QUANTITATIVE RELATIONS BETWEEN AVOIDANCE BEHAVIOR AND PITUITARY-ADRENAL CORTICAL ACTIVITY[1] .

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The rate at which monkeys pressed a lever and avoided shocks was manipulated in several ways. Measurements were also made of their plasma levels of 17-hydroxycorticosteroids. The rate at which the animals pressed the lever and the frequency with which they received shocks were both implicated as determiners of the steroid levels.

In a previous report, we described some relations between behavior and pituitary-adrenocortical activity in rhesus monkeys; plasma 17-hydroxycorticosteroid (17-OH-CS) levels provided the index of ACTH secretion (Mason, Brady, & Sidman, 1957). The plasma 17-OH-CS levels for monkeys reinforced with food on either a continuous or a fixed-ratio schedule did not rise during an experimental session. Nor did the monkeys display an adrenal cortical response when we abruptly shifted the reinforcement schedule from a low to a high fixed-ratio. However, the animals did respond to two behavioral procedures with near-maximal rates of elevation of plasma 17-OH-CS levels.

One of the effective procedures was a modification of the Estes-Skinner conditioned-suppression technique (Estes & Skinner, 1941). Monkeys lever pressing for food on a variable-interval schedule were given occasional unavoidable shocks, each shock preceded by a warning stimulus. The animals typically ceased pressing the lever when the warning stimuli came on, and displayed a marked increase in plasma 17-OH-CS levels during the experimental session. The warning stimuli increased the animals' adrenal cortical activity even though shock was never administered during experimental sessions in which hormone measurements were made.

The second effective procedure was conditioned avoidance (Sidman, 1953a). Each

time the monkey pressed the lever, it postponed a brief electric shock for 20 sec. Again, associated with the avoidance behavior, there were significant cortico-steroid elevations, even in experiments in which the animal successfully avoided all shocks.

The present report describes additional experiments which were designed to clarify the relations between behavior and pituitary-adrenal cortical activity.

GENERAL PROCEDURE

The subjects were rhesus monkeys (Macaca mulatta), weighing 3 to 5 kg. To eliminate repeated catching and handling, these monkeys remained in a chair-type restraining apparatus throughout the experiments (Mason, 1958). A description of the initial increase and subsequent adaptation of 17-OH-CS levels to such restraint appears elsewhere (Mason, Harwood, & Rosenthal, 1957). Immediately before and after the experimental sessions, blood samples were obtained from the animals from an indwelling cardiac catheter exteriorized at the top of the head. From Monkey M-672, the blood sample was taken from the leg. These samples were immediately centrifuged and the plasma separated and stored in the frozen state until analyzed. The Nelson-Samuels method (Nelson & Samuels, 1952; Harwood & Mason, 1956) was used to determine the concentration of free 17-hydroxycorticosteroids in each sample. Sessions in which blood samples were collected never occurred more frequently than twice each week.

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Attached to the restraining chair were a hand lever (modified telegraph key), a panel of stimulus lights, a loudspeaker for auditory stimuli, and a pair of wires to the foot rests for administering electric shock. In all cases, the animal's lever-pressing response was the reinforced response. Lights in the stimulus panel, located in front of the monkey, were turned on at the start of each experimental session, and were turned off at the end. Automatic relay and timing circuits located in a separate room programed and scheduled the events in each session. Lever-pressing responses, stimuli, and shocks were recorded both on electromagnetic counters and on a Gerbrands cumulative recorder.

EXPERIMENT I:

MANIPULATION OF RESPONSE-SHOCK INTERVALS

After we had established a positive correlation between avoidance conditioning and steroid levels (Mason, Brady, & Sidman, 1957), we wanted to examine quantitatively the relations between steroid levels and some of the variables relevant to avoidance behavior. What features of the avoidance procedure were involved in the steroid elevations?

One of the variables known to be relevant behaviorally in our avoidance situation is the response-shock interval, *i.e.*, the length of time the animal postpones the shock with each avoidance response (Sidman, 1953b). Would the steroid changes also be correlated with the duration of the response-shock interval?

Procedure

Avoidance behavior was conditioned in two monkeys, M-6 and M-288, in the following manner. While in the restraining chair, the animal was shocked every 4 sec (shock-shock interval). The shock duration was fixed at approximately 0.5 sec, and the intensity was 5 to 10 ma. However, each time the monkey pressed the lever, it postponed the next shock for 20 sec (response-shock interval). Only a downward movement of the lever served to postpone shock; the monkey did not postpone shock by holding the lever down. As soon as the animal began to press the lever sufficiently often to indicate to the experimenter that some conditioning had occurred, the shock-

shock and response-shock intervals were both set at 20 sec. (For the remainder of the experiments, the two intervals were kept equal to each other, so that it will be necessary to specify only the response-shock interval.) The response-shock interval was then gradually increased to a value of 180 sec for Monkey M-6 and 240 sec for Monkey M-288.

