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CHANGES IN PROGRESSIVE-RATIO PERFORMANCE UNDER INCREASED PRESSURES OF AIR[1]

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Rats performed on progressive-ratio schedules that required an increasing number of responses for each successive reinforcement. The number of responses required increased until the subjects failed to complete the next ratio in the sequence within 15 min. Response-ratio increments of two responses, five responses, and 20 responses were investigated. The size of the final completed ratio generally increased with increases in the progressive-ratio step size. Increased pressures of air in a hyperbaric chamber led to both increases and decreases in terminal ratio size, with the differential effects depending on both air pressure and on the size of the progressive-ratio increment. Changes in the number of responses in the final ratio were related to increased pressures of nitrogen, as similar pressures of helium produced few effects.

A baseline for measuring changes in operant performance without reference to rate of responding was described by Hodos (1961) and termed a progressive-ratio schedule. On a progressive-ratio schedule, reinforcement follows the nth response (the fixed-ratio requirement) and the ratio requirement is increased by a constant step size after each successive reinforcement. The ratio requirement continues to increase by the step size after each reinforcement until the organism either fails to respond or fails to complete the next ratio within a specified time period. The size of the final ratio has been shown to be sensitive to a range of variables affecting operant performance (Hodos, 1961; Hodos, 1965; Hodos and Kalman, 1963; Thompson, 1972).

In the present experiment, a progressive-ratio schedule was used to assess the effects on operant performance of a range of increased pressures of air. Breathing air under increased atmospheric pressures has been reported to produce effects similar to alcohol, hypoxia, and early stages of anesthesia (Bennett, 1966). The effects have been attributed to the nitrogen content of air at elevated pressures and have been termed nitrogen narcosis. Nitrogen narcosis is reported to occur when organisms breathing compressed air are exposed to raised pressures of 45 psi (3 kg/cm^2) or more while diving to depths deeper than 100 ft (30 m) in open water, or are exposed to simulated depths in hyperbaric chambers (Bennett, 1966; Bennett, 1969; Miles, 1969).

METHOD

Subjects

Three male albino rats (NMRI:0 [SD], Sprague-Dawley derived) designated Subjects 25, 26, and 27, approximately 60 days old at the beginning of the study, were maintained at 80% of their free-feeding weights.

Apparatus

The experimental chamber was a rat cage, specially manufactured by Harvard Instrument Company, that contained two response levers and a food hopper mounted on the front wall. Only the right lever, which required a minimum force of approximately 0.10 N to operate, was used. A pellet feeder located behind the front wall dispensed 45-mg Noyes pellets into the hopper. A houselight was

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mounted on top of the front wall and a pilot light was mounted above each lever. During most baseline sessions, the cage was mounted inside a ventilated sound-reducing enclosure. All pressure sessions, as well as a number of baseline sessions, were conducted with the rat cage mounted inside a Bethlehem hyperbaric chamber (Figure 1) capable of increases in internal pressure to 1000 pounds per square inch (70 kg/cm^2), which is comparable to a simulated depth of 2250 ft (685 m) of sea water. The chamber was penetrated with several threaded openings for pressure-fitted connectors to gas supplies and scheduling equipment. Scheduling and recording of sessions were accomplished by a system of solid-state digital logic modules.

Procedure

The subjects performed seven days a week. Sessions were preceded and followed by a blackout condition of variable length, during which lights in the chamber were off. During a session, the houselight and the light above the right response lever remained illuminated.

Baseline sessions. The subjects were trained by the method of successive approximation to press the response lever. Thereafter, a single response produced a food pellet. The only event coincident with reinforcement was a click produced by the feeder operation. The subjects were then exposed to a progressive-ratio schedule during which the ratio increment was five responses. Five responses were

