The interaction of diet and stress in rats: high-energy food and sucrose treatment.

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Exposure to inescapable shock typically reduces eating and body weight in rats. The present study examined the modulation of stress effects by presress diet and poststress sugar availability. Maintenance on a high-fat, high-energy food attenuated stress-induced weight loss and anorexia and increased high-energy food selection when a low-energy wet mash was the only alternative. Access to sugar after stress also reduced short-term weight loss; among rats maintained on high-energy food, body weight was spared absolutely. The dependence of stress effects on pre- and poststress diet alternatives may speak to individual differences in the stress–eating relationship in humans. More generally, these results support a conceptualization of stress in terms of metabolic challenge and the integrated reorganization of energy regulatory processes.

Increased energy utilization decreases food consumption (Friedman, Tordoff, & Ramirez, 1986). Stress and a neurohormonal analog mobilize stored fuels through glycolysis and lipolysis (Rickards et al., 1996; Rivest, Deshaies, & Richard, 1989; for a review, see Sapolsky, 1992). These rapid metabolic responses could mediate stress-induced anorexia. Thus, weight loss may indeed be a cause as well as a consequence of reduced eating after stress.

If the diverse effect of stress on bodily and behavioral function reflects an organized shift in energy regulation, then environmental variables that control energy balance should modulate stress effects. The metabolic consequences of stress and effects of diet on physiological stress sequelae have received some attention (Brennan, Job, Watkins, & Maier, 1992; Hülsmann, 1978; Servatius, Ottenweller, Gross, & Natelson, 1993; Tannenbaum et al., 1993). However, how energy balance influences the behavioral impact of stress is largely unexplored.

One major determinant of energy balance is the diet on which an animal lives. Standard laboratory chow is approximately 60% complex carbohydrate and only about 10% fat in terms of utilisable calories—approximately 25% of the diet is nonnutritive bulk by weight. Rats maintained on this low-energy diet readily utilize stored fuel when circumstances demand it, thus reducing the need to forage and eat. Conversely, diets rich in fat and calories bias fuel partitioning towards fat storage (Donato, 1987; Ramirez & Friedman, 1990). High-energy diets increase weight gain and adiposity and decrease readiness to mobilize stored fuel. Fat oxidation during metabolic challenges is attenuated, leaving the need to eat relatively unaffected.

Conceptualizing stress as a metabolic challenge leads to the prediction that a stressor’s impact on body weight, food selection, and caloric intake will depend critically on the nature of the animal’s diet prior to stress treatment. Rats maintained on a low-energy diet will readily mobilize stored fuel when stressed. Lipolysis and fat oxidation will be expressed as weight loss and reduced food intake (Dess et al., 1988, 1989; Paré, 1965). In contrast, rats maintained on a
High-energy diet are predisposed to store fat rather than mobilize fat and thus should lose little weight when stressed. In addition, reduced lipolysis should attenuate the suppressive effect of stress on eating. Consistent with this prediction, Vaswani, Tejwani, and Mousa (1983) found that swim stress actually increased food intake among rats maintained and tested on a high-fat diet.

High-energy feeding should influence not just how many calories are procured, but also how they are procured. Stressed rats can limit their risk of additional harm by procuring many calories in little time. Indeed, meal patterning analyses indicate that stress reduces meal frequency and can result in compensatory increases in meal eating rate and meal size (Dess & VanderWeele, 1994; Helmstetter & Fanselow, 1993). Risk reduction also could be achieved through dietary selection. Selecting a high-energy food, such as one high in fat, yields many calories quickly. However, the fat content and caloric density of foods lack a simple sensory code, and rats must learn about these food properties (Bartoshuk, 1991; Tepper & Friedman, 1989; Tordoff, Tepper, & Friedman, 1987). Thus, we predict that stress will potentiate selection of a high-energy food only among rats that are experienced with the diet.

Availability of simple sugars also may influence energy regulation after stress. Sweet tastes reduce distress in several paradigms (Ahlers, Shurtleff, Schrot, Thomas, & Paul-Emile, 1993; Blass; Calcagnetti & Holtzman, 1992; Christensen, 1993; Dess, 1992; Minor & Saade, in press). Even a dilute sugar solution can be effective. Rats given access to a 1–2% sucrose solution after exposure to tailshock gain as much weight as do nonstressed controls (Dess, 1992). To the extent that this effect occurs centrally at early stages of the stress response, access to sucrose should decrease the impact of stress on all dependent measures, including noningestive ones.

The effects of sucrose availability may depend on the maintenance diet. It has been reported that the consumption of dilute sucrose solution increases (Dess, 1992) as does the percentage of calories consumed as sugar (Dess & Choe, 1994) among stressed rats maintained on standard chow. Rats fed a high-fat, high-energy diet may react differently. Fat and carbohydrate metabolism can synergistically increase food intake and body weight (Drewnowski, 1996; Friedman & Tordoff, 1986; Ramirez & Friedman, 1990). Moreover, metabolic biases influence behavioral responses to fat and carbohydrates. Maintenance on a high-fat diet increases consumption of oil emulsion (Tepper & Friedman, 1989) and potentiates feeding elicited by the pharmacological blockade of fat oxidation (Friedman, Ramirez, Bowden, & Tordoff, 1990). To the extent that rats fed a high-fat diet are more attuned to the availability of fats than of carbohydrates, they may be less affected by access to sugar after stress.

