Effects of Fixed-Interval and Random-Interval Escape Paradigms on Presession and Postsession Levels of Corticosterone in the Rat

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EFFECTS OF FIXED-INTERVAL AND RANDOM-INTERVAL ESCAPE PARADIGMS ON PRESESSION AND POSTSESSION LEVELS OF CORTICOSTERONE IN THE RAT

by

Duane Dregits

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Submitted to the
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My thanks go to a number of people in the Psychology and Biology Departments at Western Michigan University and the UpJohn Company in Kalamazoo, Michigan. For teaching me the aortic cannulation techniques that I used in this study, recognition must go to Dr. J. R. Weeks and his staff at the UpJohn Company. For allowing me the use of his surgical lab in which to perform the cannulations, my thanks go to Dr. Fred Gault of Western Michigan University who also served as one of my thesis committee members. For helping me learn the protein-binding assay for corticosterone, recognition must go to another thesis committee member, Dr. Leonard Beuving of Western Michigan University. For providing me with the behavioral lab necessary to realize the behavioral work, and also serving as my committee chair, my thanks to Dr. Arthur Snapper of Western Michigan University. Finally, for providing additional support and helpful criticism in bringing this thesis to an end, thanks go to Dr. Kay Malott of Western Michigan University.

Duane Dregits
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WESTERN MICHIGAN UNIVERSITY, M.A., 1980
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Mason (1968), in a discussion of the integration of psychendocrine mechanisms, noted that elements of novelty, uncertainty, and unpredictability are especially striking in their ability to elicit responses of the pituitary-adrenal systems. This seems to be true for both human and sub-human species, as well as among humans; both for those who would be clinically regarded as "normal" and for those who would be regarded as "disturbed". Additionally, for disturbed hospitalized patients, "involvement" or "trying" are variables which he points out to be especially important to stimulating this system to increase the levels of corticosterone in urine and plasma.

Weiss (1971a, b, c) has addressed himself similarly in some recent studies to the influence of predictability, and the interaction of predictability and avoidance/escape responding on gastric ulcer formation, circulating levels of corticosterone, and related indices of "psychosomatic stress". In these studies, predictability was manipulated by the use of discriminative stimuli ("warning signals") that reliably preceded electric shock.

From the results of one of these studies (1971a), Weiss formulated and tested (1971a, b, c) a model of the predictability-responding interaction and consequent ulceration.

Stress ulceration is said to be a function of two variables: the number of coping attempts an animal makes, and the amount of appropriate feedback which these coping attempts produce. ...Hence, the first proposition is that ulceration tends to increase monotonically as the number of responses, or coping attempts, increases. The theory states, however, that expression of the foregoing relationship is completely dependent on a second variable—the
consequences of coping attempts, or, in operational terms, the stimulus feedback from responses. ... If responses immediately produce stimuli that are not associated with the stressor, ulcerogenic stress will not occur. If, on the other hand, responses fail to produce such stimuli, then ulcerogenic stress will occur. Stimuli that are not associated with the stressor and that follow a response are called relevant feedback, ... (Weiss, 1971a)

Relevant to the current study, Weiss also added that "shock termination is a very large change in the stimulus situation", and therefore "excellent feedback". Using this model, Weiss accounts for both his own results and the severe ulceration which developed during high-frequency free-operant avoidance lever-pressing of monkeys in an experiment by Brady, Porter, Conrad, and Mason (1958) known as the "executive monkey" experiment (Brady, 1958). Since discriminative stimuli do not precede shock in free-operant avoidance paradigms, high-relevant-feedback comes only from shock termination (escape responding). Thus, the ulceration of the "executive monkeys was due to high-frequency responding in a low-relevant-feedback situation according to Weiss.

