BEHAVIORAL REGULATION OF GRAVITY: SCHEDULE EFFECTS UNDER ESCAPE-AVOIDANCE PROCEDURES¹

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Squirrel monkeys were restrained in a centrifuge capsule and trained to escape and avoid increases in artificial gravity. During escape-avoidance, lever responses reduced centrifugally simulated gravity or postponed scheduled increases. The effect of variation in the interval of postponement (equal to the duration of decrease produced by escape responses) was studied under a multiple schedule of four components. Three components were gravity escape-avoidance with postponement times of 20, 40, and 60 sec. The fourth component was extinction. Each component was associated with a different auditory stimulus. Rate of responding decreased with increasing postponement time and higher mean g-levels occurred at shorter intervals of postponement. Effects of the schedule parameter on response rate and mean g-level were similar to effects of the schedule on free-operant avoidance and on titration behavior maintained by shock.

Behavioral and biological effects of gravity have been the subject of scientific inquiry since before the turn of this century. Much of the earlier literature has been reviewed by Frankel and Gunn (1961, pp. 216-243). Because the magnitude of gravitational acceleration varies but little at the earth's surface, most early investigation was concerned with orienting behavior as influenced by the direction of stimulation. Subsequently, much research has been directed at establishing thresholds and elucidating sensory mechanisms for both angular and linear acceleration (e.g., Guedry, 1965; Wendt, 1951). Although gravity is among conditions providing stimuli to all earth organisms, linear accelerations have been studied much less extensively than angular accelerations.

Recently, research on the biological effects of conditions encountered in spaceflight has

brought attention to the analysis of behavior in response to gravitational changes. A general analysis of the behavioral effects of gravity may take its departure from a classification of the possible functions of gravitational stimulation in the control of behavior. For example, gravitational stimuli may have eliciting functions with respect to specific reflexes, or discriminative and reinforcing functions with respect to learned behavior.

The present paper is concerned with the reinforcing properties of increases above normal earth gravity. Increased gravity can be physiologically noxious, and indeed, lethal (e.g., Wunder, Lutherer, and Dodge, 1963). Recent evidence indicates that increased effective weight can also be aversive (or, negatively reinforcing), in that it may generate behavior that functions to terminate or minimize increases. Experiments using centrifugally produced artificial gravity have shown that animals rotating at constant angular velocity minimize increases in their effective weight by locomotion to the shortest available radius (Belleville, Clark, and Lange, 1964; Broderson and Lange, 1969). Escape and avoidance behavior have also been conditioned and maintained under operant conditioning procedures, using increased artificial gravity as the aversive stimulus (Clark, Martin, Lange, and Belleville, 1969; Clark, Lange, and Belleville, 1971). In these experiments, squirrel monkeys were restrained in a centrifuge capsule and provided with a

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lever switch. Operation of the switch enabled subjects to avoid or escape increase in artificial gravity. In the absence of responses, angular velocity was arranged to increase from a lower limit up to some upper limit. When the lower limit was exceeded, each lever depression produced an interval of decreasing artificial gravity (escape behavior). Subsequent responses reset the interval, and each response at the lower limit postponed the onset of the next gravity increase (avoidance behavior). Avoidance and escape behavior resulting in low mean levels of artificial gravity were conditioned and maintained under this procedure.

The present paper reports an extension of this procedure designed to establish that gravity avoidance has functional properties similar to avoidance maintained by other aversive stimuli. The chief parameters of the procedure are the upper and lower limits of artificial gravity, the rate of change between these, and the interval by which responses postpone gravity increases (the same as the duration of decrease produced by an escape response). In this experiment, the postponement time was manipulated to determine its effect on the rate of responding and on the mean level of artificial gravity maintained. To obviate the necessity for successive restabilization of behavior at different values of the schedule parameter, a multiple schedule was used (Ferster and Skinner, 1957). The multiple schedule had four components, each correlated with a distinctive auditory stimulus. Three components were gravity avoidance with different values of the postponement interval. The fourth component was gravity avoidance extinction, in which artificial gravity remained at the lower limit of the schedule and responses were ineffective.