The following two experiments demonstrate the modulation of a stressor's impact by prestress maintenance diet and poststress sugar availability. Measures of body weight, food selection, and total caloric intake provided an ingestional profile of stress effects, and an open-field test provided a test of whether stress modulation generalized to noningestive processes.

Experiment 1

Rats were maintained on either a corn oil–chow mash or a water–chow mash diet for 4 weeks prior to stress treatment. Compared with the water–chow mash, the corn oil–chow mash is a food with a carbohydrate base that is also high in calories and proportion of calories derived from fat (viz., a high-energy food). This combination of characteristics is particularly effective at promoting fat storage and weight gain (Ramirez & Friedman, 1990). Our intentional confounding of dietary fat and caloric density also models naturally occurring diets in which the proportion of calories from fat and caloric density often covary.

At the end of the maintenance period, half of the rats from each dietary condition were exposed to inescapable tailshock while the other rats remained in their home cages. We then gave all rats immediate, continuous access to both the high-energy food and the low-energy food for 8 days. Rats also had access to a dilute (2%) sucrose solution during the poststress test. Sucrose was provided immediately after the stress session for half of each group and was provided 24 hr later for the remaining rats. This choice procedure was used to assess effects of stress on dietary selection and to better model the circumstances of omnivores outside of the laboratory.

To examine the role of available foods in noningestive stress effects, we tested the rats for emergence latency and exploration of a novel, open field 24 hr after the stress session (cf. Minor, Dess, Ben-David, & Chang, 1994). If high-energy feeding and sucrose availability modulate stress-induced ingestive changes through a general stress-reduction mechanism, then these conditions also should reduce emotionality in this test (i.e., shorten emergence latencies, reduce defection; Royce, 1977).

Method

Rats

Sixty-eight female albino rats from the University of California, Los Angeles (UCLA) Psychology Vivarium were housed in individual cages with free access to water and Wayne Rodent Chow 8604 pellets (Teklad Premier, Madison, WI) for at least 1 week prior to the start of the experiment. The colony room was illuminated on a 12-hr light–dark cycle, with light onset at 7 a.m. Rats were 60–70 days old and weighed an average of 225 g at the beginning of the study. Treatments and measurements took place during the light phase of the cycle.

Diets

Two chow-based mash foods were used. The low-energy food consisted of water and Wayne Rodent Chow 8604 meal in a 1:1 ratio (1.62 kcal/g; 58% carbohydrate, 30% protein, and 12% fat). The high-energy food also was approximately half chow meal, but the meal was mixed with corn oil. This mash was supplemented with casein, dextrose, minerals, and vitamins to reduce the difference between the diets in terms of protein and micronutrients.
(by weight, 52% chow meal, 33% Wesson corn oil, 7% casein, 5% dextrose, 2% Jones Foster mixture, 1% Vitamin Diet Fortification mixture; the latter four ingredients from ICN Biochemicals, Irvine, CA). The caloric density of this food was 5.24 kcal/g, with 61% of utilisable calories as fat, 23% as carbohydrate, and 16% as protein.

During testing, rats had access to 2% (weight/volume) sucrose solution (ICN Biochemicals, Irvine, CA). Sucrose was presented in glass bottles and water was presented in polypropylene tubes, both with rubber stoppers and stainless-steel spouts. Fifty-four rats received mash in clear acrylic cups (6.0 diameter x 2.0 cm height) throughout the study; the other rats spilled a large amount of mash early on and thereafter received food in metal cups (4.0 diameter cm x 2.5 cm height) with lids with a 3.0 cm hole punched in the center.

**Apparatus**

The stress session was administered in individual acrylic tubes (23.0 cm length x 6.0 cm diameter). Each rat’s tail was taped to an acrylic rod extending from the tube. Two electrodes coated with electrode paste were taped to the tail 1.5 cm apart. Electric shocks were delivered to the electrodes from constant-current shock generators (Model 82400, Lafayette Instruments, Lafayette, IN). The tubes were placed in illuminated white sound-attenuating chests. White noise and a ventilation fan behind the rear wall (total 80 dB SPL) masked extraneous sound.

The open field consisted of an enclosed start box (25.0 cm x 8.0 cm x 18.0 cm), which opened near a corner of a square field (56.0 cm x 56.0 cm x 100.0 cm). The apparatus was made of black acrylic except for the clear acrylic floor. Black tape on the underside of the field 15.0 cm from the walls bisected each side and defined periphery and center. The start box was dark, and the field was illuminated by a 40-W frosted bulb located directly above the arena. A small plastic ball was placed in the center of the field at the beginning of each test. A few food pellets (Formula A, P. J. Noyes Co., Lancaster, NH) were placed in two small plastic cups located outside of the start box. Additional pellets were placed on the floor at the midpoint of each of the side walls and in each corner.

