent variable) was itself significantly influenced by genetic strain as well as by reinforcement contingencies. Because independent and dependent variables could each be related to other aspects of the experiment, a conclusion of no effect is supported: Rearing environment did not influence behavioral variability.

Further support comes from the fact that many of the present results are consistent with previous findings. For example, SHR rats were more likely to vary their lever presses than WKYs under baseline conditions in which reinforcement did not depend upon variations (Low *et al.*, 1984; Mook *et al.*, 1993; Mook & Neuringer, 1994). Previous studies have also shown the importance of reinforcement contingencies in the control of behavioral variability (Machado, 1989; Mook *et al.*, 1993; Morgan & Neuringer, 1990; Neuringer & Huntley, 1992; Page & Neuringer, 1985). In the present experiment, as well as in previous research, genetic strain and reinforcement contingencies interacted in affecting levels of behavioral variability. The findings can be summarized as follows: SHRs respond more variably than WKYs when reinforcement contingencies do not require variability. Both strains respond variably when reinforcement contingencies require such variability, with schedule of reinforcement accounting for the decreased difference between strains. (Note that under some situations, *e.g.*, in radial arm mazes and when key pressing is the operant response, SHRs continue to respond more variably than the WKYs under variability-reinforcing contingencies, but the difference between groups is smaller than in baseline; Mook *et al.*, 1993; for related work, see Morgan & Neuringer, 1990.)

Differences in body weights as a function of rearing environments have also been documented previously. In the current experiment, as well as in some previous studies, enriched animals weighed more than impover-

ished ones (*e.g.*, Perry, 1991; Wainwright, Levesque, Krempulec, Bulman-Fleming, & McCutcheon, 1993). In one such study, stimulated SHRs weighed significantly more than unstimulated SHRs, but no difference was found between weights of stimulated and unstimulated WKYs (Niewiadomska & Lukaszewska, 1987). Furthermore, a number of studies show that impoverished animals weigh more than enriched ones (Renner & Rosenzweig, 1987), a finding opposite to ours. One factor that may help to explain these different results—enriched animals weigh more than impoverished animals in some studies, but less in others—is the feeding regime under which subjects are maintained. In the present case, subjects were maintained on a 22-hr food deprivation regimen, thereby permitting the study of food-reinforced responding, whereas in most other studies, animals were maintained on a free-feeding regimen. Fiala, Snow, and Greenough (1977) suggested that, under free-feeding conditions, impoverished animals might eat more than enriched animals because the impoverished subjects have few alternative activities and nothing to gnaw on besides the freely available food. Further research is necessary to compare body weights in subjects maintained with *ad lib* food versus restricted feeding under enriched versus impoverished rearing conditions. Another aspect of the weight data deserves further study. By the end of Part 2, the enriched WKYs weighed more than the enriched SHRs, a difference in weights in the same direction as for mature animals raised under normal conditions in the Charles River breeding colony (personal communication). (At weaning, SHR and WKY weights are approximately equal.) On the other hand, at the end of Part 2, the impoverished WKYs weighed considerably less than the impoverished SHRs. Said differently, the impoverished SHR weights were relatively close to the enriched SHR weights, whereas the impoverished and enriched WKY weights differed significantly. Thus, with respect to body weights, the SHRs may have been protected from the effects of environmental impoverishment.

The current results parallel a number of findings when children with ADHD are compared with normal controls. Higher levels of variability in SHRs than WKYs, smaller changes in performance by SHRs as a func-

tion of changed reinforcement contingencies (FR 4 to vary), and lower frequencies of on-task behavior (i.e., longer ITTs) are analogous to effects reported for ADHD children (Aman & Turbott, 1986; Barkley, 1981, 1990; Chee, Logan, Schacher, Lindsay, & Wachsmuth, 1989; Douglas, 1972; Zentall, 1984; Zentall, Falkenberg, & Smith 1985). The present results therefore support the conclusion of Sagvolden et al. (1992) that SHRs can serve as a model of some aspects of human ADHD.