After the animal had begun to press the lever at a relatively stable rate, an intravenous catheter was inserted, as described. Subsequent avoidance sessions were approximately 2 hr long, and were no more frequent than twice weekly. Blood samples were drawn from the animals immediately before and immediately after each session.

With Subject M-6, the response-shock interval was then reduced, in successive stages, from 180 sec to 20 sec to 2 sec. With Subject M-288, the sequence was 240, 20, 2, 1, 0.75, and 0.5 sec, respectively.

Results

When the response-shock interval was decreased, the animals usually increased the rate at which they pressed the lever (Sidman, 1953b). Figure 1 illustrates the avoidance behavior of Monkey M-6 during the final session at each response-shock interval. The behavior of Monkey M-288 was similar, although its rate changes were not so great.

Figure 2 shows the total responses per session and the corresponding steroid changes for Monkey M-6. The steroid response is given in terms of the difference between the animal's plasma levels before and after the experimental session; positive values indicate that the plasma steroid levels increased during the session, and the negative values indicated that these levels decreased. Trends from one session to another indicate variations in the amount of steroid *change*.

At the longest response-shock interval, there was little or no steroid increase. When the response-shock interval was changed from 180 to 20 sec, both the steroid levels and lever-pressing rates increased, but the steroids then declined from a near-maximal value. Reducing the response-shock interval to 2 sec again caused the animal to increase its rate of lever pressing, and there was a second rise in steroid levels to the maximal value; but, again, the amount of steroid rise was less during the final session.
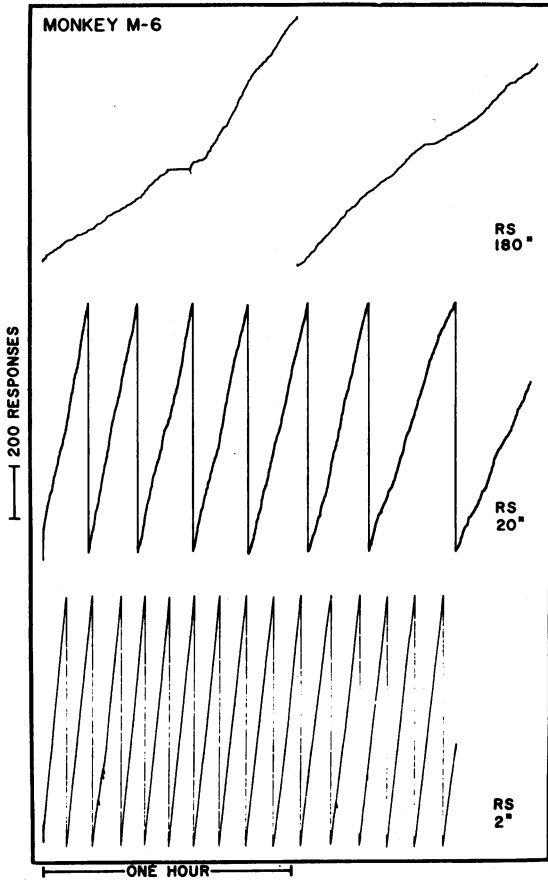
Fig. 1. Cumulative records of the final session at each value of response-shock (RS) interval. The occasional oblique marks indicate shocks.
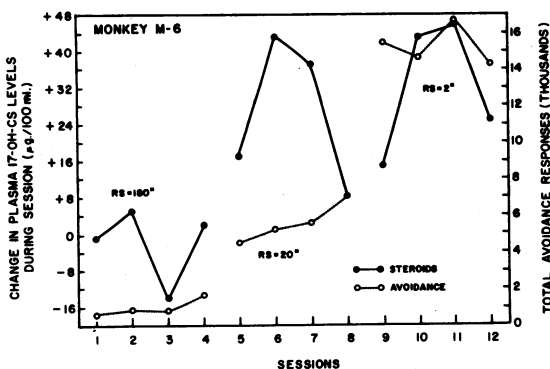

Fig. 2. Response rates and steroid changes at each response-shock (RS) interval.

Some striking discrepancies in detail occur between the magnitude of the behavioral and hormonal changes. For example, the large steroid increase during Session 6 cor-

responds to a relatively small change in the monkey's rate of avoidance responding. The amount of steroid change decreased considerably during Session 8, even though the response rate continued to increase. Again, in Session 9, the extremely high rate at which the monkey pressed the lever was accompanied by only a small increase in steroids. Thus, although we may draw the general conclusion that steroid changes and response rates are both inverse functions of the response-shock interval, we cannot explain all the hormonal changes solely with reference to the concurrent level of avoidance behavior.