**Procedure**

During a 4-day baseline period, all rats were given the low-energy food and were weighed daily. Because the low-energy food was a wet mash version of the chow pellets on which the rats had been raised, its flavor was familiar. This procedure therefore served to adapt the rats to eating mash from the food cup and to the daily weighing and handling procedures.

The experiment used a 2 x 2 x 2 between-groups design, with maintenance diet, stress, and sucrose availability as variables. The following description of the assignment of rats to treatment conditions and final group sizes are summarized in Table 1. After the baseline period, rats were assigned to one of two dietary conditions, matched for body weight and food consumption. Rats in one condition (low energy) received the low-energy food for 4 weeks, and the others (high energy) received the high-energy food for 4 weeks. During this time, 3 rats were eliminated from the study: one who emptied the food cup every day, one who cut her lip slightly, and one who suddenly lost weight on Days 9–10.

After 4 weeks of low-energy or high-energy feeding, rats were assigned to treatment conditions that differed with respect to stress and poststress sucrose availability. Half of each dietary group was exposed to a single session of 100 inescapable tailshocks (5 s, 1.0 mA) on a 60-s variable-time schedule (range = 20–230 s), after which they were returned to their home cages (shock condition). Two rats were eliminated from the study at this time because of injury. The other rats remained in their home cages (no-shock condition). All rats received both the low-energy and the high-energy food immediately following the stress session. Half of the shocked rats and half of the home-cage controls also received a 2% sucrose solution and water immediately after the stress session (immediate-sucrose condition); the remaining rats received only water to drink for 24 hr (delayed-sucrose condition).

All rats were tested in the open field 24 hr after the stress session. Rats were transported in their home cages to a darkened room adjacent to the testing room 30 min prior to testing. During the test, observations were made by two investigators who were nominally blind as to the experimental condition of the rat. The oily coat of several high-energy rats betrayed their prestress diet condition, but all group assignments with respect to stress or sucrose availability were unknown at the time of observation.

A test began with placement of a rat in the start box by Observer A, who opened the door to the field after approximately 20 s. Head-out (ears across threshold), front-out (front paws and shoulders across threshold), and full emergence (base of tail across threshold) latencies were timed by Observer B. After full emergence, the door to the start box was lowered. While a rat was in the open field, Observer A counted peripheral line crosses, and Observer B counted entrances to the center, rearing, and grooming bouts. After 10 min, the rat was returned to its cage by Observer A; a maximum latency of 600 s was recorded for failure to emerge. Number of pellets remaining and fecal boli were counted. Missing pellets were replaced, and the floor of the apparatus was sponged and towelled dry. After all rats had been tested for emergence, each rat was placed directly into the field with the door to the start box closed for another 2 min of observation. Line crossing, grooming, eating, cumulative time in the center of the field, and defection were recorded. At the completion of this test, rats were returned to the colony room.

All rats had access to a 2% sucrose solution and water as well as to the low-energy and high-energy foods for an additional 7 days. Body weight, sucrose intake, and consumption of each food were recorded daily between 8 and 10 a.m. All foods were made fresh daily.

**Statistical Analyses**

The data from the three experimental phases were analyzed separately. First, data on each dependent measure from the maintenance period were analyzed in four 7-day blocks by using a mixed-design Diet x Block analysis of variance (ANOVA). Next, data on each dependent measure for the first 24-h poststress period were analyzed with a 2 x 2 x 2 between-group
DIET-STRESS INTERACTIONS

Figure 1. Experiment 1: Mean (+SEM) body weight and daily caloric intake in rats maintained on a high-energy food or on a low-energy food for 4 weeks. The overall mean for a 4-day baseline period (BL) is shown for comparison.

(Diet X Stress X Sucrose Availability) ANOVA, followed by orthogonal contrasts to interpret interactions. Finally, data from the recovery week (Test Days 2–8) were analyzed with a 2 X 2 X 2 X 7 mixed-design ANOVA, with diet, stress, and sucrose availability as between-group variables and test day as a repeated measure. Two-way or three-way interactions among between-group variables were interpreted with orthogonal contrasts by using appropriate error terms from the ANOVA. Contrasts performed to interpret interactions involving test day compared the relevant conditions with respect to change from the beginning to the end of the recovery phase (Test Day 8 – Test Day 2).

Test statistics were evaluated for significance at \( \alpha = .05 \). All significant test statistics are reported.

Results

Maintenance Period

Figure 1 shows the effect of maintenance diet on body weight (upper panel) and average daily caloric intake (lower panel). Rats fed the high-energy food gained weight faster than did rats fed the low-energy food. A Diet X Block ANOVA on these data yielded a block effect, \( F(3, 195) = 529.99 \), and a Diet X Block interaction, \( F(3, 195) = 8.51 \). High-energy rats consumed more calories than did the low-energy rats during the first week, after which caloric intake was comparable in the two groups. A Diet X Block ANOVA on these data yielded a block effect, \( F(3, 195) = 4.85 \), and a Diet X Block interaction, \( F(3, 195) = 23.35 \).