METHOD

Centrifugation as a Substitute for Gravity

Centrifugal force is equivalent to gravitational attraction in that it acts on each particle of the subject and the sum of all these forces is in equilibrium with the reaction of supporting structures, such as a floor or seat. At the earth's surface accelerations greater than the mean gravitational acceleration, g , (about 9.81 ms^{-2}), can be maintained for extended periods only by centrifugation. During rotation at constant angular velocity, ω , and constant radius, r , a mass is acted on by the vector sum of

the centrifugal acceleration, $\omega^2 r$, and the gravitational acceleration, g . The magnitude of this resultant acceleration, a , is $(g^2 + \omega^4 r^2)^{1/2}$, or in units of g , $a = (1 + \omega^4 r^2)^{1/2}/g$. Weight (force) is the product of mass and acceleration. Hence, the ratio of the effective weight of a mass during rotation to its "normal" weight is the same as the ratio, a/g , of resultant to gravitational accelerations. Hence, g is the customary unit of acceleration, although it is not a unit of force or weight. In this paper, resultant acceleration is also referred to as "artificial gravity" or "g-level" and resultant force is called "effective weight". Since resultant acceleration is a function of both centrifuge angular velocity, ω , and radius of rotation, r , artificial gravity may be manipulated by changing either of these variables.

The relations above hold during steady state rotation at constant angular velocity and radius. Changes in angular velocity or movement of a subject with respect to the rotating system introduce additional, transient accelerations. Angular acceleration, $d\omega/dt$, is the time rate of change of angular velocity and is equivalent to a tangential linear acceleration of magnitude $r (d\omega/dt)$. That is, a subject facing the axis of rotation during centrifugation is subjected to a lateral force during changes in angular velocity. In addition, a transient Coriolis acceleration is imposed whenever a mass has velocity with a radial component relative to the rotating coordinate system. For the special case of radial motion, the Coriolis acceleration is tangential and the magnitude is $2\omega(dr/dt)$, where dr/dt is the time rate of change of radius. Thus, radial motion and angular acceleration give rise to similar lateral forces. In the present experiment, transient accelerations occurred as a function of time or were produced by responses. Their relation to gravity avoidance behavior is considered in the discussion section. A more complete account of the mechanics of centrifugation can be found in textbooks (e.g., Den Hartog, 1961).

Subjects and Apparatus

Three adult male squirrel monkeys, *Saimiri sciureus*, with no previous experimental history, were restrained during experimental sessions inside a capsule mounted on a 50-ft (15 m) diameter centrifuge with programmable capsule radius and angular velocity. The centrifuge and capsule is shown in Figure 1. The

capsule was gimballed so that during rotation, the resultant of gravitational and centrifugal accelerations always acted along the axis of the subject's trunk. Monkeys were restrained in a primate chair with only the head and arms free. A response lever (Lehigh Valley, LVE 1405R) was mounted directly in front of the subject and a pilot light was above the lever at eye level. Each depression of the lever produced a brief flash of the pilot light and an audible relay click. Auditory stimuli (white noise, tone, or train of clicks) could be presented in the capsule. During experimental sessions the capsule was illuminated and subjects were observed via closed-circuit TV.

Events in the capsule were transmitted to the control and recording apparatus through slip rings. The centrifuge was controlled by a system of curve followers and an IBM 1800 computer. Experiments were conducted with a capsule radius of 24.5 ft (7.35 m). Scheduled increases or decreases in angular velocity maintained a constant time rate of change in re-

sultant acceleration at $1g/30s$. In all programs, the lower limit of artificial gravity was 1.05 g (at 0.646 rad/s). During the earlier part of preliminary training, the upper limit was 2.05 g (at 1.532 rad/s). Subsequently, the upper limit was 2.55 g (at 1.754 rad/s).

The control system was arranged so that increases or decreases in artificial gravity could be made contingent on time or on events recorded from the capsule. In avoidance-escape procedures increases were time dependent and decreases were response contingent. All schedules were arranged by the IBM 1800, which also acquired and processed data. The centrifuge was controlled by curve followers which were controlled in turn by the computer. Lever responses were recorded on a cumulator and the resultant linear acceleration was recorded on a strip chart recorder, which indicated the output of an accelerometer on the capsule. Mean g-levels were computed from the integrated elapsed time in each tenth of the total g-range.

Fig. 1. Fifty-foot diameter behavioral centrifuge for research on artificial gravity. An animal capsule with gimballed mount and windshield can be seen on the near arm. Both rotation rate and capsule radius are remotely programmable. During rotation, the capsule orients in the direction of resultant acceleration. Control and recording circuits are wired through slip rings over the axis of rotation. The machine is controlled by curve followers and an IBM 1800 series computer.