The Weiss model does not appear to fit well the data of all free-operant avoidance studies however. Explicitly, in the studies described in the Mason (1968) review, corticosterone levels were generally elevated in the initial sessions, but these levels returned to baseline levels—sometimes they dropped below—by approximately the fourth session, while the number of avoidance responses increased across sessions. Applying the Weiss model here, we should expect the levels of corticosterone to either remain elevated in later sessions or elevate even further since (1) the association is no different in later sessions than in early ones, and (2) the number of low-relevant-feedback avoidance responses...
responses is actually higher in later sessions than in earlier ones. We might expect the levels of corticosterone to drop slightly after the situation loses its novelty, but we should not expect these levels to drop to baseline if the animal engages in much low-relevant-feedback responding. Because these expectations are not realized, the role of shock frequency versus psychological factors such as predictability, avoidability, and escapability, may have to be reassessed with respect to the corticosterone response.

Weiss and Mason have both stated, as have others, that psychological variables are more important than shock frequency in determining the circulating levels of corticosterone. The Mason, et al. avoidance data just cited may evidence the fact that early in avoidance, when an animal is making the transition from an experimentally naive subject to an experienced avoider, the predictability-responding interaction is maximally important, because it provides the animal with information necessary to reduce shock frequency. Once the transition has been made however, these variables may no longer be of utmost importance. We might thus consider the possibility that the Weiss model is only applicable to transition-state responding: while for steady-state responding, the activity of the pituitary-adrenal system is directly determined by shock frequency, as in non-avoidance and non-escape situations (Pare, 1970). It should be noted that the Weiss studies were not longitudinal, but single session studies which lasted either 24 or 48 hours.

It is also interesting that although a positive correlation obtains in the Weiss studies between low-relevant-feedback responding and levels of corticosterone, a negative correlation is reliably obtained in those avoidance studies which manipulate or measure
corticosteroids independently and treat responding (conditioned avoidance, intertrial, or "exploratory") as the dependent variable (Bohus, 1970; Bohus & DeWied, 1966; Bohus & Endroczi, 1965; Bohus & Greven, 1968; Bohus & Lissak, 1963; Bohus, Nyakuas & Endroczi, 1968; DeWied, 1967; DeWied, 1968; DeWied, Bohus, & Greven, 1968; Endroczi & Fekete, 1971; Greidanus, 1967; Levine, 1968; Mason, Brady, & Tolliver, 1968; Van Delft, 1970; Wertheim, Connor, & Levine, 1967). Although these data do not contradict Weiss, they appear to evidence an inhibitory function of corticosteroids on responding that makes presession levels of corticosterone a variable of interest. Especially relevant in this regard is the study of Wertheim, et al. (1967) which showed a shift in interresponse-time distributions in free-avoidance toward longer interresponse times when dexamethasone—a potent synthetic glucocorticoid—was injected presession.

There were three objectives in the present study. The first objective was to determine if adaptation to shock develops in escape paradigms in which high-relevant-feedback is obtained only by an escape response, as in free avoidance, and where the number of intrasession and intersession shock exposures is invariant for all subjects. The second objective was to determine if the response of the pituitary-adrenal system is affected by the predictability of an aversive electric shock stimulus when the predictability is determined not with discriminative stimuli, as in the Weiss studies, but temporally. The third objective was to determine if presession levels of corticosterone are predictors of intrasession lever-press performance.
The primary interest here is whether or not escape and avoidance situations are alike, and if so, to learn how well the Weiss model applies to at least two situations which are non-discriminated.
METHOD

Subjects

The subjects were Sprague-Dawley derived male albino rats from the colonies of the UpJohn Company, Kalamazoo, Michigan. The age of the subjects at the beginning of experimentation was approximately 90 days. Their body weights ranged from 317-417 grams at the end of the experimental sessions. Food consumption and water consumption were ad libitum throughout experimentation, and body weight was monitored daily. No subject had been used in any prior experiments.