One source of the fluctuations in the steroid measurements may have been day-to-day variations in the time course of the steroid change. Previous data have indicated that the animal's steroid level may sometimes become maximal and then begin to decline before the end of a 2-hr session (Harwood & Mason, 1957). In such instances, the measurement at the end of the session would yield a spuriously low estimate of the steroid change that had occurred.

A second source of variability may have been the number of shocks the animal received. In Sessions 1-4, at a response-shock interval of 180 sec, Monkey M-6 received 3, 1, 1, and 1 shocks, respectively, and pressed the lever at a relatively low rate, as Fig. 2 shows. In Session 5, with the change to a response-shock interval of 20 sec, there were 2 shocks. The following session was neither plotted nor numbered in Fig. 2 because technical difficulties prevented analysis of the blood samples; however, there were 5 shocks. This temporary increase in shock frequency could conceivably have produced the subsequent large steroid changes in Sessions 6 and 7. However, the continuing rise in the monkey's rate of lever pressing again brought the number of shocks it received down to 1, 1, and 0 in Sessions 6, 7, and 8, respectively, perhaps thereby producing the lowered steroid level of Session 8. In Session 9, with a decrease in the response-shock interval to 2 sec, the number of shocks the animal received rose to 25; and in the subsequent sessions, it was 6, 13, and 4, respectively. In spite of the relatively high shock frequency during the preceding sessions, however, the amount of steroid increase dropped during the final session.

Figure 3 shows the response rates and steroid changes for Monkey M-288. Again, we see both steroid change and response rate inversely related to the .response-shock interval. However, this animal was quantitatively different from Monkey M-6 in its steroid reactivity. Except for Sessions 9, 12, and 15, its steroid output during each session actually decreased; but the amount of this decrease grew less as the response-shock interval was changed from 240 sec. We observe here a lessening influence of the diurnal cycle, which normally manifests itself as a drop in the steroid level (Mason, 1958). The adrenocor-
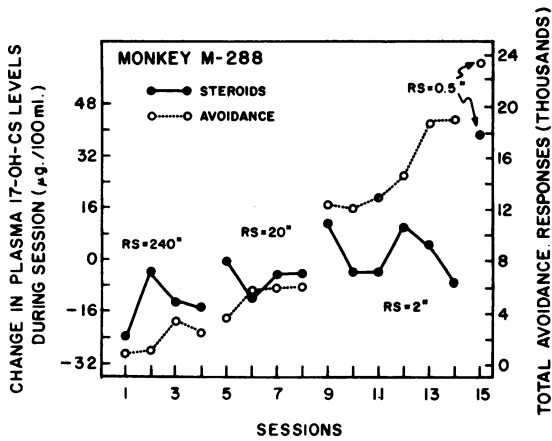

Fig. 3. Response rates and steroid changes at each response-shock (RS) interval.

tical response maintained its relative resistance even though the monkey increased its rate of lever pressing approximately eightfold as the response-shock interval was decreased to 2 sec.

Shock frequencies increased slightly as the response-shock interval decreased, with the largest changes occurring when the animal was initially exposed to a new interval. During the first four sessions, the monkey received 1, 0, 2, and 0 shocks, respectively; at a response-shock interval of 20 sec, the successive number of shocks was 7, 0, 1, and 1; and at the 2-sec response-shock interval, there were 11, 3, 1, 4, 9, and 1 shocks per successive session.

Following Session 14, Monkey M-288 was exposed to a single session each in which the response-shock interval was 1 sec and 0.75 sec. The monkey did not increase its rate of lever pressing during these sessions, and its steroid changes were within the range shown when the response-shock interval was 2 sec. A single

subsequent session at a response-shock interval of 0.5 sec, however, brought about a relatively large increase in both avoidance behavior and steroid levels, as Session 15 of Fig. 3 shows. The number of shocks the animal received in this session also increased drastically to 411.

Discussion

Previous data have demonstrated that high rates of lever pressing generated by fixed-ratio schedules of food reinforcement do not increase the steroid levels (Mason, Brady, & Sidman, 1957). In broad outline, however, we may say with reasonable assurance that in the avoidance situation, higher rates of lever pressing produced by shorter response-shock intervals will be accompanied by higher steroid levels. Although the source of the steroid increase is not clear, there are four outstanding possibilities:

(a) The animal's rate of avoidance responding and its steroid level may both be independent consequences of the response-shock interval.

