

RESPONSE SUPPRESSION PRODUCED BY VESTIBULAR STIMULATION IN THE RAT¹

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Seven rats were trained to stable performance levels on either Fixed Ratio 47, Variable Ratio 47, Variable Interval 1-min, or Fixed Interval 1-min schedules of food reinforcement. Subjects were then tested for sensitivity to vestibular stimulation from rotation, using an ascending method of limits technique with increments in velocity of one revolution per minute every 5 min. Centrifugal forces were minimized by locating the test chamber over the axis of rotation. Response rates decreased in all subjects as a function of increasing rotation speed. In addition, characteristic differences in the patterns of response decrement were found between subjects on ratio and on interval schedules. Repeated tests indicated high intra-subject reliability in sensitivity to rotation. Similarities of these data to "motion sickness" phenomena in other species were noted. It is suggested that this behavioral approach provides a sensitive and quantifiable technique for assessing the effects of vestibular stimulation in animals.

Recent experiments have shown that significant psychophysiological changes are produced when subjects make head movements during rotation at slow angular velocities. Although centrifugal forces are minimal, a variety of symptoms, including nystagmus, nausea, vomiting, and reduced locomotor activity, typically occur in a wide range of species (Graybiel, Clark, and Zarriello, 1960; Eskin and Riccio, 1966; Meek, Graybiel, Beischer, and Riopelle, 1962). Since these changes do not occur, or are greatly attenu-

ated in subjects with damaged labyrinths (Clark and Graybiel, 1961; Meek *et al.*, 1962; Riccio, Igarashi, and Eskin, 1966), the immediately effective stimuli are considered to be complex accelerational forces acting on the semicircular canals. Behavioral assessment of the effects of slow rotation on animals has been largely limited to the use of observational ratings of activity level or more simply to measurement of the exposure speed which induces vomiting. In view of the increasing interest in proprioceptive feedback and, more specifically, in interactions of vestibular stimulation with performance, it seemed of interest to provide a more sensitive and quantifiable behavioral index of rotation effects. Accordingly, the present study sought to assess the effects of continuous rotation on rats by measuring changes in ongoing operant response rates.

METHOD

Subjects

Seven male albino rats of the Sprague-Dawley strain, 125 to 150 days old at the start of the experiment, were maintained at 75 to 80% of their free-feeding weight throughout the experiment.

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Apparatus

The test chamber consisted of a standard Gerbrands demonstration box 9-in. long, 8-in. wide, and 8-in. high, with clear plastic sides and aluminum ends. The operandum, a 2-in. wide bar, mounted in one end 2-3/4 in. above the floor, required about a 20-g force through a downward excursion of 1/8 in. to close the microswitch. Responses were automatically reinforced with P. J. Noyes 45-mg rat pellets delivered into a hopper at the lower left-hand corner of the front panel by a solenoid pellet dispenser. To minimize centrifugal forces, the test chamber was mounted on a turntable so that the rat's head, while pressing the bar, was over the axis of rotation. The entire unit was driven by a 2-hp constant torque dc motor, having a maximum speed of 29 rpm and an accuracy of $\pm 1\%$. Slip rings provided electrical connections between the test chamber on the turntable and the programming and recording equipment nearby.

Procedure

Two subjects were assigned to each of the following reinforcement schedules: fixed ratio (FR) 47; variable ratio (VR) 47; and variable interval (VI) 1-min. One subject received fixed interval (FI) 1-min training. After initial magazine and continuous reinforcement (CRF) sessions, subjects were trained on their designated schedule of reinforcement until levels of responding stabilized. Ten to 20 daily sessions lasting 1 to 2 hr were usually required to stabilize performance.

After this training, the effects of rotation were investigated using a method analogous to an ascending method of limits. For the first 5 min at the start of the test session, the turntable was stationary. Thereafter, rotation began at 1 revolution per minute (rpm) and increased in stepwise fashion in single rpm increments every 5 min. About 1 to 2 sec were required to change speed. Since stopping and starting could introduce unwanted side effects at higher velocities, rotation was continuously applied until the subject failed to respond at two consecutive speeds, or until the maximum speed of 29 rpm was reached and maintained for 15 min, whichever occurred first. After the criterion was met, the turntable was stopped, deceleration requiring 3 to 4 sec. The subject was left in the chamber for an additional 15-

to 25-min recovery period and then returned to the home cage after testing. At least 24 hr, and usually longer, were allowed before the next test was given.

Under this procedure total exposure time and speed of rotation increase together. To separate this confounding of two possible variables, the subject on FI 1-min received several tests in which the 1-rpm increases occurred every 2.5 min rather than 5 min.

To assess the possible influence of vision on motion sickness, one of the rats on the FR schedule and one on the VR schedule worked in open chambers. Visual stimuli were excluded for the other five rats by completely enclosing the Gerbrands box.