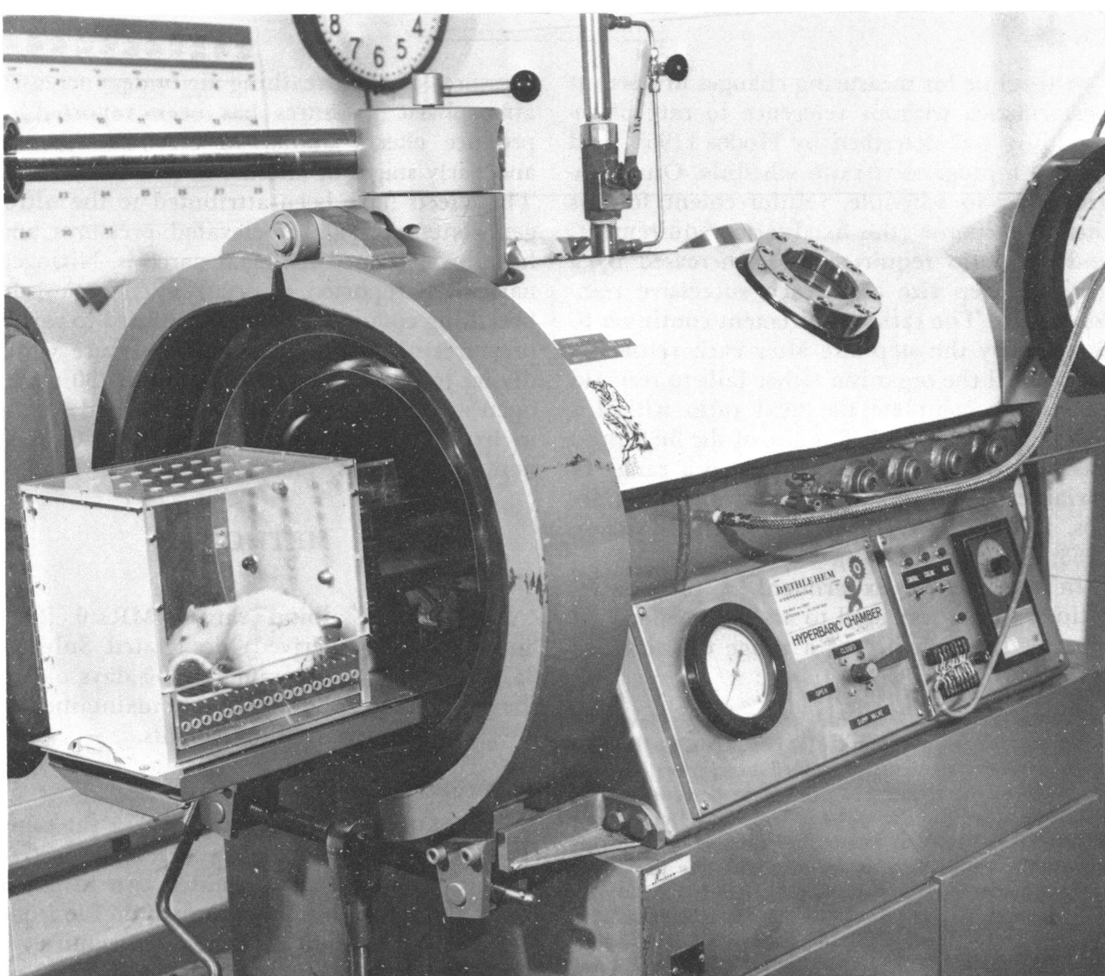

Fig. 1. Hyperbaric chamber opened with rat cage mounted on slides.

Table 1

Order of Conditions

Schedule	*Subject* 25	26	27
Progressive-ratio 5	B*-82 sessions	B-84 sessions	B-81 sessions
	111.3 psi Air	111.3 psi Air	111.3 psi Air
	111.3 psi Air	111.3 psi He	111.3 psi Air
	111.3 psi He**	111.3 psi Air	111.3 psi He
	111.3 psi Air	89.0 psi Air	133.5 psi Air
	111.3 psi Air	44.5 psi Air	133.5 psi Air
	89.0 psi Air	44.5 psi He	133.5 psi He
	89.0 psi He	89.0 psi He	44.5 psi Air
	133.5 psi He	89.0 psi Air	89.0 psi Air
	44.5 psi Air	89.0 psi He	89.0 psi Air
	44.5 psi Air	89.0 psi Air	111.3 psi Air
	133.5 psi Air	111.3 psi He	44.5 psi He
	44.5 psi Air	133.5 psi Air	111.3 psi Air
	—	44.5 psi Air	111.3 psi Air
Progressive-ratio 20	B-47 sessions	B-44 sessions	B-40 sessions
	111.3 psi Air	111.3 psi Air	111.3 psi Air
	111.3 psi Air	44.5 psi Air	44.5 psi Air
	44.5 psi Air	133.5 psi Air	89.0 psi Air
	111.3 psi Air	89.0 psi Air	133.5 psi Air
	133.5 psi Air	133.5 psi Air	111.3 psi Air
	44.5 psi Air	44.5 psi Air	111.3 psi Air
	89.0 psi Air	—	133.5 psi Air
	133.5 psi Air	—	—
Progressive-ratio 2	B-45 sessions	B-50 sessions	B-49 sessions
	44.5 psi Air	111.3 psi Air	111.3 psi Air
	111.3 psi Air	44.5 psi Air	44.5 psi Air
	44.5 psi Air	133.5 psi Air	44.5 psi Air
	133.5 psi Air	44.5 psi He	89.0 psi He
	89.0 psi Air	89.0 psi He	111.3 psi He
	133.5 psi Air	89.0 psi Air	89.0 psi Air
	44.5 psi Air	133.5 psi Air	133.5 psi Air
	89.0 psi Air	111.3 psi He	133.5 psi Air
	—	44.5 psi Air	89.0 psi Air
	—	111.3 psi Air	89.0 psi Air
	—	44.5 psi Air	133.5 psi He
	—	—	44.5 psi He
Progressive-ratio 5	B-23 sessions	B-27 sessions	B-19 sessions
	89.0 psi He	111.3 psi Air	133.5 psi Air
	111.3 psi He	133.5 psi Air	133.5 psi He
	—	89.0 psi He	89.0 psi He
	—	133.5 psi He	133.5 psi He
	—	111.3 psi He	