Apparatus

The experimental operant chambers measured 20.2 cm L x 12.5 cm W x 15.3 cm H. Each was constructed of plexiglas with the interior walls lined with 1.016 mm aluminum plates. The floor consisted of a grid of aluminum tubes, 3.3 cm apart, and .6 cm in diameter, which traversed the length of the chamber. The sequence, 1 ma shock was delivered through these grids from the rearmost grid, forward. For each grid, shock was delivered for .03 seconds, with the onset of shock for a given grid occurring with the offset of the prior grid in the sequence. When shock was terminated on the fourth grid, the sequence again began with the rearmost grid. When an animal made an escape response, shock always terminated with the fourth grid in the sequence. An escape response consisted of a press on a Lehigh Valley rodent lever (Lehigh Valley Electronics, Fogelsville, Pennsylvania) located 2.54 cm from the left side of the chamber. The chambers were housed in sound...
attenuating enclosures which contained speakers delivering white noise from a Grason Stadler (Model 1048) noise generator, and a 0.96 watt houselight (#1819, Chicago Miniature Lamp Works, Chicago, Illinois).

The collection of behavioral data, and the control of experimental procedures including shock delivery were by a SKED run-time system (SKED User's Group, Kalamazoo, Michigan) operating on a PDP-8/e minicomputer (Digital Equipment Corporation, Maynard, Massachusetts), with the operant chambers interfaced to the computer via State Systems Incorporated (Kalamazoo, Michigan) input and output cords and relay panels.

Blood Withdrawal

Two weeks prior to the start of baseline conditions, an aortic cannula was chronically implanted in each animal by the technique of Weeks (1974). Such a device allowed blood withdrawal without venipuncture, so the confounding stress of venipuncture was circumvented. Blood was withdrawn into heparinized 1 ml disposable syringes while the animals were restrained with a towel wrapped around their bodies. Animals were adapted to towel wrapping during the two week recovery period following surgery and preceding the baseline conditions described below. During the days of the second baseline condition and experimental sessions, blood was drawn immediately prior to session start and immediately upon session termination. Blood was also drawn at corresponding times during the initial baseline condition, when home cage levels of corticosterone were determined. All samples for all conditions were drawn between 5:30 and 6:30 p.m., and placed in 10 x 75 mm culture tubes until preparation for storage.
Baseline Conditions

Two baseline conditions were used in the present study, each of which lasted one week. The first, Baseline 1, involved removing each animal from his home cage, withdrawing .4-.45 ml of blood from the subject, returning him to his home cage, and repeating this procedure 45 minutes later. This daily procedure provided an index of the normal resting state of corticosterone in the subjects at points in time corresponding to that of session start, and that of session end, and thus served as a control for passage of time. Since a rat has a blood volume of approximately 20 ml, withdrawing this quantity of blood daily, over this period of days, resulted in no apparent health problems for the subjects. No behavioral data were collected during this baseline condition.

The second baseline condition, Baseline 2, was identical to the first, but with three modifications. First, during the 45 minute interval between blood withdrawals, the subjects spent their time in the experimental chambers rather than in their home cages. Second, the free-operant level of lever-press responding was monitored. These changes provided the subjects with a period of adaptation to the experimental chambers, and also provided an indication of whether or not placement in such a chamber would produce elevated levels of lever-press responding and corticosterone as a result of relative confinement, novelty, restraint, or some property of the chamber itself. The stimulus conditions in the chamber during Baseline 2 consisted of a white houselight and white noise. Third, blood was withdrawn every second day, rather than every day.
Experimental Sessions

The first day following the week of Baseline 2 was the initial day of experimental sessions. Animals had been assigned randomly, prior to Baseline 2, to what would be one of two treatment groups: (1) fixed-interval escape, or (2) random-interval escape. For neither group was there an external stimulus which preceded shock.

In the fixed-interval paradigm, FI-30 sec, each animal was exposed to scrambled shock 30 seconds after the offset of the prior shock. There was no opportunity to avoid shock, but an animal could immediately escape shock by pressing a rodent lever. If such a response did not occur within 8 seconds after shock onset, shock was terminated, and the timing of the next 30 second interval between shock deliveries began.