RESULTS

Figure 1 shows the effect of increasing rotation speeds upon responding under the ratio schedules of reinforcement during three tests. The final training session, which served as a control for simple satiation effects, is also shown. The principal characteristic of the test curves was an abrupt drop when an angular velocity of 9 to 11 rpm was reached. The steepness of this gradient can be seen from the fact that 1 to 3-rpm increments in rotation speed were sufficient to reduce responding from 100% to 0% of baseline levels. As the control session indicates, the rats showed no systematic change in response rates during a comparable period of time without rotation. No appreciable effects of rotation speeds below 8 rpm appeared in any animal. Rat 1 characteristically slowed responding more gradually than did the other three. Although absolute response rates differed, each animal was quite consistent for the three sessions, both in terms of baseline rates and the speed at which responding ceased. The median speeds at which each of the four rats stopped responding were 9, 11, 11, and 11 rpm. No appreciable difference existed between the fixed- and variable-ratio schedules as measured by the rotation speed at which responding stopped or the time course of the performance decrement. The same indices showed no difference between rats with and without visual cues during rotation.

The time after rotation stopped until the first response occurred (latency) provided an index of the persistence of rotation effects. The

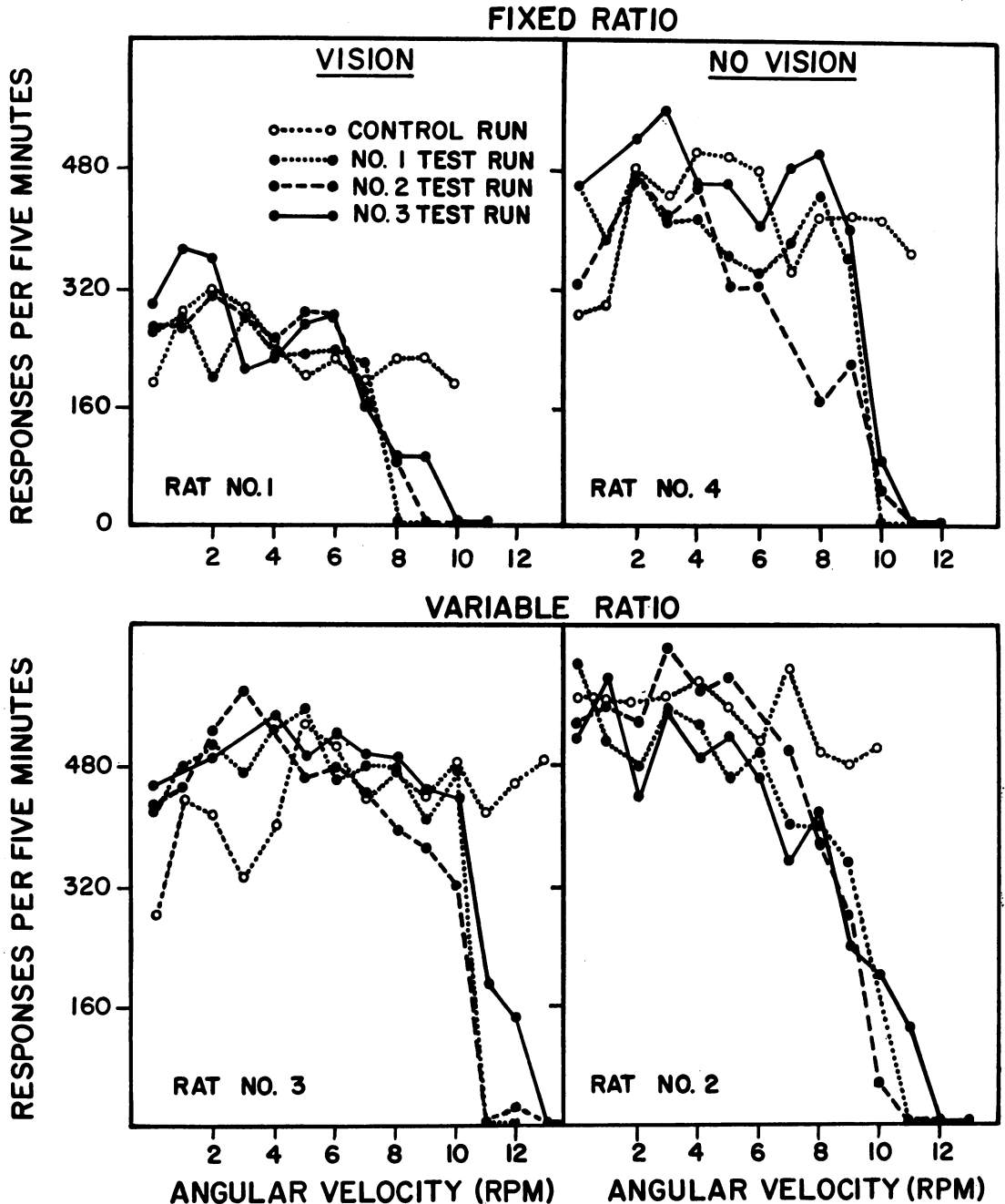


Fig. 1. Effects of increasing rotation speed upon bar-pressing rates in rats on FR 47 or VR 47 schedules of food reinforcement. Control runs reflect response rates at 5-min intervals without rotation.

median latencies for resumption of initial bar-pressing after the three rotation tests were: 36, 36, 108, and 180 sec for Rats 1 to 4, respectively. Subsequent response rates also provided an index of the after-effects of rotation. Although each animal resumed bar-pressing on

all sessions after the wheel had stopped, subjects typically required 10 to 20 min to recover to 75% of their baseline level.