*Baseline sessions
**Helium sessions

required to produce the first reinforcement, 10 responses the second reinforcement, 15 responses the third, and so on. The session was terminated when the subject did not complete the next ratio in the sequence within 15 min. The subjects were then exposed to progressive-ratio schedules with ratio increments of two responses and 20 responses, and again to an increment of five responses. The order of conditions is shown in Table 1.

Air-pressure sessions. After initial baseline sessions on the progressive-ratio schedule with a ratio increment of five responses, but before actual pressure sessions began, the subjects were exposed to a number of control sessions with the rat cage mounted in the hyperbaric chamber to allow the subjects to adapt to the chamber and the noise of gas flow. Compressed air was allowed to flow into the chamber; however, all chamber valves were left open so that ambient pressure was maintained and only noise level was manipulated.

Following baseline sessions on each progressive-ratio schedule, the subjects were exposed to four hyperbaric pressures while breathing compressed air. The four pressures of air investigated were 44.5 pounds per square inch or psi (3.1 kg/cm^2), 89.0 psi (6.3 kg/cm^2), 111.3 psi (7.8 kg/cm^2), and 133.5 psi (9.4 kg/cm^2). These four pressures are equal to 4.0, 7.1, 8.6, and 10.1 atmospheres absolute and are the pressures impinging on an organism at depths of 100 ft (30 m), 200 ft (61 m), 250 ft (76 m), and 300 ft (91 m) of sea water. The subjects were exposed to the four pressures on each progressive-ratio schedule in different orders. Several determinations were made for some pressures. At least six baseline sessions were conducted between successive hyperbaric exposures. The order of exposure to each pressure is presented in Table 1. Compression rate to the desired pressure was 10 ft (3 m) per minute. Chamber temperature was maintained between 23° and 27°C.

Helium-pressure sessions. On the progressive-ratio schedules with ratio increments of two and five responses, the subjects were exposed to increased pressures breathing a helium-oxygen mixture. An 80% helium and 20% oxygen mixture was used to keep the oxygen percentage similar to that used during pressure exposures with compressed air (roughly 80% nitrogen and 20% oxygen). The helium mixture was used as a control for the nitrogen content of compressed air in the sense that it allowed measurement of the effects of pressure *per se,* and raised pressures of oxygen on progressive-ratio performance in the absence of nitrogen. Compression rate to the desired pressure breathing helium-oxygen was the same as used with compressed air (10 ft per minute). Several observations were made for some pressures. The order of exposure to each pressure breathing helium-oxygen is shown in Table 1.

Baseline and pressure probe. During several baseline sessions and an exposure to 133.5 psi on the progressive-ratio schedule with a ratio increment of five responses, the session was terminated as usual for Subjects 26 and 27 when the subjects failed to complete the next ratio scheduled within 15 min. In each instance, the chamber was darkened for 30 sec, the response ratio was reset to the initial value of five responses, the houselight and light over the response lever were turned back on, and the session was restarted.

RESULTS

Baseline. Performance on the progressive-ratio schedules was measured in terms of the number of responses emitted in the final completed ratio. This measure for baseline sessions and the four pressures for each progressive-ratio schedule are presented in Figure 2. The point plotted for baseline sessions (B) is the mean of 15 sessions preceding the initial hyperbaric exposure on each progressive-ratio schedule and the brackets indicate the range of the number of responses in the last completed ratio. For all three subjects, the size of the final ratio generally increased with increases in the step size of the progressive-ratio schedule. Cumulative response records of baseline performances on the three progressive-ratio schedules are presented for one subject on the left of Figure 3. Baselines showed rather constant running rates, with most of the changes reflected in gradual lengthening of the pause, *i.e.,* the period of no responding preceding the first response of each ratio.