Poststress Measures

Body weight. Figure 2 shows body weight, expressed as change from a prestress baseline, for the 24 hr after the stress session and for the ensuing week of recovery. In the first day after the stress session, rats previously maintained on a low-energy food gained less weight than did those previously maintained on a high-energy food. Overall, shock reduced weight gain, but its impact varied as a function of maintenance diet and sucrose availability. Among low-energy rats, shock reduced weight gain regardless of whether

Figure 2. Experiment 1: Body weight (as change from prestress baseline weight) for the 24 hr after the stress session (Test Day 1) and the following week of recovery in groups that had been maintained on a high-energy or a low-energy prestress diet and then were exposed to inescapable tailshock or no shock. All rats had access to both foods during testing, as well as access to 2% sucrose beginning either immediately (upper panel) or 24 hr after (lower panel) stress.
sucrose solution was available. Shock also reduced weight gain among high-energy rats unless sucrose solution was available immediately after stress.

Each of these assertions is supported by results from a mixed-design ANOVA, which yielded effects of diet and stress, $F_{(1, 55)} = 9.92$ and 29.13, respectively, and interactions of stress with diet and sucrose availability, $F_{(6, 330)} = 5.59$ and 4.79, respectively. Contrasts comparing shocked to nonshocked groups in each of the four Diet × Stress × Sucrose Availability conditions showed that the reduction of weight gain by shock was significant in the low-energy/sucrose, low-energy/no-sucrose, and high-energy/no-sucrose conditions, $t_{(55)} = 2.65, 5.24, \text{ and } 2.43$, respectively, but not in the high-energy/sucrose condition.

In the ensuing week, weight gain among shocked rats continued to lag behind that of controls. With respect to prior maintenance diet, the Day 1 trend was reversed: high-energy rats gained less weight than did low-energy rats. A Diet × Stress × Sucrose Availability × Test Day ANOVA yielded effects of test day, $F_{(6, 330)} = 34.54$, and of diet and stress, $F_{(6, 55)} = 97.76$ and 133.05, respectively; the interactions of test day with diet and stress were also significant, $F_{(6, 330)} = 32.56$ and 20.91, respectively. Contrasts confirmed that weight gain from Day 2 to Day 8 was lower among shocked rats than nonshocked controls, $r_{(385)} = 10.09$, and was lower among high-energy rats than low-energy rats, $r_{(385)} = 12.65$.

**Diet selection.** Figure 3 shows daily consumption of the high-energy food during testing as a percentage of total calories consumed. On the first test day, high-energy rats consumed a smaller percentage of their calories in the form of the high-energy food than did low-energy rats. The effect of stress on the consumption of the high-energy food depended on the availability of the sucrose solution. When the sucrose solution was available, shock reduced selection of calories from the high-energy diet; when sucrose was not available, consumption of the high-energy diet after shock was at least as high as in the absence of shock. This pattern was independent of maintenance diet. A mixed-design ANOVA on these data yielded a main effect of diet and a Stress × Sucrose Availability interaction, $F_{(1, 55)} = 59.21$ and 4.39, respectively. A contrast comparing shocked to nonshocked groups given access to sucrose solution was significant, $r_{(55)} = 2.08$; shocked and nonshocked groups not given sucrose solution did not differ.

During recovery, consumption of the high-energy food changed little in the low-energy groups but increased over days in the high-energy groups. Shock increased consumption of the high-energy diet during recovery only among high-energy rats given delayed access to sucrose solution. A Diet × Stress × Sucrose Availability × Test Day ANOVA yielded effects of diet, $F_{(1, 55)} = 23.39$, and test day, $F_{(6, 330)} = 5.08$, as well as several two-way interactions: Stress × Sucrose Availability, $F_{(1, 55)} = 4.63$; Test Day × Diet, $F_{(6, 330)} = 3.39$; and Test Day × Sucrose Availability, $F_{(6, 330)} = 2.59$. Most importantly, the Diet × Stress × Sucrose Availability interaction was significant, $F_{(1, 55)} = 4.32$. This interaction was interpreted by performing simpler ANOVAs (Diet × Stress × Test Day) on data from each sucrose availability condition. The Diet × Stress interaction was significant only in the delayed-sucrose condition, $F_{(1, 28)} = 6.33$. Among delayed-sucrose groups, a contrast comparing the effect of shock in the low-energy condition to the effect of shock in the high-energy condition confirmed the greater effect of shock in the latter, $r_{(28)} = 5.02$.

The pattern of results for selection of the low-energy food need not have been the mirror image of that for high-energy food selection given the availability of a third source of calories (sucrose solution), but it basically was. The low-energy food data mirrored the high-energy diet data shown Figure 3. In addition, results of all statistical analyses were the same, except, of course, that the mean differences were in the opposite direction.

Sucrose consumption, expressed as a percentage of total daily calories, is shown in Figure 4. On the first test day (upper panel), sucrose consumption was affected only by prior maintenance diet: Low-energy rats, whose maintenance diet was high in carbohydrates, consumed a higher percentage of calories as sucrose solution than did high-
energy rats. A Diet X Stress ANOVA on the Test Day 1 data from the immediate-sucrose groups yielded only an effect of diet, \( F(1, 27) = 4.50 \).