The effects of increasing intensities of rotational stimulation on VI and FI schedules of reinforcement are shown in Fig. 2 and 3,

respectively. Two representative test runs and a control run extending over a comparable period of time, but without rotation, are presented for each rat. Again, response rates decreased as rotation speed increased, but performance on interval schedules declined more gradually than on ratio schedules. Moreover, responding continued at a low rate through very high rotation speeds.

The major disruption of responding occurred at rotation speeds comparable to those of ratio schedules. Although complete suppression did not occur, all three subjects showed a 50% reduction in response rates between 10 and 13 rpm, and 75% suppression by 14 to 15 rpm. As Fig. 3 also indicates, reducing the test duration at each speed by one-half did not appreciably affect the speed at which suppression occurred.

The cumulative records provide further information on the pattern of response decline during rotation. Representative cumulative records of performance under four reinforcement schedules are shown in Fig. 4 and 5. Pen reset occurred at the onset of each change in rpm. On ratio schedules, the reduced emission of responses reflected prolonged periods of no responding, the running rate being virtually unaffected. If the animal responded at all, it responded as rapidly as during low rotation speeds and control sessions. As might be expected from the known stability of responding on FR schedules (Ferster and Skinner, 1957), the periods of no responding always occurred after reinforcement and thus were essentially increased pause times. On the VR schedule, the period of no responding did not always coincide with the postreinforcement period. The abrupt break-off in responding which sometimes occurred part way through a VR response run is also typical (Ferster and Skinner, 1957).

In contrast with ratio schedules, the decreased rates on interval schedules were characterized by generally intermittent responding. With VI subjects, the reduced response rate was a result of increased pausing after non-reinforced as well as reinforced responses. The major effect on the FI schedule was an increase in the postreinforcement pause, but as rotation speed increased the terminal rate itself was also disrupted.

Behavior during rotation was observed in several cases when an open chamber was used.

In addition, several other animals were observed on occasion through closed circuit TV. At speeds producing response suppression, the rats on ratio schedules typically moved away from the lever, and after a period of grooming or tail chewing, curled up on the floor of the cage. The animals on interval schedules would frequently lie down between lever presses, or engage in tail chewing and grooming behavior.

EXPERIMENT 2

While performance on all four schedules of reinforcement was suppressed by comparable rotation intensities, attributing the differential patterns of change between ratio and interval schedule to the schedules themselves raised several further questions. The possibility remained that individual differences between rats accounted for the differential performance changes. Another possible confounding factor concerned the density of reinforcement. Animals on VI 1-min and FI 1-min schedules received about five pellets at each rpm (since each exposure speed lasted 5 min) while the ratio animals, due to their high response rates, obtained approximately twice as many pellets. If partial satiation and rotational stimulation were interacting to influence response rates, it is conceivable that the fewer reinforcements received on interval schedules could "stretch out" performance over a longer period and therefore allow subjects to reach a higher rotation speed. The purpose of the following ancillary experiment was to examine interval and ratio performance when these factors were balanced.

Procedure

Rats 8 and 9, previously on VI 1-min, were switched to schedules of VI 30-sec and FR 50, respectively. After reaching stable performance levels on these schedules, the animals were given three rotation tests following the usual procedure. Subsequently, Rat 9 was also put on an FR 100 schedule, allowed to stabilize, and tested again.

Results

Figure 6 shows the performance on VI 30-sec. As with VI 1-min, responding continued at low rates through 29 rpm. The higher response rate on VI 30-sec seemed to result in a somewhat steeper decrement than previously,