(b) The steroid level may be a direct consequence of the number of shocks the animal has received, either in the current session or in the immediately preceding ones. The rate at which the animal presses the lever may affect the steroid level only indirectly by altering shock frequency.

(c) Steroid level may be a direct function of the rate at which the animal presses the lever and avoids shocks. If so, this would be a true "psychosomatic" phenomenon.

(d) Steroid level may be a compound function of more than one of the above factors: response-shock interval, shock frequency, and rate of avoidance responding.

In the next two experiments, we manipulated other variables than the response-shock interval, in order to determine whether the steroid changes were specific to this factor.

EXPERIMENT II:

DISCRIMINATED *VS.* NONDISCRIMINATED AVOIDANCE

In Experiment I, no exteroceptive warning stimulus preceded impending shocks (nondiscriminated avoidance). When an animal is given warning stimuli (discriminated avoidance), it tends to wait until the stimulus comes on before pressing the lever, so that its

rate of avoidance behavior is lowered (Sidman, 1955). By providing the animal with warning stimuli, we can change its rate of lever pressing without altering the response-shock interval. In this experiment, then, we undertook to investigate possible covariations between the monkey's steroid level and its rate of lever pressing when the procedure was changed from discriminated to nondiscriminated avoidance and vice versa.

Procedure

Monkey M-488 was' first conditioned with the nondiscriminated avoidance procedure, as described in Experiment I. After conditioning had taken place with a shock-shock interval of 5 sec and a response-shock interval of 20 sec, both intervals were set at 20 sec. When the avoidance behavior had stabilized, a catheter was inserted and blood samples were secured before and after several nondiscriminated avoidance sessions.

The discriminated avoidance procedure was then initiated. The monkey still postponed shock for 20 sec with each lever press, so that the response-shock interval was unchanged; but a warning signal (tone) came on if the animal waited 15 sec without pressing the lever. The tone remained on for 5 sec and terminated with a shock if the animal still did not press the lever. If it did press the lever, the tone was immediately turned off and a new cycle began. Whenever the animal pressed the lever prior to the tone, it postponed the tone's onset for 15 sec. The only difference in procedure, then, was the presence of the tone during the 5 sec immediately before an impending shock.

The discriminated avoidance procedure was continued until the monkey's rate of lever pressing had dropped to a level which permitted frequent occurrences of the tone, and blood samples were again taken. Following this series, the warning signal was eliminated, and the procedure returned to nondiscriminated avoidance. A final series of blood samples was again taken.

Similar manipulations were carried out with Monkey M-672, except that the initial conditioning procedure was discriminated avoidance, and the two procedures were alternated twice.

All experimental sessions were 2 hr long and occurred no more frequently than twice

weekly during the periods when blood samples were taken.

Results and Discussion

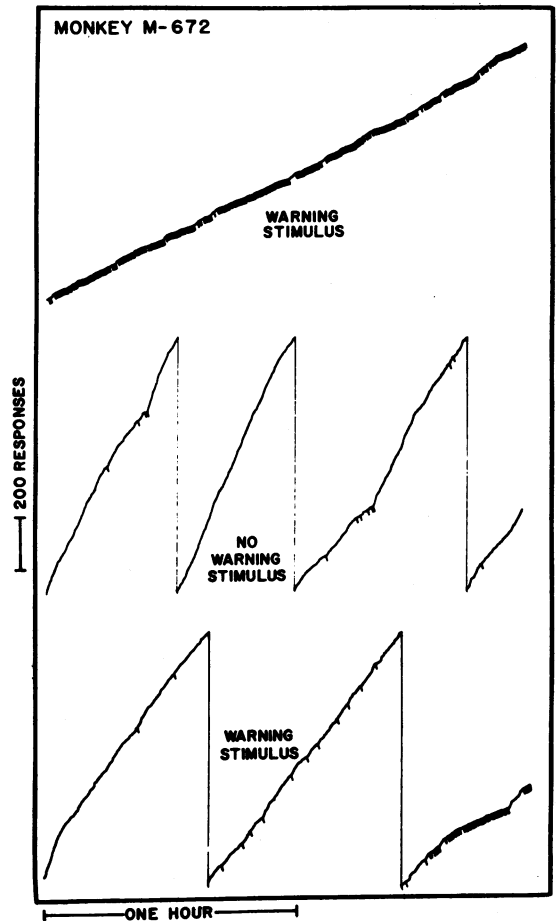Figure 4 shows characteristic response rates of Monkey M-672. After its original training

Fig. 4. Cumulative records of the first exposure to the discriminated avoidance procedure (upper record); the subsequent exposure to nondiscriminated avoidance (center record); and the return to the original discriminated avoidance procedure (lower record). In the upper and lower records, the oblique marks indicate warning stimuli; in the center record, the marks indicate those points at which a warning stimulus would have come on if the procedure had been discriminated avoidance.

on discriminated avoidance, the animal pressed the lever at a relatively low rate; it frequently paused for at least 15 sec, as the large number of warning signals indicates (upper record). When the warning stimulus was removed, the monkey increased its response rate, rarely pausing as long as 15 sec (center

record). The return to discriminated avoidance (lower record) was not continued long enough to bring the animal's response rate down to its original level, but the change was sufficiently great to increase the number of 15-sec pauses.