Air-pressure sessions. The effects of exposure to increased pressures of air depended upon the value of the progressive-ratio schedule (Figure 2). On the progressive-ratio schedule with a ratio increment of two responses (top portion of Figure 2), pressures of 44.5 and 89.0 psi increased the size of the final ratio above baseline values. At 133.5 psi, performance tended to be below baseline or near the lower limit of baseline ranges. The increase in performance above baseline at 44.5 and 89.0 psi may be seen in the cumulative response records in the top row of Figure 3 for Subject 26. The running rates appeared not to differ from baseline performance. However, the cumulative records show a decrease in pause times associated with the larger ratios at 44.5 and 89.0 psi. An example of the decrease in final ratio size at 133.5 psi for Subject 26 is presented in the top row of Figure 3. The pause times were decreased but the running rates began to be

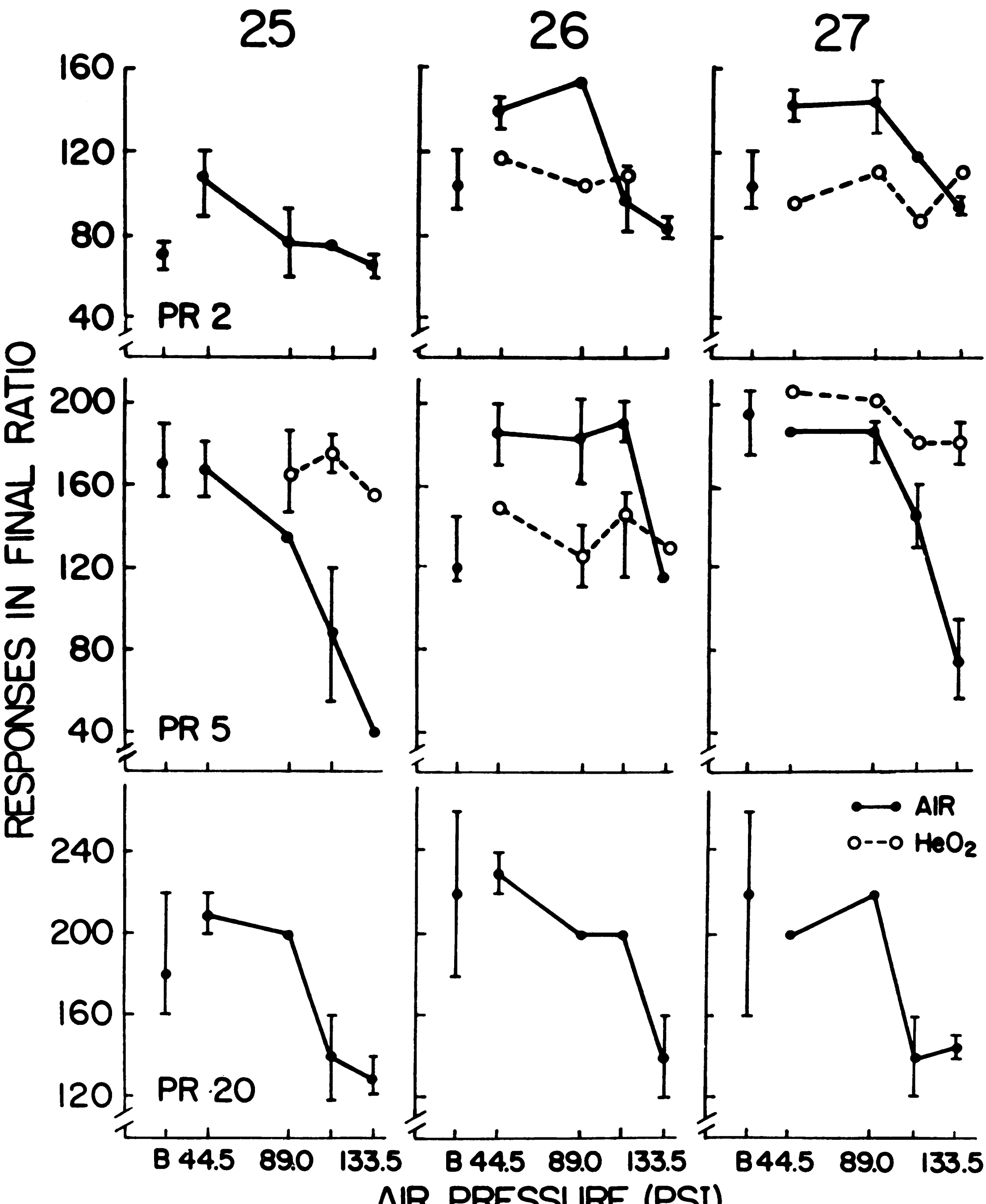

Fig. 2. Pressure-effect functions for four pressures of air. Number of responses in the final completed ratio are shown for three progressive-ratio (PR) values for the four pressures. The points plotted are the means, and the brackets for all points indicate the ranges of multiple observations. Filled circles indicate exposures to increased pressures of air and unfilled circles indicate exposures to increased pressures of a 80% helium-20% oxygen mixture.

disrupted at the higher ratios under this pressure. Similar changes were shown by the other two subjects.

On the progressive-ratio schedule with a ratio increment of five responses, shown in the center portion of Figure 2, Subjects 25 and 27