Sucrose consumption increased overall during the recovery week, but the amount of increase varied as a function of maintenance diet, stress, and sucrose availability on the first test day. Specifically, the increase over days was greater for rats that had been maintained on a high-energy diet, were shocked, or had sucrose available on the first test day. In addition, access to sucrose at the beginning of testing generally elevated sucrose consumption among low-energy rats but had little effect on high-energy rats. Because the Stress X Test Day interaction is difficult to discern in Figure 4, means for shocked versus nonshocked groups are shown collapsed across maintenance diet and sucrose availability conditions in Figure 5.

A Diet X Stress X Sucrose Availability X Test Day ANOVA on recovery data yielded a main effect of test day, \( F(6, 330) = 8.48 \), and interactions between test day and stress, diet, and sucrose availability, \( F(6, 330) = 9.14, 2.21 \), and 2.47, respectively. Contrasts pertinent to each of these interactions confirmed that the increase over days in sucrose consumption was enhanced by prior high-energy feeding, \( r(385) = 2.46 \), by shock, \( r(385) = 5.91 \), and by immediate access to sucrose, \( r(385) = 2.31 \). The Diet X Sucrose Availability interaction also was significant, \( F(1, 55) = 5.77 \); a contrast comparing the difference between immediate versus delayed sucrose groups in the high-energy condition with that in the low-energy condition was significant, \( r(55) = 3.28 \).

**Total caloric intake.** Total daily caloric intake on each test day is shown in Figure 6. On the first test day, caloric intake was reduced by prior high-energy feeding and by exposure to shock. Though shock reduced caloric intake in both high-energy and low-energy conditions, its impact was greater in the low-energy condition. Unlike the preceding dependent variables, total caloric intake on Day 1 was unrelated to the availability of sucrose solution. A Diet X Stress X Sucrose Availability ANOVA yielded effects of diet and stress, \( F(1, 55) = 61.81 \) and 64.22, respectively, and a Diet X Stress interaction, \( F(1, 55) = 4.77 \). The reduction in caloric intake by shock was significant in both the high-energy and low-energy conditions, \( r(55) = 4.53 \) and 7.18, respectively, but the difference between shocked and nonshocked groups was larger in the low-energy condition, \( r(55) = 3.63 \).

During recovery, caloric intake was greater in low-energy (vs. high-energy) groups, nonshocked (vs. shocked) groups, and delayed-sucrose (vs. immediate-sucrose) groups. In addition, calorie consumption generally increased over days. In sharp contrast to the results for body weight and diet selection, the effects of maintenance diet, stress, sucrose availability, and test day were independent of each other. A Diet X Stress X Sucrose Availability X Test Day ANOVA yielded main effects of test day, \( F(6, 330) = 26.85 \), of diet, stress, and sucrose availability, \( F(1, 55) = 50.47, 20.22, \) and 4.10, respectively. No interactions were significant nor even nearly so (\( ps > .20 \)).
**Open-field behavior.** Each measure of open-field behavior was analyzed for effects of maintenance diet, stress, and sucrose availability. Maintenance diet and sucrose availability were unrelated to open-field behavior. Two effects of stress, however, were significant. Shock increased full-emergence latency; latency averaged 401.4 s for shocked rats versus 269.5 s for nonshocked rats, $F(1, 54) = 4.85$. On the other hand, the average number of line crossings after direct placement in the open field was 4.5 crossings for shocked rats versus 2.8 crossings for nonshocked rats, $F(1, 54) = 5.05$. The heightened activity of the shocked rats shows that their longer emergence latencies were not due to motoric retardation. Increased activity in the field, accompanied by longer emergence latencies and more defecation, is more consistent with an interpretation in terms of stress and emotionality (Krahn, Gosnell, Levine, & Morley, 1988; Royce, 1977).

**Discussion**

Maintenance on a high-energy food had the expected effect on caloric intake and weight gain. Access to a high-energy food transiently increased energy intake: During the first week of high-energy feeding, caloric intake was elevated compared with baseline food consumption and compared with access to a lower-energy food. Caloric intake during Weeks 2-4 in the high-energy condition returned to baseline levels and was slightly lower than in the low-energy conditions. Despite this decline in caloric intake from the first to subsequent weeks of high-energy feeding, weight gain accelerated among high-energy rats relative to low-energy rats. These findings replicate those of other studies, which also provided morphometric and biochemical evidence of increased adiposity after high-energy feeding (Jen, Greenwood, & Brasel, 1981; Ramirez & Frieder, 1990). Greater body weight yield per calorie consumed and increased adiposity indicate a metabolic shift toward fat storage in the high-energy condition.

Two findings in Experiment 1 are of special importance. The first concerns the modulation of the stressor's acute effect on weight loss by maintenance diet and sucrose availability. Results in the low-energy condition replicate those obtained in other studies of rats fed standard chow pellets or mash: Stress reduced weight gain in the first poststress day (Dess et al., 1988, 1989). Results for the first test day among high-energy rats given sugar solution immediately after shock (see upper panel, Figure 2) were quite different: Weight gain in this group was identical to that of nonstressed controls.