In the random-interval paradigm, RI-30 sec, scrambled shock was presented on an average of once every 30 seconds from the prior shock offset. This schedule was produced by making the probability of shock presentation 0.033 in each consecutive second.

Sessions began with the onset of a houselight and white noise as during baseline conditions. Each daily session was terminated upon the offset of the 90th shock delivered. Shock exposures were thereby identical in number for each group of subjects. Blood was withdrawn frequently during early sessions, and intermittently, at the convenience of the experimenter, during later sessions until the 45th day of escape training.
Blood Processing and Analysis

Following each day's experimental session, within 20 to 30 minutes after blood had been withdrawn from the subject, blood serum was separated from red blood cells via centrifugation and pipeting. Individual plasma samples were frozed at -20 degrees Celsius until the time of assaying. Assaying was done by a competitive protein-blood radioassay (Murphy, 1967).

Behavioral Measures

During Baseline 1, no behavioral measures were recorded. During Baseline 2, however, total free operant lever presses were recorded while the subjects were in the experimental chambers. During the escape sessions, the following behavioral measures were obtained for each group.

1. Time distribution of responses in the intershock interval.
2. Escape latency of each escape response, and a daily mean escape latency for each subject.
3. Total number of lever presses during the intershock interval.
4. Total number of escape lever presses.
5. Total number of lever presses (3 and 4).
6. Total shocks not escaped by an escape lever-press.
7. Total shock onsets.
RESULTS

Figure 1 displays the mean escape latencies and their associated standard deviations for FI and RI subjects on shock-exposure days when blood was withdrawn. Escape response latencies reached their minimum levels by the third to seventh day of shock exposure. This minimum level was maintained especially well for FI subjects.

Figure 2 shows the mean number of lever presses that occurred in the intershock interval for FI and RI subjects on the days of blood withdrawal. For FI subjects in general, a continual decline in the number of lever presses occurred across sessions. Similarly for RI subjects, there was also an overall decline in lever pressing across sessions; but the trend was somewhat bi-modal, with the number of intershock responses rising in later sessions. The number of intershock responses of RI subjects was about twice that of FI subjects during the final session.

Figure 3 indicates both presession and postsession levels of circulating corticosterone in both FI and RI subjects during the shock sessions, and during the pre-shock control sessions. Baseline 1 data are represented as a mean of all days during that period since the data of Baseline 2 are nearly identical to Baseline 1 and provides a means of comparison with escape sessions. On the first day of exposure to the chamber, Day 8, postsession corticoid levels elevated in subjects of both groups. However, by the third day of exposure to the chamber in this condition, these levels remained at presession levels. For some subjects,
- FIXED-INTERVAL GROUP
- RANDOM-INTERVAL GROUP

INTER-SHOCK INTERVAL RESPONSES

DAYS

15 16 17 19 22 25 28 31 34 38 43 51 60
the postsession levels often fell beneath presession levels. This had also been seen during Baseline 1, indicating that it probably was not a manifestation of some property of the chamber. During the Baseline 2 condition, approximately 12.6 free operant bar presses per subject per session were emitted, with a range of 0 to 47 responses across all subjects and sessions. One the first day of shock exposure, there was an abrupt elevation in postsession corticoids. These elvations persisted for subjects in both FI and RI conditions, despite an overall decrease in intershock responses across sessions. The FI postsession levels are generally beneath the RI postsession levels in the latest sessions; but, this is generally due to the influence of one subject, S7, which displayed an abrupt drop in postsession levels at session 28. For both FI and RI subjects, presession levels of corticosterone were similar to control sessions, and were not different for FI and RI subjects.