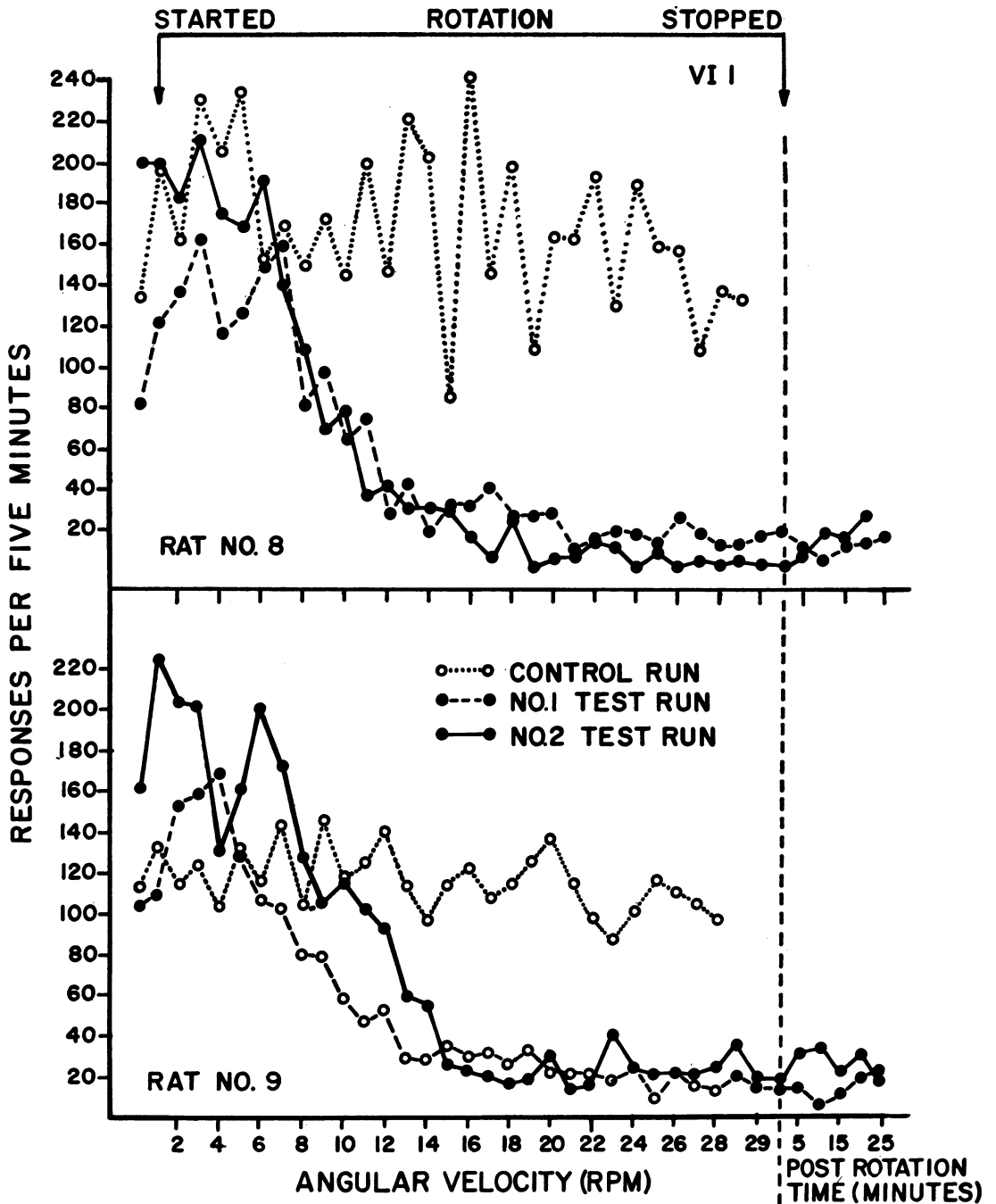


Fig. 2. Effects of increasing rotation speed upon bar-pressing rates in rats on VI 1-min schedule of food reinforcement. Upper curve in each panel presents control rates obtained at 5-min intervals without rotation.

but as before, a low-level plateau was reached by 14 rpm despite doubling of reinforcement density. This frequency of reinforcement was comparable to that of the rats on the ratio schedules.

Data from Rat 9 on FR 50 and FR 100 schedules are presented in Fig. 7. Previously, when on the VI 1-min schedule (Fig. 2) this animal showed a gradual decline but never ceased responding. When changed to an FR