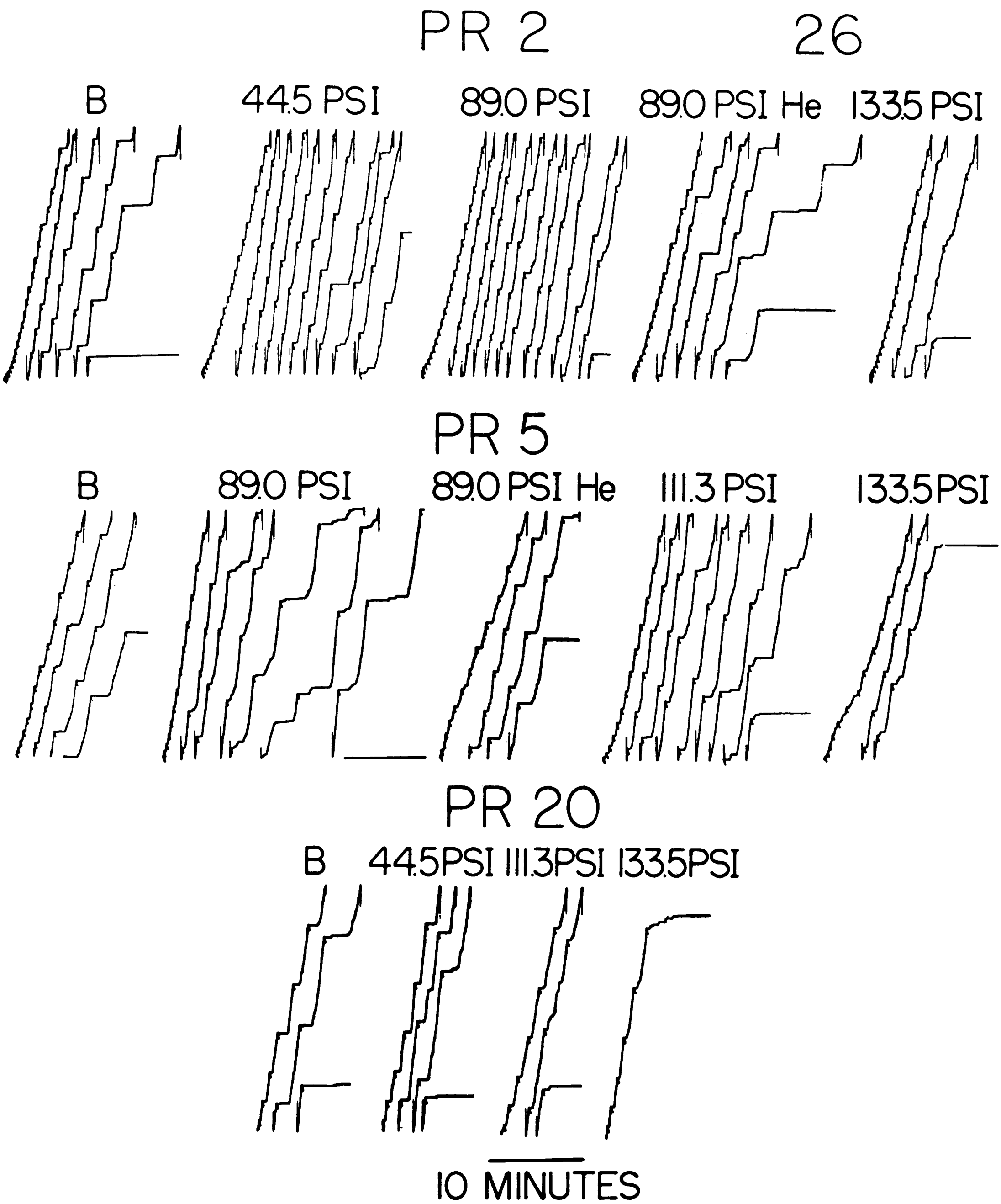

Fig. 3. Cumulative response records of entire sessions for Subject 26 at several pressures for each of the progressive-ratio (PR) schedules. Baseline sessions are indicated as B and exposures to the helium-oxygen mixture are indicated He.

showed a decrease in the size of the final ratio at 111.3 and 133.5 psi, with performance within baseline ranges or slightly below at 44.5 and 89.0 psi. Subject 26 on the progressive-ratio schedule with an increment of five responses showed increased performance at 44.5, 89.0, and 111.3 psi and a decline in performance at 133.5 psi. Examples of Subject 26's performance on the progressive-ratio schedule with a ratio increment of five responses at several pressures are shown in the middle row of Figure 3. Generally, the changes in the size of the final ratio of this subject breathing air under pressure were not accompanied by changes in running rate.

When the ratio increment was 20 responses on the progressive-ratio schedule, both the 111.3 psi and the 133.5 psi pressures generally decreased the size of the final ratio. The 44.5 psi and 89.0 psi pressures showed performances that were not outside baseline ranges. Cumulative response records showing performance changes at three pressures on the progressive-ratio schedule with an increment size of 20 responses are shown in the bottom row of Figure 3 for Subject 26. Aside from changes in the size of the final ratio completed, major changes due to different pressures appeared in changes in pausing, with little changes in running rates.

The effects of breathing air under pressure on the size of the terminal ratio completed can also be evaluated by plotting per cent change in control final ratio size against control ratio size for each pressure as shown in Figure 4. The data plotted in this manner suggest an overall relation between the relative amount and direction of change under pressure and the size of the final ratio completed during baseline control sessions. The upper left portion of Figure 4 shows that at 44.5 psi, there is a tendency for performance to increase relatively more when the number of responses in the final ratio of control sessions is small rather than large. At 89.0 and 111.3 psi, performance is increased above control for small control ratio values and decreased below control for larger control ratio values. At 133.5 psi, shown in the lower right of Figure 4, performance is decreased below control values relatively more for larger control ratio values than for smaller ratio values. A comparison of the four regression lines in Figure 4 shows that at the lowest pressure (44.5 psi), most of the data points are above control values and with increasing pressures, more of the data points are below control values, with all data points below control values at the highest pressure (133.5 psi).