The data of individual subjects were examined closely, and it was found that Figures 1, 2, and 3 accurately portray individual subject phenomena, not just averaging artifacts. It was also found that days when shock-shock responding was exceptionally high or exceptionally low were not necessarily days when presession and/or postsession corticoid levels were exceptionally high or low. Lever-press levels and corticosterone levels did not show any positive or negative correlations. Any given subject was just as likely to display a corticosterone level of 50 ug/100 ml plasma on a day when he made 35 intershock lever presses as on a day when he made 120 intershock lever presses.

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Also, the subjects did not display a peak corticosterone response. On one particular day, subject S1 displayed an extremely elevated postsession level of corticosterone that was approximately 30 ug/100 ml higher than any other day (70 ug/100 ml). It is assumed that this was due to the additional physical stress which the animal provided for himself by trying, almost successfully, to extract his cannula. This extreme elevation implies that the postsession levels of corticosterone displayed by the subjects during the shock sessions are probably not the maximum levels that can be achieved. In other studies (Hussian, 1974) done in the same laboratory as the assays of this study, it had been found that heat, cold, or restraint "stress" could elevate corticosterone levels to 100+ ug/100 ml plasma in this strain of rats.

Subject S5 is also a subject of special interest. A broken wire going to one of the four large shock grids in the chamber of S5 forced an accidental ABA design which contrasted escape with the development of what might be regarded as "passive avoidance". Although the chamber was tested before every session, the flaw was not immediately apparent since the grid initially would fail only when the chamber door was closed—disturbing the wire—and the chamber was tested with the door open. In the earliest sessions, a door closure would only open the circuit to this grid intermittently. The problem gradually worsened however, until it lost its intermittency around day 34, when the subject learned to "passively avoid" by remaining only on this grid. It was at this point that the exact problem became obvious and the chamber repaired. There was a pronounced drop in postsession
corticosterone levels at day 31 to 25 ug/100 ml, and a further drop to presession levels (10 ug/100 ml) on day 34. Postsession levels had been averaging 50 ug/100 ml prior to these days. On day 35, when the chamber was repaired so the subject could no longer avoid shock, postsession levels immediately rose to 40 ug/100 ml. This elevated level persisted in later sessions, indicating a sharp contrast between corticosteroid levels when the animal was avoiding, and when he was escaping. This suggests the primary importance of shock frequency in paradigms where the animal is helpless in latering this frequency.

The relationship between escape latencies and both presession and postsession corticosterone levels, and the relationships between intershock responses and both presession and postsession corticosterone levels were examined carefully for each subject; but not enlightening correlations emerged. The time distribution of responses was also evaluated with respect to presession and postsession levels of corticosterone, and no consistent relationships were found. However, it was observed that most non-escape responses occurred during the first 3-6 seconds of the shock-shock interval. Table 1 displays the percent of shock-shock responses that were emitted by each rat in the first 3 seconds of the shock-shock interval. As can be seen from this table, most intershock responses occurred shortly after shock offset across all sessions. On some days, all of these responses occurred within 3 seconds of shock offset for subjects S5, S9, and S6.
<table>
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DISCUSSION

The present study produced three main results: (1) postsession levels of corticosterone remained elevated in all escape sessions, for all subjects, displaying little habituation; (2) presession levels of corticosterone remained low, and seemed to bear little relationship to intrasession responding; (3) when a lever-press response did occur, it generally occurred after a salient change in the environment. Specifically, escape lever presses were emitted shortly after electric shock onset, and most intrashock lever presses occurred within 3-6 seconds of shock offset.