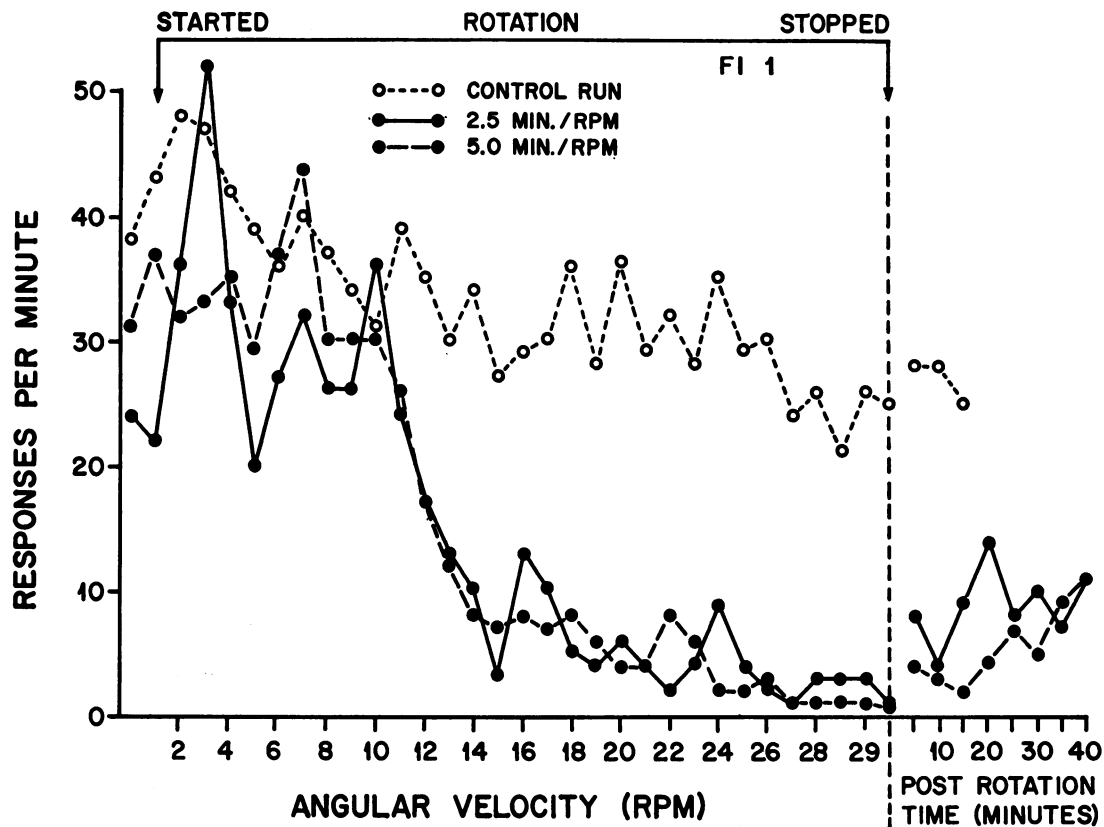


Fig. 3. Changes in response rate on FI 1-min as a function of rotation speed under two durations of exposure. Rate for 2.5-hr session without rotation is shown in control run.

schedule, the rat's behavior was in all respects comparable to the other FR subjects. When the FR 50 was increased to FR 100 in order to reduce reinforcement frequency, responding still ceased abruptly, and at a slightly lower rotation speed.

DISCUSSION

These data show that slow rotation markedly depresses food-reinforced responding in the rat and that the magnitude of behavioral change is a function of stimulus intensity. That the lowered response rate is not attributable to food satiation is demonstrated by maintenance of response rates over comparable time periods in control sessions, by postrotation recovery, and by the similarity of response functions under widely different durations of exposure to each rpm (5 min *vs.* 2.5 min). The latter finding also indicates that within the exposure limits used here, it is the absolute rotation speed, not the cumulative effects, that disrupts responding.

It should be emphasized that centrifugal forces in this study were minimal, increasing less than 0.01 G. Further evidence that suppression was not due to impaired motor capacity for bar-pressing is provided by the data from ratio-schedule subjects. Performance decrements reflected increased pause durations, rather than a disruption of the actual running rate. If the subject responded at all, the rate was as rapid and efficient as during nonrotation sessions.

The basis for the response suppression seems to be the aversiveness of rotation, but whether this is due to a specific punishment effect or more general malaise is not clear. Since each movement during rotation generates unusual proprioceptive stimulation (Guedry and Montague, 1961), a second contingency is superimposed on the reinforcement schedule. Thus, the situation may be analogous to the operant punishment condition where the same response that produces food also produces shock. As a number of experiments have shown, responding diminishes or ceases as the