Procedure

Preliminary training. After being adapted to the restraining chair, all three monkeys were placed on board the centrifuge for three "operant level" sessions during which the level of random responding on the lever was determined under rotation. These and all subsequent experimental sessions were 2 hr in duration. Sessions occurred twice a week for each subject throughout the experiment. During the three operant level sessions subjects were rotated continuously at 1.05 g (0.646 rad/s) in the presence of a white noise. Lever depressions produced a click and flash of the pilot light but had no other scheduled consequences. By the third session, lever responses were rarely emitted by any subject.

Following operant level determination, subjects were placed on a gravity avoidance discrimination schedule. This schedule consisted of alternating periods of extinction at 1.05 g in the presence of white noise (S—) and gravity avoidance in the presence of a tone (S+). During extinction, artificial gravity remained at 1.05 g and responses had no effect on the centrifuge. At the onset of avoidance-escape periods, artificial gravity was scheduled to increase to the upper limit. A response produced a 20-sec period of decreasing acceleration. Subsequent responses within 20 sec reset this interval until the lower limit of gravity was reached. At the lower limit, each response postponed the onset of the next increase by 20 sec from the time of response (response-g or RG interval = 20 sec). Thus, during avoidance-escape components, responses either initiated a period of deceleration, or postponed the onset of increases in artificial gravity. By responding at least once every RG seconds, the subject could produce and maintain the minimum gravity. On the other hand, interresponse times greater than the RG interval imposed increased acceleration. This procedure differs from the usual free-operant avoidance-escape schedule (Sidman, 1953) because changes in acceleration must be imposed gradually. The procedure has some properties of titration schedules (Weiss and Laties, 1959).

All subjects received 30 two-hour sessions of avoidance discrimination training over 15 weeks. During the first 12 sessions, the upper limit of artificial gravity was 2.05 g and alternating periods of extinction (S—) and avoid-

ance (S+) were 15 min in duration. During the last 18 sessions, the upper limit of gravity was increased to 2.55 g and S— duration was 10 min with S+ duration 20 min. The RG interval remained at 20 sec during avoidance components.

Multiple gravity avoidance schedule. After training on avoidance discrimination with the RG interval at 20 sec, all three monkeys were placed on the multiple avoidance schedule. The multiple schedule had four components, each associated with a different auditory stimulus. Three components were gravity avoidance with different values of the schedule parameter. The RG intervals with their associated stimuli were 20 sec (high frequency tone), 40 sec (low frequency tone) and 60 sec (train of clicks). The fourth component was avoidance extinction (S—) in the presence of white noise. Experimental sessions were 2 hr in duration with one 15-min exposure of each RG interval in each hour. RG intervals occurred in descending order in the first hour and in ascending order in the second hour. Each avoidance component was followed by a 5-min exposure of S— at 1.05 g. The upper limit of resultant acceleration remained at 2.55 g and the rate of change at 1g/30s. All three monkeys received 22 sessions under the multiple schedule. Sessions occurred twice a week with at least two days between sessions.

RESULTS

The development of discriminated gravity avoidance behavior during preliminary training of one subject (Monkey 60) is illustrated in Figure 2. The upper record shows cumulative responses during the last of three 2-hr control sessions for random responding on the lever (operant level). During operant level sessions, subjects were rotated continuously at 1.05 g. The lower three pairs of records show concurrent cumulative response and accelerometer recordings at different stages of discriminated gravity avoidance training. Complete sessions are shown for the first and last days of training with an upper limit of 2.05 g during avoidance and for the last day of the 18 days of training with an upper limit of 2.55 g. Each session consisted of four extinction components in the presence of white noise (S—) alternating with four escape-avoidance components in the presence of tone (S+). The mean g-level