Figure 5 shows the session-by-session lever-pressing rates and steroid levels. Moderate
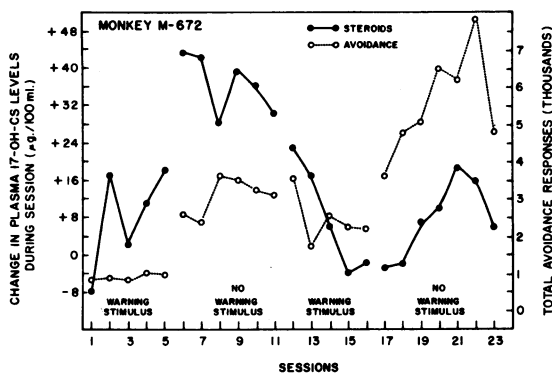

Fig. 5. Response rates and steroid changes during successive cycles of discriminated and nondiscriminated avoidance.

steroid rises were associated with the relatively low response rates during the initial discriminated-avoidance cycle. There was a single shock in Session 1, and no shocks in Sessions 2-5. Steroid fluctuations do not appear to be correlated with changes in either response rate or shock frequency.

After removal of the warning stimulus, the animal increased its rate of lever pressing and showed a much larger increase in plasma steroid levels than previously. The number of shocks in Session 6 jumped to 134, but decreased in the subsequent sessions to 102, 3, 1, 2, and 2, successively. Along with the decline in shock frequency, there was a suggestion of a decline in the magnitude of the steroid change.

With reintroduction of the warning stimulus, the animal's response rate dropped, but not to its original level. However, the amount of steroid rise gradually fell below the average value of the initial five sessions. During this phase, the animal received 1 shock in Session 13, 2 shocks in Session 14, and none in any of the other sessions.

The second time the warning stimulus was eliminated, the response rates and steroid levels again increased. Both changes were more

gradual this time. Shock frequency increased, but not to so great an extent as before; the number of shocks in Sessions 17-23 were 5, 3, 1, 1, 1, 1, and 0, respectively.

Again, we may draw the general conclusion that the animal's steroid output and its lever-pressing rate covary. This does not favor the response-shock interval as a specific determiner of the steroid level, since the response-shock interval was constant throughout.

Although we still cannot decide in favor of response rate or shock frequency as a determiner of the steroid level, these data do lend some support to the notion that the steroid changes are a function of the number of shocks the animal has received. For example, the steroid rises during the second cycle of nondiscriminated avoidance were considerably less than during the first cycle, consistent with the lower number of shocks the monkey received during the second cycle. Also, the steroid rises during the second cycle were smaller even though the rates of avoidance responding were much higher than during the first cycle of nondiscriminated avoidance.

Similar conclusions may be drawn from the data of Monkey M-488 (Fig. 6). The steroid
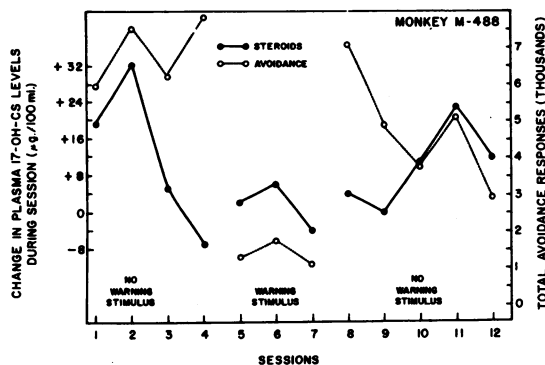

Fig. 6. Response rates and steroid changes during nondiscriminated and discriminated avoidance.

changes correlated with nondiscriminated avoidance were generally larger than those which accompanied discriminated avoidance. Within each cycle, however, there was little detailed correspondence between changes in response rate and changes in steroid levels. During the initial sessions, for example, the steroid increase seemed to adapt out, in spite of the high rate of lever pressing that the animal maintained. During the final cycle,

the trends reversed; *i.e.,* response rate declined while the steroid level went up.