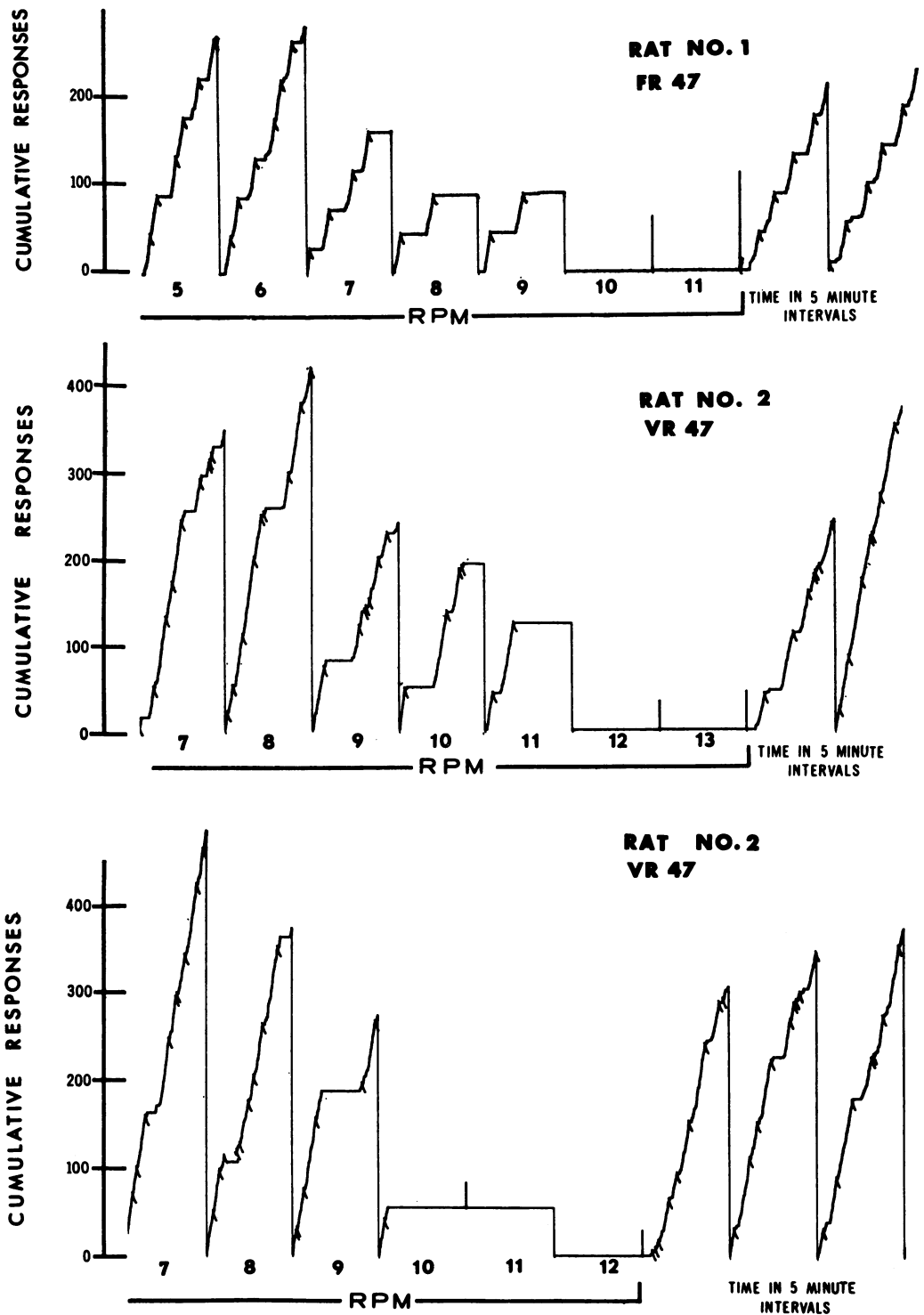


Fig. 4. Representative cumulative records showing prolonged pauses during rotation on FR and VR reinforcement schedules. Pen reset indicates the end of 5-min intervals. The bottom panel illustrates cessation of responding independent of reinforcement on a VR schedule. Failure of the pen to reset resulted in raised baseline at 11 rpm. Postrotation recovery is evident in all cases.