Helium-pressure sessions. When helium replaced the nitrogen of the breathing mixture under pressure, the size of the terminal ratio completed generally remained within control baseline ranges for all subjects. In Figure 2, the unfilled circles in the top and middle row indicate exposures to each helium pressure. The unfilled circles with brackets are the means of several observations and the brackets indicate the ranges. The performance of Subject 26 at 89.0 psi breathing the helium-oxygen mixture is shown in the cumulative response record presented in the top row of Figure 3 for the progressive-ratio schedule with a ratio increment of two responses, and in the middle row of Figure 3 for the progressive-ratio schedule with a ratio increment of five responses.

Probe sessions. During the probe sessions on the progressive-ratio schedule, Subjects 26 and 27 began to respond again when the schedule was reset to the initial value of five responses after a usual session terminated. Responding was reinstated at the restart of a session on both baseline sessions and at a pressure of 133.5 psi. Figure 5 shows the cumulative response record for Subject 26 at 133.5 psi on the probe session. When the final ratio was not completed within 15 min, the houselight and light over the response lever went off. Thirty seconds later, the session was restarted with the progressive-ratio schedule set at a ratio of five responses (A in Figure 5), at which point the subject again began to respond.

DISCUSSION

The present study indicated that the size of the final ratio completed on a progressive-ratio schedule is a sensitive measure of the effects of increased pressures of air on performance without reference to response rate. Running rates observed in the cumulative records often showed little or no change, yet the size of the terminal ratio completed did change under increased pressures. Examples were also seen where running rates appeared disrupted, but little change occurred in the terminal ratio size. The size of the ratio that is completed does not appear directly related to modification of response rate and gives different information.