Although the frequency of shocks did not vary greatly, it was somewhat higher during nondiscriminated avoidance. The animal received 2, 1, 1, and 2 shocks in Sessions 1-4, respectively; no shocks in Sessions 5-7; and 2, 3, 7, 2, and 2 shocks in Sessions 8-12.

EXPERIMENT III:

THE EFFECTS OF UNAVOIDABLE SHOCKS DURING NONDISCRIMINATED AVOIDANCE

If unavoidable, or "free," shocks are periodically administered to a monkey during a session of nondiscriminated avoidance, the animal's rate of avoidance responding will increase, and will remain high for a considerable period of time (Sidman, Herrnstein, & Conrad, 1957). This experiment was designed to evaluate the effects of free shocks on the steroid response.

Procedure

Three monkeys, M-734, M-738, and M-619, were conditioned to avoid shock with a response-shock interval of 20 sec. The interval was then changed to 2 sec, and several blood samples were taken for steroid analysis. The response-shock interval for Monkey M-619 was then further reduced to 1 sec, and blood samples were again taken.

In subsequent sessions, free shocks were administered to the animals at a rate of one every 5 min. The free, or unavoidable, shocks were delivered on schedule, even though the animals were successfully postponing most of the avoidable shocks. Blood samples were also taken at the beginning and end of the free-shock sessions. Monkey M-738 was then returned to avoidance without free shocks.

Results

Figure 7 presents the data for Monkey M-734. When the response-shock interval was 2 sec, the relatively stable lever-pressing rates were accompanied by moderate steroid rises during each session. The animal received 1, 0, and 9 shocks during Sessions 1-3, respectively. When the monkey was given free shocks, both its lever-pressing rate and its steroid levels rose immediately. During the last two sessions,
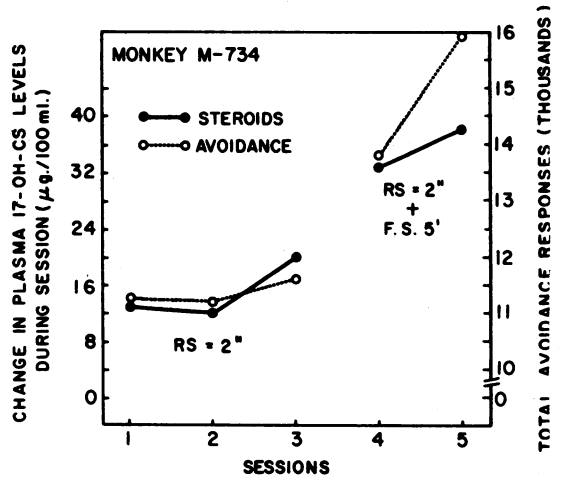

Fig. 7. Response rates and steroid changes during nondiscriminated avoidance with a response-shock (RS) interval of 2 sec, and during nondiscriminated avoidance with a free shock (F.S.) administered every 5 min.

the monkey received 21 and 33 shocks, respectively.

Monkey M-619 (Fig. 8) displayed a slight increase in its steroid levels during the initial sessions with a response-shock interval of 2 sec. This increase gradually disappeared during successive sessions, however, and it was replaced by the normal diurnal drop, even though the response rate did not change systematically. The animal received no more than 3 shocks during any of these sessions.

When the response-shock interval was decreased to 1 sec, the animal pressed the lever at a higher rate. Although the steroid levels did not increase markedly during these ses-
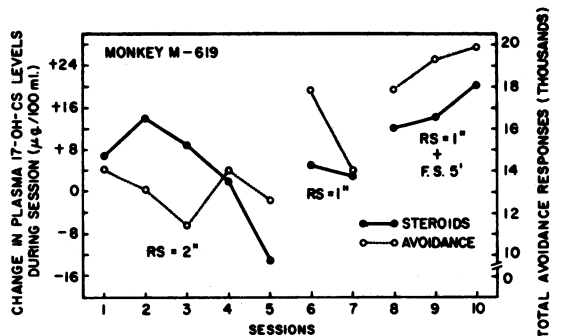

Fig. 8. Response rates and steroid changes during nondiscriminated avoidance with response-shock (RS) intervals of 2 and 1 sec, and during nondiscriminated avoidance with a free shock (F.S.) administered every 5 min.

sions, they no longer displayed the drop which had been evident when the response-shock interval was 2 sec. There were 15 shocks in Session 6, and only 3 shocks in Session 7. When free shocks were given to Monkey M-619 the trends shown by Monkey M-734 were replicated. The response rates and steroid levels both increased. The number of shocks administered during the final sessions of this experiment were 24, 23, and 30 shocks, respectively.