MONKEY 60

OPERANT LEVEL DAY 3

GRAVITY AVOIDANCE 1.05-2.05g DAY 1

GRAVITY AVOIDANCE 1.05-2.05g DAY 12

GRAVITY AVOIDANCE 1.05-2.55g DAY 18

Fig. 2. Performance of Monkey 60 at selected stages of preliminary training under gravity avoidance discrimination. The upper record (Operant Level, Day 3) shows the last of three control sessions for random responding during rotation at 1.05 g. A 2-hr recording has been cut into 1-hr segments and overlapped. The response pen incremented at each lever depression and reset at the end of the session. The other records show concurrent response and accelerometer recordings with the time scale compressed. In each case, a 2-hr session is shown. The upper record of each pair is a cumulative response recording; the lower record represents the concurrent output of an accelerometer on the centrifuge capsule. The response pen incremented at each lever depression and reset at the end of each schedule component. In addition, the response pen was displaced downward whenever the resultant acceleration increased or was at the upper limit, and was released when gravity was decreasing or at the lower limit.

maintained during avoidance components is indicated above each pair of records. The response-g interval was 20 sec in all avoidance components. It can be seen that responding in S+ increased gradually over the first 12 sessions with an upper limit of 2.05 g. The mean g-level maintained in S+ decreased concomitantly. The discrimination was also well maintained, with very few lever responses occurring in S-. After the upper limit of artificial gravity was increased to 2.55 g, the duration of S+ components was increased to 20 min and the duration of S- exposures was decreased to 10 min. The lower pair of records in Figure 2 show the per-

formance of Monkey 60 on the last day of preliminary training with the increased upper limit of artificial gravity. The rate of responding in S+ was higher, although periods of several minutes at 2.55 g still occurred occasionally. With the increased upper g-limit, the average level maintained during S+, was slightly below that seen previously.

The purpose of preliminary training was to condition avoidance and escape behavior and establish the discrimination between gravity avoidance and extinction. After the 30 sessions of avoidance discrimination illustrated in Figure 2, all three monkeys were trained on the

MULTIPLE GRAVITY AVOIDANCE SCHEDULE 1.05-2.55g

MONKEY 60

MONKEY 61

MONKEY 65

Fig. 3. Final performance of three monkeys under the multiple gravity avoidance schedule. Concurrent recordings of responding and accelerometer output are arranged as in Figure 2. The order of presentation of the three avoidance schedules is indicated above the upper pair of records (Monkey 60). The event pen under cumulative records was displaced during avoidance components and released during extinction (S-). Each component of the multiple schedule was associated with a different auditory stimulus.

multiple avoidance schedule for 22 biweekly sessions. Performance of all three subjects during the last session under the multiple schedule is shown in Figure 3. Both response and accelerometer recorders operated as in Figure 2. The order of occurrence of the three RG intervals is indicated above the upper pair of records (Monkey 60). Each 15-min exposure of an avoidance component was followed by a 5-min period of extinction at 1.05 g. The records show the entire final session, except for the last 5 min in S—.

Figure 3 shows that rates of responding for all three monkeys were related to the RG interval, the highest rates obtaining under the shortest postponement times. In the data of Monkeys 60 and 61, the frequency and duration of increases in acceleration were also related to the schedule parameter. Longer and

more frequency increases in gravity were tolerated at shorter RG intervals. On the other hand, Monkey 65 maintained very nearly the minimum gravity at all times regardless of the schedule.

Figure 4 presents the relationship between response rates and mean g-levels, on the one hand, and the RG interval, on the other hand. Points represent the mean of the last five sessions under each component of the multiple schedule for each animal. Response rates in S— are also plotted. It is apparent that Monkey 61, and to a lesser degree, Monkey 60, tolerated higher mean g-levels at shorter postponement times. Monkey 65 behaved so as to maintain similar g-levels under different schedules by increasing response rate at shorter postponement times. Response rates of Monkey 60 were also a decreasing function of the RG interval. In

Fig. 4. Mean g-level and mean response rate as functions of the schedule parameter for three monkeys trained under the multiple gravity avoidance schedule. Each point represents the mean of the last five of 22 sessions. Standard errors are plotted about mean response rates. Standard errors of mean g-levels were too small to be indicated.

the case of Monkey 61, however, response rate was increased only at the shortest RG interval (20 sec), and the g-level varied with the schedule parameter more than rate of responding did. The discrimination between S- and the other schedule components was well maintained in Monkeys 60 and 65. Monkey 61, however, displayed about the same response rate in S- as at the longer RG intervals.