What accounts for this striking conservation of weight? Stress did significantly reduce caloric intake in the high-energy/immediate-sucrose condition; selection of the high-energy food also was slightly reduced. Indeed, suppression of caloric intake by stress was somewhat greater in that condition than in the high-energy/delayed-sucrose condition (see filled symbols in upper vs. lower panel, Figure 6), yet weight was protected more completely. Clearly, the weight sparing was not due to a compensatory increase in eating or selection of high-calorie food. The attenuated impact of shock on caloric intake after high-energy feeding is consistent with reduced fat oxidation (Friedman, 1992). Thus, the pattern of results across dependent measures implicates a metabolic shift away from fat mobilization in the weight sparing observed in the high-energy/immediate-sucrose condition. How various physiological and behavioral correlates of such a shift (e.g., thermoregulation, activity level) might contribute to this effect could be examined in future work.

A second important finding is the dramatic effect of maintenance diet and sucrose availability on diet selection during recovery from stress. During recovery, selection of calories from the high-energy food increased only among rats maintained on the high-energy food and not offered sucrose immediately after stress. On the first test day, this effect could have been due to the unavailability of a third diet alternative (sucrose solution) for the delayed-sucrose groups. However, this pattern persisted in the rest of the test period, during which sucrose was available to all groups. Thus, the availability of sucrose immediately after stress modified diet selection later, when the dietary alternatives were the same for all groups. This finding provides a clear example of critical roles for both prestress and poststress dietary conditions in the ingestive impact of stress.

All rats were shifted from a single food to a choice of foods, one of which was relatively novel, when the test

**Figure 6.** Experiment 1: Total caloric consumption for the 24 hr after the stress session (Test Day 1) and the following week of recovery.
phases began. This situation prompts the question of whether some aspects of food selection are interpretable in terms of neophobia, or the generalized avoidance of novel flavors (Domjan, 1977). Neophobia should have led the low-energy rats to prefer the familiar low-energy food over the high-energy food, which they encountered for the first time during testing. The high-energy rats should have preferred the familiar high-energy food, although this tendency might have been weakened by their earlier experience with the low-energy food in pelleted and mash form. If stress increases flavor neophobia (Job & Barnes, 1995), the preference for the maintenance diet should have been enhanced in both the low-energy and the high-energy conditions. Finally, these preferences should have been strongest early in testing and then diminished because of the increasing familiarity of the foods and of recovery from stress.

None of these patterns occurred. Overall, low-energy groups selected more calories from the novel high-energy food with which they had no prior experience, and the high-energy groups initially selected more calories from the relatively novel low-energy food. This dietary neophilia runs counter to rats' legendary neophobia (Naim, Brand, & Kare, 1986; see also Rolls, Rowe, & Rolls, 1982), as well as to explanations in terms of nutritional deficiencies of either diet (e.g., protein; Castonguay, Hirsch, & Collier, 1981).

If enhanced neophobia controls food selection after shock, then food selection on the first test day should have depended critically on maintenance diet. It did not: The effect of stress on the selection of the high-energy food on the first test day was independent of maintenance diet. The stress-induced potentiation of high-energy food selection among high-energy rats was weaker on the first test day than on subsequent days and did not occur at all when sucrose was available immediately after stress. If the latter effect was attributable to a stress- (and neophobia-) reducing effect of sucrose, then sucrose availability also should have increased selection of a novel food by low-energy rats soon after shock. To the contrary, access to sucrose reduced selection of the novel food by stressed low-energy rats on the first test day. The dependence of the stress-induced high-energy food selection on both maintenance diet and poststress sucrose availability and its recruitment over test days are inconsistent with a neophobia explanation.

The potentiated fat selection after stress is explained most simply in terms of the metabolic bias toward fat storage created by prior high-energy feeding. When subjected to a metabolic challenge, high-energy fed rats less readily mobilized stored fat and thus selected the higher energy diet alternative; stress-induced glucocorticoid elevation could mediate this effect (Castonguay, 1991). This interpretation is supported by the absence of potentiated high-energy food selection when stressed high-energy rats were given another source of readily utilized energy (sucrose) with which to supplement their diet.

Experiment 2

In Experiment 1, immediate access to a sugar solution modulated virtually all effects of stress on ingestion. This new evidence of sugars' power to influence stress and ingestion is consistent with earlier work (Ahlers et al., 1993; Blass, 1992; Dess, 1992; Minor & Saade, in press). However, Experiment 1 provided a conservative test of sugars' effects for at least two reasons. First, the sugar solution was dilute. A faster and more robust effect of stress on, for instance, selection of calories as sugar has been obtained with a more concentrated (24%) solution (Dess & Choe, 1994). Second, all groups had access to sucrose after the first test day. Although such a design is useful in terms of localizing any effect of sucrose availability to the first 24 hr of testing, it provides no means of assessing how some potentially important features of recovery from stress might differ as a function of the sugar availability. For example, immediate access to sucrose protected against weight loss in the 24 hr following stress in the high-energy condition. Shocked rats' weight gain then stalled, despite continuous sucrose availability. Indeed, high-energy rats that had been shocked just managed to maintain their body weights near prestress levels. This outcome raises the question of whether access to a richer sugar solution might protect against stress in an absolute sense—that is, promote frank weight gain.