Monkey M-738 (Fig. 9) showed similar results. Moderate steroid rises accompanied the
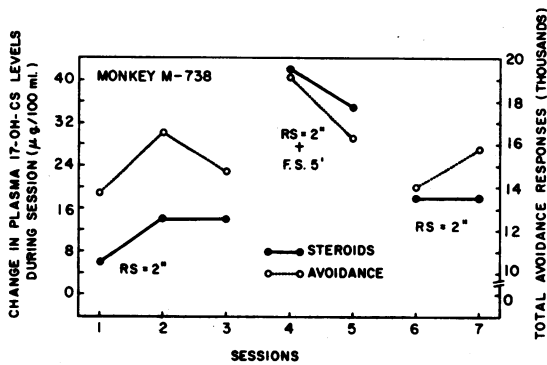

Fig. 9. Response rates and steroid changes during nondiscriminated avoidance with a response-shock (RS) interval of 2 sec; during nondiscriminated avoidance with a free shock (F.S.) administered every 5 min; and during a return to the original condition without free shock.

animal's initial exposure to a response-shock interval of 2 sec. There were 2, 4, and 9 shocks during each of these sessions, respectively. Introduction of the free shocks produced an immediate rise both in response rates and steroid levels. The number of shocks during these sessions was 27 and 44 shocks. The removal of the free shocks brought both the response rates and steroid increases back approximately to their former levels, with the animal receiving 9 shocks and 3 shocks during the final two sessions.

Discussion

The administration of free shocks to the animal provides us with a third operation through which we can manipulate the plasma steroid level. Like the other operations, however, this one also changes both shock frequency and lever-pressing rate at the same time.

EXPERIMENT IV:
THE EFFECTS OF UNAVOIDABLE SHOCKS DURING AVOIDANCE EXTINCTION

In the preceding experiments, variations in the animals' steroid output seemed at times to be correlated with the rate at which they pressed the lever to avoid shock; at other times, the steroid output seemed correlated with the number of shocks the animal had received. The independent effects of lever-pressing rate and shock frequency could rarely be disentangled. This experiment evaluated the contribution of shock frequency to the animal's steroid response; shock frequency was kept constant while the rate of lever pressing declined.

Procedure and Results

The subject of this experiment was Monkey M-672. Its previous experience had been with the nondiscriminated avoidance procedure, at a response-shock interval of 20 sec (Experiment II), and it was beginning to show only relatively small steroid changes (Fig. 5). Immediately after its last session in Experiment II, the procedure was changed to avoidance extinction. The animal was no longer shocked if it failed to press the lever. However, it was given a brief, unavoidable shock every 2 min. Blood samples were taken from the animal before and after its first exposure to this new procedure of avoidance-extinction-plus-free-shock.

By comparing the first session of Fig. 10 with the last session of Fig. 5, we see that the free shocks produced marked rises in the animal's rate of lever pressing and in its steroid output, consistent with the data of Experiment III.

With continued extinction, the monkey's rate of lever pressing gradually declined, in spite of the free shocks it received every 2 min (Sidman, Herrnstein, & Conrad, 1957). When the animal had almost completely ceased pressing the lever, blood samples were again taken before and after each of four sessions. The question we asked here was a relatively simple one: as the animal's lever-pressing rate declines in extinction, while the shock frequency is maintained by the administration of free shocks, will the steroid output decline
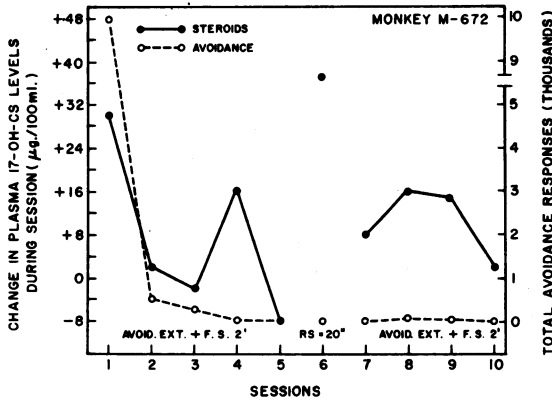
Fig. 10. Response rates and steroid changes when the avoidance response is extinguished while the animal is given free shocks every 2 min.

along with the response rate or will it remain constant along with the shock frequency?

The results appear in Sessions 2-5 of Fig. 10. These were separated from Session 1 by a large number of extinction periods, during which the response rate had dropped nearly to zero. Except for Session 4, steroid increases were virtually absent. Steroid levels had dropped, along with the lever-pressing rate, even though the animal was consistently receiving more shocks per session than it had ever experienced before. We had apparently succeeded in implicating the animal's rate of lever pressing as a determiner of the steroid change.