The Weiss model discussed earlier addresses itself to the first result. However, the interpretation of this result with respect to the Weiss model is difficult. If we accept Weiss' assertion that shock termination provides excellent high-relevant-feedback because it provides a very large change in the stimulus situation, then the data of the present study do not support the Weiss model. Since, in later sessions, the RI subjects made considerably more intershock lever presses (low-relevant-feedback responses) than the FI subjects, the FI rats might have been expected to display lower levels of postsession corticosterone in these sessions than RI subjects. This result did not occur, but maybe shock termination does not provide relevant feedback. Shock offset, or termination, probably does not have the same predictive utility with regard to shock onset that the termination of a discriminative stimulus preceding shock onset would have, and this predictive utility may be what gives an environmental change relevance. Saying, as Weiss does, that shock
termination provides relevant feedback because it is furthest removed in time from shock onset than any other event and is a salient change in the environment seems to be a poor operational definition of relevance. If this is true, then a failure for a difference to arise between fixed-interval and random-interval subjects may be due to the fact that there was no such thing as a high-relevant-feedback response for subjects of either group. Whether or not shock termination provides high-relevant-feedback seems to be a question worthy of investigation itself, and not a fact which should be accepted a priori. Thus, trying to apply the Weiss model to schedules which do not use discriminative stimuli may be premature at this point. Although Weiss reports that 70% of his animals emitted primarily escape responses, when shock is part of a stimulus complex made up of discriminative stimuli preceding shock, and the shock itself; termination of shock by an animal emitting an escape response in his paradigm may be quite a different thing than the termination of shock in the paradigm used here.

It might be true that shock termination does provides high-relevant-feedback, but the difference between the ratios of the non-escape and escape responses between the two groups of subjects simply is not great enough for a difference in the response of the pituitary-adrenal system to manifest itself.

Presession levels of corticosterone were completely inadequate predictors of performance during the sessions for all subjects. Variability of presession levels of corticosterone across sessions was not very great however, so it is difficult to assess in these experiments the true impact of presession levels on responding.
The presession levels would actually have to be altered by the experimenter in order to provide a true test of the influence of these levels on responding within a session. This was not done in this study as only naturally occurring levels were of interest here and it was not known how sensitive the relationship between presession levels of corticosterone and intrasession responding would be.

The fact that most responses occurred immediately after some kind of stimulus change—either shock onset or shock offset—is interesting, but, probably should not have been unexpected since responding to the stimulus change of shock onset in the form of an escape response is the only type of responding that was favorably consequated, that conseuation being shock offset. The responses that occur shortly after shock offset in the intershock interval may be primarily aggressive responses elicited by the presentation of shock. It may be useful to consider the study of Basset, Cairncross, and King (1973). These researchers found that shock delivered in an irregular fashion produced a greater corticosterone response than shock delivered in a regular fashion only if both were "signaled" by the presentation of a tone stimulus preceding shock. This was true in situations in which there was no response contingency whatsoever, and also, in situations in which there was an escape contingency. They also found that when shock was presented in an irregular-signaled fashion, the escape responses had no effect on the corticosterone response. Comparable levels of corticosterone were produced by irregular-signaled shock delivery when there was an escape contingency and when there was not. The results of the Basset, et al. study and the results of
the present study, along with the Weiss and Mason, et al. studies suggest that avoidance situations and escape situations are truly different with regard to the corticosterone response, and some interactions between the corticosterone response and responding. Any generalization from one situation to the other may be inappropriate at this time.

There also appears to be a difference between the influence of predictability on the corticosterone response, when it is manipulated temporally, and when it is manipulated with "warning signals"; this may be due to differential feedback.
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FIGURE LEGENDS

Figure 1. The mean latencies per day of escape lever presses for fixed-interval subjects and for random-interval subjects. The sessions indicated are those which were immediately preceded by, and immediately followed by, blood withdrawal.

Figure 2. Mean number per day per group of responses which occurred during the intervals between shock offset and the next shock onset for fixed-interval and random-interval subjects. The sessions indicated are those which were immediately preceded by, and immediately followed by, blood withdrawal.

Figure 3. Mean concentration of corticosterone in blood plasma per day per group for fixed-interval and random-interval subjects. Shown separately are mean postsession levels and mean presession levels for each group of rats on those days (Days 18-60) when the subjects were placed in their experimental chambers. Corresponding levels for the preceding days (Days 1-7) are indicated as two pooled mean values for all subjects across these days.