Experiment 2 was designed to answer this question. We maintained rats on the high-energy food for 28 days and then exposed them to a session of inescapable tailshock. Thereafter, rats continued to receive the high-energy food and water. Half the rats also received continuous access to a 24% glucose solution. Body weight and caloric intake were measured for 3 days. Of interest was whether access to a concentrated sugar solution would prevent the decline in body weight and caloric intake typically precipitated by the tailshock stressor.

Method

Rats

Twenty experimentally naive female rats from the UCLA colony, weighing approximately 225 g each, were maintained as described in Experiment 1. Treatments and measurements took place in the light phase of the 12-hr light-dark cycle.

Apparatus

The high-energy food and shock apparatus were as described in Experiment 1. A 24% (weight/volume) glucose solution also was used.

Procedure

Water and pelleted chow intake were measured for 48 hr to obtain baseline measures of ingestion. All rats were fed the high-energy food for the next 4 weeks. Because the effect of high-energy feeding on body weight and food consumption is well documented (see Experiment 1), these measures were sampled at three 3-day periods at the beginning, middle, and end of this phase rather than daily. All rats then were exposed to 100 inescapable tailshocks (5 s, 1.0 mA) on a variable-time 60-s schedule (range = 20–230 s). Stress sessions occurred between 9 a.m. and noon. Rats were returned to their home cages and received a fresh supply of high-energy food and water immediately after the stress.
session. Ten rats also received a 125-ml bottle of 24% glucose solution. The rats, food cups, and glucose bottles were weighed daily for 3 consecutive days. The high-energy food and glucose were replaced with a fresh supply each day.

Results and Discussion

Maintenance Period

Weight gain and daily caloric intake during high-energy feeding are shown in Figure 7. The values and pattern for each variable approximate those for high-energy rats in Experiment 1.

Poststress Measures

The glucose group consumed a large percentage of their calories as glucose. The mean percentage was highest on the first test day (74%, SEM = 3%), decreasing significantly to 55% (SEM = 3%) and 56% (SEM = 3%) on the remaining two days, F(2, 18) = 17.10. Nonstressed rats typically consume about 50–60% of their calories as concentrated sugar solution (Castonguay et al., 1981). Thus, the 74% sugar selection observed here on the first test day is considerably higher than is typical for nonstressed rats. This finding is consistent with the elevated selection of calories as sugar among stressed rats relative to nonstressed controls in a previous study (Experiment 2, Dess & Choe, 1994). Results from the second and third test days, on the other hand, resembled norms for nonstressed rats.

Figure 8 depicts body weight and total caloric intake during the test period. Access to concentrated glucose solution increased weight gain and caloric intake. Moreover, both measures were above baseline levels when glucose was available. A Glucose Availability × Test Day ANOVA yielded an effect of glucose availability on body weight and caloric intake, Fs(1, 18) = 58.49 and 6.64, respectively. The test day effect was significant for caloric intake, F(2, 36) = 35.37. Comparison of each group to its own baseline showed that the glucose group was above baseline in terms of body weight and caloric intake, ts(18) = 2.46 and 5.98, respectively. On the other hand, the no-glucose group did not gain weight after stress and was below baseline in terms of caloric intake, t(18) = 6.05. Thus, access to glucose protected these ingestive processes absolutely.

The failure of the no-glucose rats to gain weight in the few days after stress replicates and clarifies the failure of high-energy rats in Experiment 1 to gain weight. In Experiment 1, all rats were given both the high-energy and low-energy foods during testing. Rats previously maintained on the high-energy food initially selected most of their calories from the low-energy alternative, which could have contributed to their caloric deficit and failure to gain weight after stress. In Experiment 2, however, no-glucose rats were given only the high-energy food during testing, with the same outcome. This result reinforces the conclusion that the
reduction of weight gain by stress in Experiment 1 was not a byproduct of diet selection. The effect apparently reflects modulation of metabolic regulation rather than behavioral energy regulation by stress.

General Discussion

The regulatory shift hypothesis was developed within a framework that casts stress as a metabolic challenge: The task for the stressed animal is to meet its metabolic needs without unduly exposing itself to further harm. How and whether this task will be accomplished is a function both of characteristics of the animal, such as body fat and metabolic bias, and of the environment, such as resource structure and predator pressure. The effects of prestress and poststress diet reported here can be viewed in terms of the path dependencies this framework implies. A bias toward energy storage because of high-energy feeding attenuates the weight loss experienced soon after stress by rats maintained on a standard high-carbohydrate diet (e.g., present Experiment 1; Dess et al., 1988; Paré, 1965). Potentially selection of high-energy food is a behavioral efficiency that reduces feeding time (Dess & VanderWeele, 1994; Helmstetter & Fanselow, 1993). Immediate access to sucrose may reduce selection of the high-energy food because sweet tastes inherently signal the availability of readily utilizable calories among omnivores (Garcia & Garcia y Robertson, 1984) and because sweet tastes ameliorate distress (Ahlers et al., 1993; Blass, 1992; Calganetti & Holtzman, 1992; Christianson, 1993; Dess, 1992; Minor & Saade, in press). Stress reduction would reinforce sugar consumption, thus increasing sugar consumption during recovery. In the present study, the intake of dilute sucrose solution by shocked rats surpassed that of nonshocked controls in both diet conditions 72–96 hr after stress, a gradual recruitment that is consistent with a role for learning in the effect (see also Dess, 1992).