DISCUSSION

Although the analysis of aversive control over behavior has proceeded largely through the use of electric shock, the techniques developed have been applied to the study of aversive properties of a variety of other stimuli. Thus, illumination (Keller, 1941), noise (Harrison and Tracy, 1955), and temperature (Carlton and Marks, 1958; Weiss and Laties, 1961) are among the conditions that have been shown to maintain escape or avoidance behavior under appropriate conditions. The present results, together with our previous experiments using similar procedures (Clark *et al.*, 1969; 1971), establish increased effective weight as one of these conditions. Not only are increases above normal earth gravity physiologically noxious to earth organisms, they are also behaviorally aversive in that responses that terminate or postpone them can be conditioned and maintained.

In the present experiment, gravity avoidance behavior was brought under multiple schedule control. Such control may have at least two sources. Differences in responding during different schedule components could be based directly on differences in the schedules, as in a mixed schedule. Or, responding could be based on discriminative control by the stimuli associated with different schedule components. The pattern of responding seen most often in Monkey 65, and occasionally in other subjects, suggests responding under the multiple schedule was partially under discriminative control of the associated stimuli. Thus, Monkey 65 (Figure 3) typically initiated responding in avoidance components immediately upon stimulus onset and before any increase in artificial gravity. This indicates that discriminative control of gravity avoidance may be similar to stimulus control of operants maintained by other reinforcers.

The effect of variation in the gravity avoid-

ance schedule parameter is similar to that seen in avoidance maintained by other aversive stimuli. In general, higher rates of responding are generated and higher mean g-levels are tolerated at shorter postponement times. In free-operant avoidance maintained by electric shock, response rates increase with decreasing response-shock intervals, the point of maximum responding depending on the shock-shock interval (Sidman, 1953). Where the response-shock and shock-shock intervals are equal, both response and shock rates decrease with increasing postponement times (Clark and Hull, 1966). Finally, in fractional escape from shock under titration schedules, higher shock intensities are tolerated where the interval between increments is shorter (Weiss and Laties, 1959). Thus, functional properties of gravity avoidance behavior in relation to the schedule parameter are similar to those obtained with other reinforcers.

It is likely that avoidance of increased effective weight is a mechanism of the gravity preference behavior obtained in locomotion experiments. In these experiments (*e.g.*, Belleville *et al.*, 1964; Broderson and Lange, 1969; Lange and Belleville, 1971), there is a spatial gradient of the magnitude of acceleration so that the imposed level depends on the subject's position. Under several spatial configurations, animals locomote to and remain near 1.0 g. Experiments with operant procedures suggest that the obtained patterns of locomotion depend on escape from and avoidance of increases in effective weight.

In the present experiment, changes in artificial gravity were produced by varying angular velocity (rotation rate) at a fixed radius. Where the subject is immobile and where differences in radius of different parts of the body are negligible with respect to the radius to the center of mass, different combinations of angular velocity and radius that produce the same resultant acceleration are physically equivalent. Within the range of values employed here, experiments have also shown that both gravity avoidance behavior and stimulus generalization gradients are functions of resultant linear acceleration and not of angular velocity or radius *per se* (Clark *et al.*, 1971; McCoy and Lange, 1969; McCoy, Love, and Miller, 1971). Linear acceleration produces deformations of the body, changes in inertial forces against supporting structures, increases in work required

to execute body movements, and pressure gradients in fluid columns such as the cardiovascular system. Cutaneous, kinesthetic, proprioceptive, and labyrinthine receptors are stimulated. Stimulation of these receptors depends on displacement of receptor organs or adjacent structures. Displacement occurs as a function of acceleration. Thus, directly or indirectly, acceleration provides the adequate stimulus in these modalities. While we have not tried to establish the sensory basis of gravity avoidance, it is not surprising that, with the qualifications noted above, similar changes in linear acceleration have similar behavioral effects whether produced by changing angular velocity, or radius, or both.

It has been suggested that the transient angular or Coriolis accelerations produced during changes in artificial gravity have a role in the maintenance of gravity escape or avoidance. There is reason to suppose that these transients are themselves aversive because of their labyrinthine effects (Riccio and Thach, 1966). Under the kind of procedure used here, it is also possible that transients may provide discriminative stimuli for impending changes in resultant linear acceleration. It should be noted, however, that these procedures do not generate behavior that avoids angular or Coriolis accelerations. The subjects behave so as to reverse or avoid imposed increases in resultant linear acceleration. The response patterns generated actually result in an increased frequency of transient angular accelerations.

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