The main question raised, however, was whether enriched environmental rearing conditions would cause performances by this putative animal model of human ADHD to approximate those of control subjects (i.e., would enrichment cause behavior of SHRs to approximate that of control WKYs, and would impoverishment increase behavioral differences). As described above, rearing conditions had no observable effect on behavioral variability. With respect to some other measures (e.g., trials per session and intertrial times), the impoverished SHR rats generally behaved more like the WKYs than did the enriched SHRs. Thus, a conservative conclusion is that environmental enrichment did not change the behavior of SHRs in the direction of control WKYs. Additional tests are needed (e.g., utilizing different enrichment procedures, different measures of variability, and different behavior). Also, further consideration must be given to the possibility that enrichment may increase differences between SHRs and WKYs, possibly because of differences in emotionality and reactivity of the two strains. Although the present study indicates that enrichment did not narrow the differences between a model of ADHD and control subjects, animal experiments can provide only hypotheses concerning human populations, and caution must be observed not to assume relevance of animal-model results before they are validated. One such hypothesis is that environmental enrichment will not result in more normal behavior by children with ADHD. Indeed, for some behavior, the opposite may be found (i.e., environmental enrichment may increase differences between ADHDs and controls). Another hypothesis is that raising a child in an impoverished environment will not cause ADHD. Both of these hypotheses are consistent with

Barkley's conclusion that "little if any evidence supports the notion that ADHD can arise purely out of social or environmental factors" (Barkley, 1990, p. 105).

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Received April 7, 1995
 Final acceptance August 9, 1995

APPENDIX A

Individual animals' *U* values and intertrial times (ITT) averaged over the last three sessions of each phase in Part 1. Each line represents an individual animal.

	FR 4		Vary	
	<i>U</i> value	ITT (s)	<i>U</i> value	ITT (s)
Enriched SHR	.725	13.27	.809	15.85
	.819	15.87	.852	10.48
	.808	13.52	.904	9.60
	.312	13.30	.851	12.47
	.758	12.87	.802	10.78
Impoverished SHR	.868	11.38	.862	6.93
	.314	10.02	.753	6.33
	.537	10.50	.774	6.73
	.109	10.90	.822	7.05
	.064	11.12	.898	8.50
Enriched WKY	.132	7.72	.781	8.70
	.152	7.65	.785	9.20
	.398	10.18	.742	7.77
	.129	7.32	.796	7.68
	.273	7.87	.831	8.35
Impoverished WKY	.106	10.25	.951	7.65
	.160	10.77	.737	11.00
	.233	10.75	.778	7.00
	.165	7.73	.880	6.70
	.228	8.30	.889	8.50

APPENDIX B

Individual animals' *U* values and intertrial times (ITT) averaged over the last three sessions of each phase in Part 2. Each line contains data from an individual animal.

	FR 4		Vary		Yoke	
	<i>U</i> value	ITT (s)	<i>U</i> value	ITT (s)	<i>U</i> value	ITT (s)
Enriched SHR	.350	10.20	.743	7.60	.134	7.52
	.896	10.13	.904	8.82	.872	7.30
	.935	8.53	.913	6.65	.916	6.65
	.627	10.53	.821	7.75	.574	6.75
	.554	9.63	.852	8.32	.775	7.23
Impoverished SHR	.566	9.93	.884	5.87	.853	6.32
	.334	9.68	.912	6.47	.615	6.75
	.945	8.88	.941	6.68	.918	7.00
	.699	8.97	.940	6.02	.841	5.77
	.828	8.33	.808	6.02	.692	5.97
Enriched WKY	.294	8.70	.938	7.05	.914	7.12
	.302	9.20	.834	9.77	.451	7.58
	.506	7.77	.894	6.78	.408	5.78
	.396	7.68	.805	6.45	.344	5.82
	.440	8.35	.688	6.48	.566	5.90
Impoverished WKY	.004	8.03	.841	6.37	.582	5.62
	.492	9.17	.783	6.72	.373	6.07
	.540	8.12	.874	5.35	.687	5.70
	.033	7.32	.811	5.58	.677	4.88
	.464	7.25	.930	6.07	.702	5.60