The conservative ingestive strategy proposed in the regulatory shift hypothesis also is consistent with the longer emergence latencies after stress observed in the open-field test (see also Minor et al., 1994; Rosellini & Widman, 1989). Reluctance to venture forth into unfamiliar places reduces the likelihood of encountering danger, and endogenous fuel provisioning permits the animal to play it safe for a time. Unlike the ingestive measures, though, emergence latency was not modulated by maintenance diet or sucrose availability. This result argues against generic stress reduction or augmentation by these dietary manipulations. In another study, however, access to a high-fat, high-sugar food after stress did partially restore exploration of a maze to the level of nonshocked controls (Miller & Dess, 1996). Which noningestive measures of distress are sensitive to dietary conditions remains to be systematically examined.

Prior high-energy feeding provided only transient alleviation of the suppressive effect of stress on body weight in Experiment 1 (Test Day 1; see Figures 2 and 7). Access to a concentrated sugar solution, however, provided greater and longer lasting protection of body weight, and, unlike dilute sucrose, prevented caloric intake from dropping below baseline levels (see Figure 8). This is not to say that concentrated sugar solution eliminated the effect of shock on caloric consumption. In fact, had a glucose/no-shock group been included in Experiment 2, it quite likely would have consumed more calories than did the glucose/shock group (Dess & Choe, 1994). The present data do, however, permit the conclusion that weight loss and anorexia are not inevitable consequences of the rather potent stressor of inescapable shock.

This study involved female rats, and sex and its concomitants are related to stress vulnerability. For example, acute restraint significantly elevates plasma corticosterone levels in female rats only during one phase of the estrus cycle (Baron & Brush, 1979). Therefore, the robustness of the stress effects reported here may have varied as a function of individual rats’ hormonal status. The effects of stress described here, however, cannot reasonably be attributed to sex-specific hormonal processes. Stress sessions were administered to several sets of 4–8 rats on 6 different days. Even if the rats’ estrus cycles were synchronized, the staggering of sessions ensured that the stress occurred at all phases of the rats’ estrus cycles. Thus, variations in sensitivity to stress over the estrus cycle may have introduced some noise, but no systematic effects, into the data set.

Whether the effects reported here generalize to male rats is an empirical question. However, there is little reason to expect that the results would be qualitatively different for males. High-energy feeding increases weight gain and adiposity in both male and female rats (Jen et al., 1981). With respect to stress, the suppressive effect of tailshock on body weight and food intake previously reported for male rats (Dess et al., 1988, 1989) was observed in the present study among female rats fed a diet with the same macronutrient profile (low-energy condition). Moreover, comparison of male and female rats in a variety of stress paradigms indicates greater vulnerability among male rats (Gray, 1987). Particularly pertinent to the present study, escape behavior is more profoundly impaired by inescapable shock (Heinsbroek, Van Haaren, Van de Poll, & Steenbergen, 1991), and body weight and food intake are more profoundly suppressed by a neurohormonal mediator of stress effects (corticotropin releasing factor; Rivest et al., 1989) in male rats than in female rats. Thus, the present study may actually underestimate the impact of these manipulations on male rats. Only further research can determine whether that is so.

Humans in emotional distress, such as life stress, anxiety, or depression, commonly experience changes in appetite and body weight. Appetite and weight decrease for some people (so-called “stress fasters”) and increase for others (“stress eaters”). A number of variables have been explored as predictors of the direction of ingestive change (Baum & Aiken, 1981; Harris, Young, & Hughes, 1984; Ruderman, 1985; Slochower, Kaplan, & Mann, 1981; Stunkard, Fernstrom, Price, Frank, & Kupfer, 1990). One reliable predictor is body weight or body mass index, with leaner people tending to lose and heavier people tending to gain appetite and weight (Slochower et al., 1981; Stunkard et al., 1990). Weight and body mass index are a function of several interacting factors, including genetics and fat and sugar.
high-energy condition may model a precondition for stress fasting, and the high-energy condition may model a precondition for stress eating.

A weakness to this parallel is the failure of stress to increase eating or body weight among high-energy rats above the level of nonstressed controls. Indeed, after the first test day, weight gain among high-energy stressed rats fell behind that of their nonstressed counterparts. The particular high-energy food used in this study may have limited its ability to promote stress eating and weight gain. During the maintenance period, this food supported only transient hyperphagia, a common finding for this type of diet (Jen et al., 1981; Ramirez & Friedman, 1990). Sustained hyperphagia and frank obesity are generated by foods that are high in both sugar and fat, are varied, or are well hydrated (Drewnowski, 1996; Ramirez, 1991; Ramirez & Friedman, 1990; Ramirez, Tordoff, & Friedman, 1989; Sclafani, 1990). Exposing rats to stress after maintenance on a high-fat, high-sugar, hydrated, “cafeteria” diet might better model the stress-eating phenomenon.

References