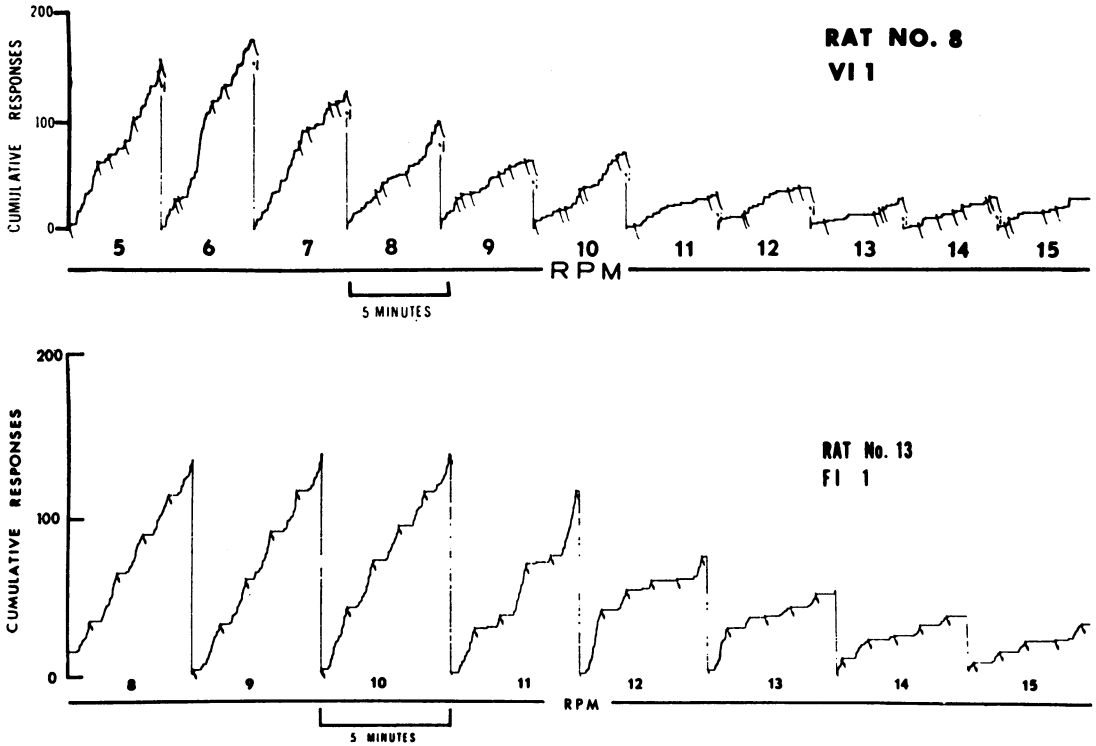


Fig. 5. Representative portions of cumulative records showing the decline in responding as a function of rotation speed on VI 1-min and FI 1-min schedules of reinforcement. Pen reset occurs after each 5-min exposure interval. Time and response scales are indicated for each subject since two different cumulative recorders were employed.

intensity of punishing noxious stimulation increases (Appel, 1963; Azrin and Holz, 1966). Since the rotation stimulation can be greatly reduced with little loss in the number of reinforcements by responding at a lower rate on interval schedules, this view might partially account for the very low but persistent response rates on interval schedules, compared with total cessation on ratio schedules.

An alternative but related explanation is that the subjects are motion-sick and consequently their behavior is not well maintained by food reinforcement. The stimulus situation is one which produces vomiting in other species. Also, one characteristic of motion sickness is that it persists after stimulation has been terminated. In this experiment, response suppression typically continued into the postrotation period, but whether the response suppression in rats is analogous to other indices of motion sickness can not readily be decided without further consensual evidence.

While the speeds which produce response suppression are largely independent of the

reinforcement schedule, the different patterns of change were contingent upon the type of schedule employed. The consistency of results among seven rats, and the finding that Rat 9 changed from a persistent, low rate at speeds above 12 rpm when on a VI schedule to no responding at these speeds when on the FR schedule, indicates that the schedule effects were not an artifact of individual differences. It seems likely that these pattern effects reflect differential probabilities of bar-pressing on the various schedules. Thus, on interval schedules the tendency to bar-press increases as a function of time since the last response, while on ratio schedules the response probability is more closely related to the chain of preceding responses.

Traditional physiological approaches to motion sickness argue that vomiting is the only reliable criterion for use with animals (Chinn and Smith, 1955). In this context it should be noted that the use of operant procedures for measuring rotation effects has the advantages of a behavioral baseline which is objective,