Changes in performance, either enhancement or decrement in terminal ratio size, under hyperbaric conditions were associated with the increment size of the progressive-ratio schedule. There were more cases of increases in terminal ratio size under increased pressure at the smallest progressive-ratio size. At the two larger progressive-ratio values, either no change or decreases in terminal ratio size occurred under pressure (except for Subject 26 on PR 5). Under baseline conditions, size of the

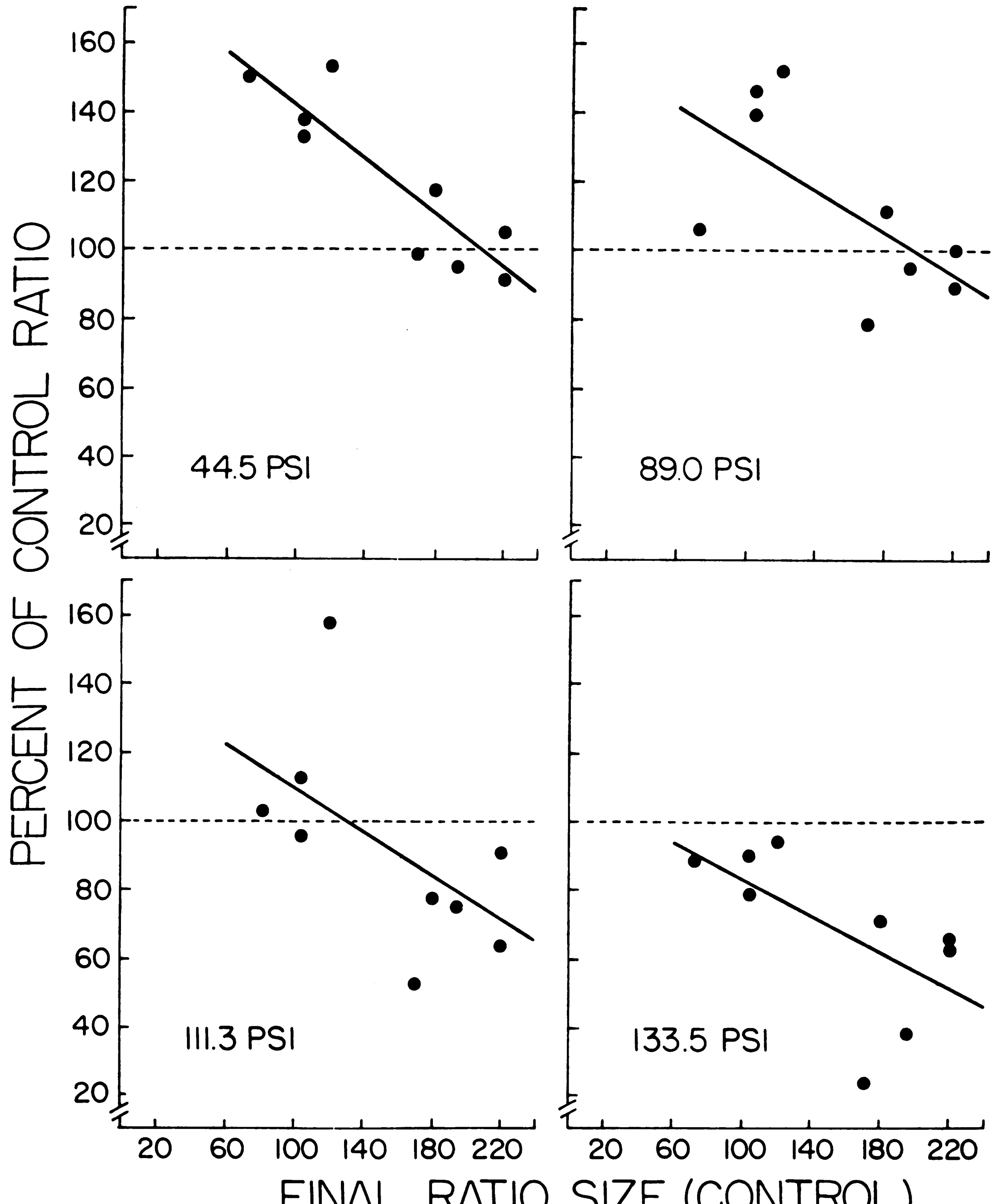

Fig. 4. Plots of the relationship between final ratio size during control sessions and the per cent change in ratio size under four different pressures of air. The points are the single and mean values depicted in Figure 2. The regression lines were calculated by the method of least squares.

final completed ratio increased with increases in progressive-ratio value. This relationship has been found over a wider range of progressive-ratio sizes (Hodos and Kalman, 1963).