The next step, however, demonstrated that shock frequency cannot be ruled out as a determiner of the steroid output. In an attempt to bring back a high rate of lever pressing, we reinstated the avoidance procedure, with the shock-shock and response-shock intervals both set at 20 sec. As Session 6 of Fig. 10 shows, the animal did not press the lever even once. The animal's long exposure to avoidance-extinction-plus-free-shock had apparently given the shock a function opposite to its usual one, making it a discriminative occasion for not responding. Monkey M-672 therefore received a shock once every 20 sec, a rate six times greater than usual. This produced a near-maximal rise in steroids, even though there was no lever-pressing behavior.

Shock frequency thus exerts its effect along some sort of a quantitative continuum. Whereas shocks every 2 min had lost their

power to produce a steroid rise in the monkey, shocks coming at a rate of one every 20 sec were able to reactivate the steroid response, even in the absence of lever-pressing behavior.

In Sessions 7-10, the 2-min free shock was reinstated, along with extinction of the animal's lever-pressing response. Some residual effects of the high shock frequency remained during these sessions.

Discussion

Experiment IV succeeded in demonstrating that shock frequency exercises an effect on steroid output independently of the animal's avoidance behavior. It also suggested that with shock frequency held constant at certain values, the animal will not show a steroid increase unless it is performing an avoidance response. Both shock frequency and lever-pressing rate appear to be implicated in the activation of the pituitary-adreno cortical system. Experiment V was designed to explore further the role of the animal's rate of lever pressing.

EXPERIMENT V

MANIPULATION OF RESPONSE RATE BY STIMULUS CONTROL

In Experiment IV, the animal's avoidance response was extinguished, and its steroid response disappeared along with the avoidance behavior, even though it continued to receive free shocks. An attempt to recondition the avoidance behavior was unsuccessful, and the additional shocks the animal received reinstated the steroid response. If a high rate of avoidance responding could be re-established without increasing the shock frequency, the nature of the correlation between response rate and steroid output would be considerably clarified.

Procedure and Results

Before its experience with free shock, Monkey M-672 had been exposed to the discriminated-avoidance procedure (Experiment II, Fig. 5). Although the animal's avoidance response had been extinguished in Experiment IV, the extinction occurred in the context of the nondiscriminated avoidance procedure. Because the response had never been explicitly extinguished in the presence of the warning stimulus, the possibility existed that it could

be reinstated by once more presenting warning stimuli to the animal.

This possibility was, in fact, realized. The animal was returned to a procedure in which it would receive a shock whenever it failed to press the lever for 20 sec, with a warning stimulus coming on 5 sec before a shock was due. With the very first presentation of the warning stimulus, the animal pressed the lever, thereby avoiding the impending shock. During the remainder of the experiment, it never failed to respond during the stimulus; therefore, it never again received a shock.

During the rest of the session in which the animal's avoidance behavior returned, the response-shock interval was gradually reduced from 20 to 7 sec. The warning stimulus still came on 5 sec before a shock was due; but instead of postponing the warning stimulus for 15 sec, each response now postponed it for only 2 sec. With the animal responding to every stimulus presentation, a relatively high response rate was generated. The same
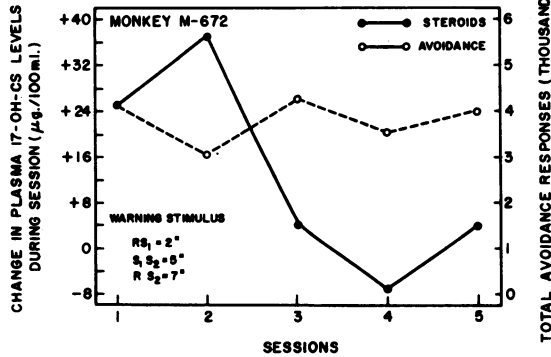

Fig. 11. Response rates and steroid changes during discriminated avoidance. Each response postponed the warning stimulus for 2 sec (RS₁), and postponed the shock for 7 sec (RS₂); the time between onset of the warning stimulus and shock (S₁S₂) was 5 sec.

conditions remained in effect during the next five sessions, and blood samples were taken before and after each session. Figure 11 shows the results.

With the reinstatement of the animal's avoidance behavior, a substantial steroid re-

sponse was again observed, even though the animal did not receive any shocks. The high steroid output was maintained for two sessions, after which it disappeared. The failure of the animal to maintain the steroid response is unexplained, and remains a problem for further investigation; but the rise during the first two sessions clearly implicates the avoidance behavior as an activator of the pituitary-adrenal cortical system, independently of the shocks.

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