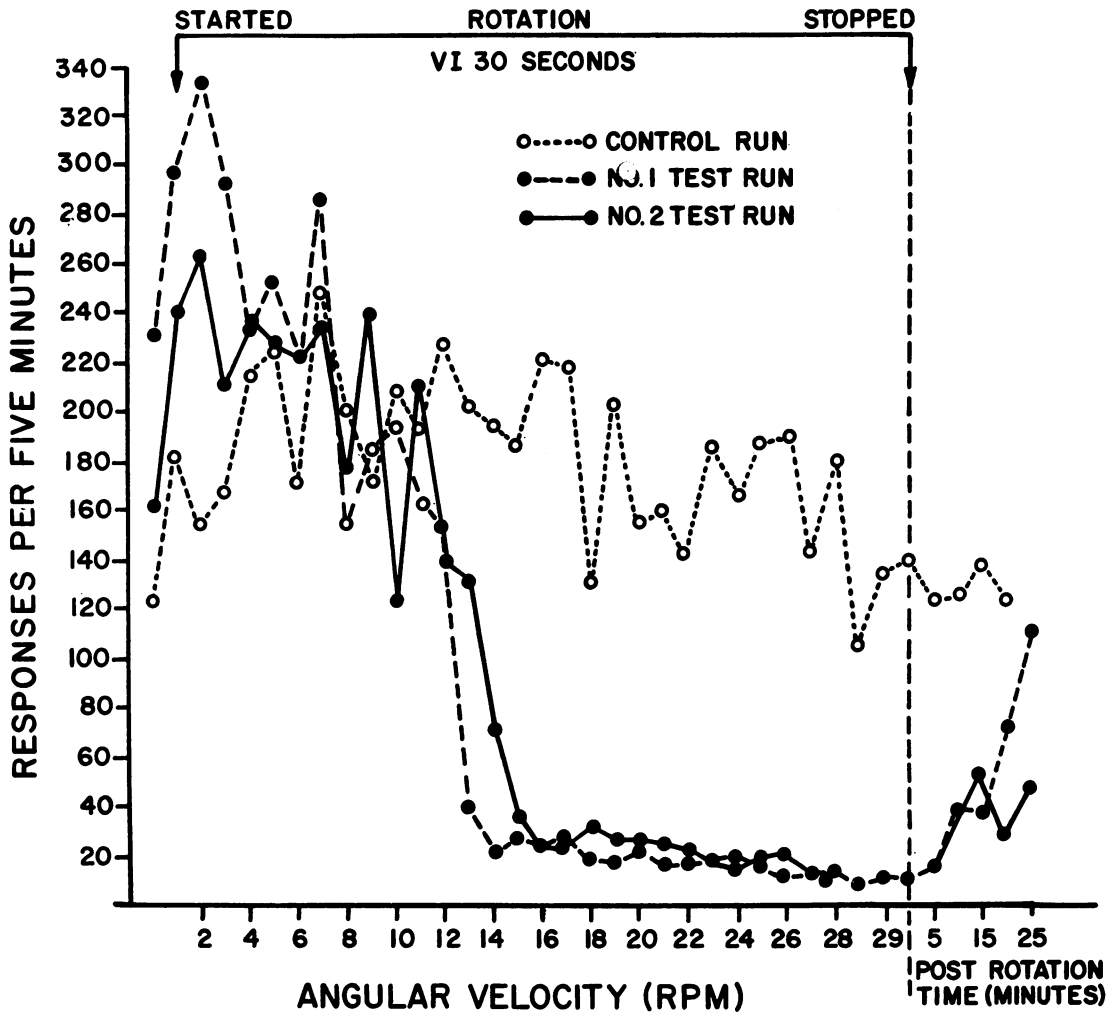


Fig. 6. Response rate decrement with increasing rotation speeds in Rat 8 on VI 30-sec schedule. No rotation occurred during control session.

stable, sensitive, and quantifiable both in regard to magnitude and time course. Moreover, the baseline can either increase or decrease, and the changes produced by rotation are reliable and repeatable both within and between subjects. Although the rat is reported to be physiologically incapable of vomiting (Hatcher, 1924), it has an intact vestibular system and appears remarkably sensitive to rotation effects. The suppression "thresholds" should be considered a conservative estimate of sensitivity, since the stimulation has to be sufficiently aversive to override reinforced responding in subjects deprived to 75% to 85% of *ad lib* weight. Also, the rat has seldom been used in vestibular stimulation research. Since response decrements occur at velocities which

produce motion sickness in man and other animals, the rat may prove to be an appropriate subject for vestibular research to evaluate the effects of drugs, prior rotation experience, and other experimental manipulations.

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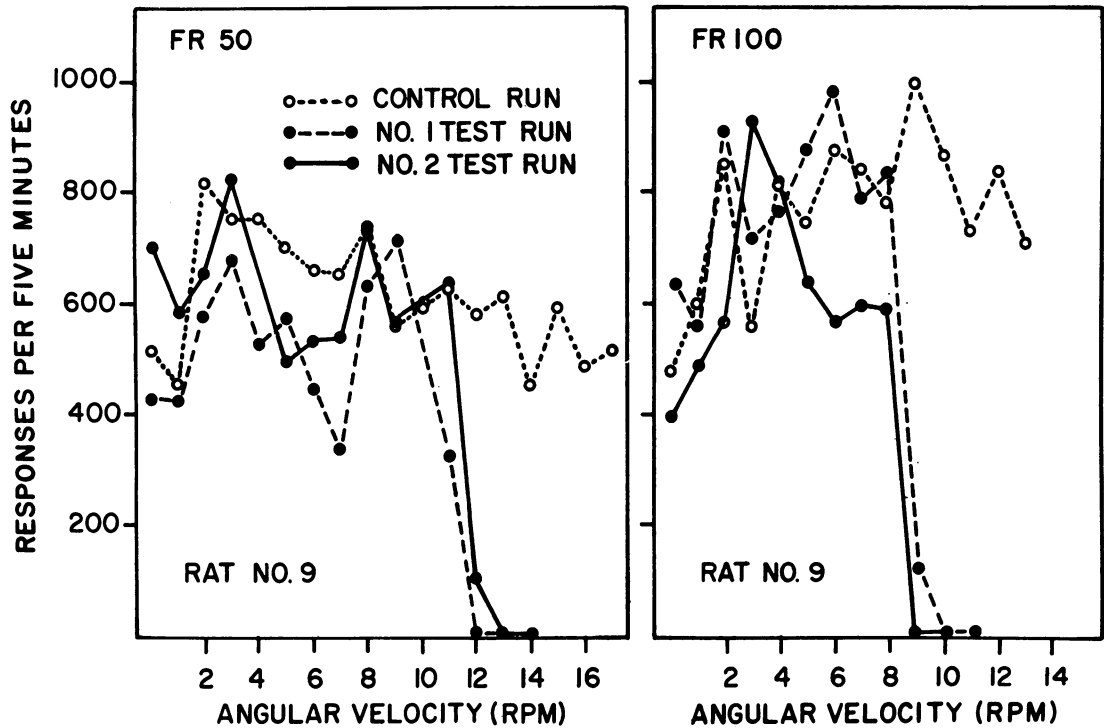


Fig. 7. Effect of rotation upon response rates in Rat 9 on FR 50 or FR 100 schedules of reinforcement. Rates during sessions of comparable length but without rotation are presented in control curves. The same subject showed persistent low rates throughout rotation when responding on VI 1-min schedule (Fig. 2).

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