A possible interpretation of the enhancement of performance under pressure is concerned with aspects of ratio schedules. If one assumes that ratio schedules have aversive

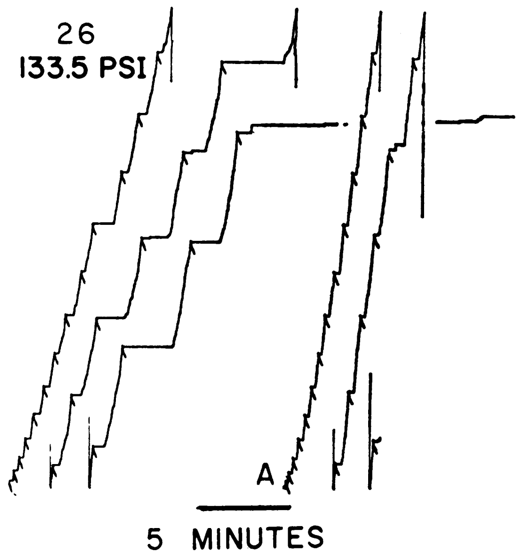

Fig. 5. Cumulative response records of Subject 26 at 133.5 psi during probe session. After the usual session ended, the progressive-ratio schedule was reset and the session was started again (at A).

properties (Azrin, 1961; Thompson, 1964; Thompson, 1965), and that under increasingly larger ratios in progressive-ratio schedules the aversive properties generally increase until the organism can no longer respond in their presence, one may interpret the enhancement of progressive-ratio performance by air under pressure as a reduction in the aversiveness of the larger ratios under the lower progressive-ratio value. Such an interpretation is in accord with the suggestion that air under pressure operates as a central nervous system depressant (Bennett, 1966). A similar interpretation has been suggested for performance enhancement on a small progressive-ratio schedule by two drugs, chlordiazepoxide and phenobarbital (Thompson, 1972). At larger progressive-ratio values, the interpretation is not applicable, as the larger pressures produced decreases in the terminal ratio size. The decrements in performance at the higher pressures do not appear to be totally related to an inability to respond due to increased pressures. The probe sessions indicated that when the subjects were exposed to the small ratios associated with the beginning of the progressive-ratio schedule, responding was reinstated. This seems to indicate that decrement in performance is related to an interaction of increased air pressures with the actual size of the larger ratios.

An interpretation of the progressive-ratio performance changes under increased air pressures that involves the dependency of the changes under pressure on obtained baseline control values is possible. The size of the terminal ratio completed under pressure appeared to be related to the size of the terminal ratio during baseline sessions. A relationship was obtained between the magnitude of pressure effects and the control baseline terminal ratio size produced by the different ratio increments. At the lower pressures, there tended to be a relatively greater increase in performance when the baseline terminal ratio size was small rather than large. At the highest pressure, there was a greater decrease in performance when the baseline terminal ratio size was large rather than small. The relationship between magnitude and direction of pressure effects and control values may be viewed as analogous to rate-dependency effects found for many drugs. Differential changes produced by drugs in response rates on fixed-ratio schedules, for example, have been shown to be inversely related to control response rate values (Waller and Morse, 1963). The relative changes in pausing observed in the present study are similar in some aspects to differential effects of drugs on pause time of small and large fixed-ratio schedules (Dews, 1958; Morse, 1962), in that certain pressures appeared to shorten long interresponse times, whereas short interresponse times were not so affected. The interpretation of the present data as similar to rate-dependency effects of drugs is only by analogy. Response rates were not obtained in the present study, only total number of responses in the final ratio was measured. However, the interpretation of the dependency of behavior changes under increased air pressures on initial baseline values is strengthened by the finding that rate-related measures of operant performance do show differential response-rate changes under similar air pressures as a function of obtained baseline rates (Thomas, 1973*b*).

The changes in performance on the progressive-ratio schedule seem to be related directly to the increased pressures of the nitrogen content of air. The size of the final ratio completed remained within baseline ranges when helium was substituted for the nitrogen content of the breathing mixture. The performance changes are not apparently the result of pressure *per se,* or the particular raised pressures of oxygen, as these were identical in both the helium mixture and air. This finding is in accord with other studies using rate-related measures that have shown that increased pressure of air produce more changes in free-operant performance than do comparable pressures of helium and oxygen mixtures (Thomas, 1973*a*; Thomas and Bachrach, 1971; Thomas, Walsh, and Bachrach, 1971) and generally supports the contention that helium has less effect on ongoing performance than does nitrogen (Bennett, 1969).

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