SHORT COMMUNICATION

Surprising Nonreward Reduces Aggressive Behavior in Rats*

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Studies with several mammalian species show that the surprising omission of an appetitive reinforcer invigorates aggressive behavior. In the present experiment, dominant and nondominant individuals within pairs of male rats were identified in pretests sessions. The dominant males were then randomly assigned to one of two groups and trained in a consummatory contrast situation. Group 32-W received exposure to 32% sucrose solution and was then shifted to water; Group W-W received exposure to water throughout the experiment. Immediately after a shift to water, nondominant males were introduced in the training box for a 5-min-long session. The previously dominant males of Group 32-W exhibited a significant decrease in aggressive attacks to nondominant pairmates, compared to the W-W dominant rats. Consummatory training in a situation involving surprising nonreward inhibits aggressive behavior. The potential connection between the present results and those obtained in experiments with inescapable shocks is discussed.

Rats exposed to a surprising reduction in the magnitude of an appetitive reinforcer not only consume less of the small magnitude than a control group always exposed to the smaller reward (a phenomenon called consummatory successive negative contrast, cSNC), but also exhibit significantly less dominance in social interactions with conspecifics. In one experiment (Mustaca & Martínez, 2000), rats received access to a 32% sucrose solution in 5-min long sessions during several days before being shifted to a 2% solution. Immediately after this postshift session, these animals were allowed interaction with control animals exposed to the 2% solution throughout the experiment. Shifted rats were more likely to be attacked by unshifted controls, than vice versa. Shifted rats were also significantly more attacked by nontrained intruders than unshifted controls. These results stand at variance with published reports indicating that surprising reward loss invigorates mammalian aggressive behavior directed at a conspecific (e.g., Dantzer, Arnone, & Mormone, 1980; Davis & Donenfeld, 1967; Frederiksen & Peterson, 1977; Gallup, 1965; Nation & Cooney, 1982; Thompson & Bloom, 1966) or at inanimate objects (Tomie, Carelli,

& Wagner, 1993; Weinstein, 1982). Similarly, extinction-induced aggressive behavior has been observed in experiments with avian species (Azrin, Hutchinson, & Hake, 1966; Haskell, Coerse, & Forkman, 2000).

For example, Azrin et al. (1966) exposed pigeons to successive periods of acquisition and extinction while a conspecific was restrained in the conditioning box. The onset of an extinction period was correlated with an increase in aggressive attacks directed at the conspecific. Using a pair of parallel runways, Gallup (1965) trained rats to run under a partial reinforcement schedule in which reinforcement and nonreinforcement fluctuate randomly and unpredictably. Rats released into a common arena after the nonreinforced trials exhibited four times as much aggressive behavior as after reinforced trials. Extinction of appetitive responses is accompanied not just by aggressive behavior (provided there is an appropriate target), but also by an increase in plasma levels of corticosteroid hormones (e.g., Coe, Stanton, & Levine, 1983; Dantzer et al., 1980; Lyons, Fong, Schrieken, & Levine, 2000), well-known markers of emotional stress (see Papini & Dudley, 1997), and by adrenal-dependent behavioral invigoration (Thomas & Papini, 2001).

There are several potentially relevant methodological differences between experiments in which reward loss leads to increased vs. decrease aggressive behavior. This experiment concentrated on a difference in the reward conditions prevailing before aggressive behavior is tested. Increased aggressive behavior has been reported in experiments involving the complete omission of an appetitive reinforcer, as it occurs in extinction (see references above). By contrast, reduced aggressive behavior was found in a situation involving a nonzero reduction in reward magnitude, from 32% to 2% sucrose solution (Mustaca & Martínez, 2000). It is possible that reduction is not the same as complete elimination or, more simply, that reward omission is a greater loss than reward reduction. Evidence for the latter may be found in experiments involving escape from a situation paired with surprising reward omissions. Daly (1969) reported faster escape from a reward-loss site in rats exposed to extinction of an appetitive response, than in rats exposed to a reduction in reward magnitude. The present experiment was designed to test the level of aggressive behavior in a consummatory analog of extinction, namely, by shifting animals from 32% sucrose solution to water. Accordingly, the control condition was provided by a group exposed to water throughout the entire experiment. Water corresponds to a 0% concentration of sucrose and thus is the consummatory equivalent of instrumental extinction. Shifted and unshifted rats were selected on the basis of pretests in which they exhibited aggressive dominance over pairmates; the submissive rats from those tests were used as intruders in tests administered immediately after postshift sessions.

Method

Subjects

The subjects were 32 Wistar rats, all male and experimentally naive. Rats were 120-150 days old at the start of the experiment and averaged 277 g in weight. They were housed in individual wire cages and exposed to a 12:12 hr of light:dark cycle (light on from 8:00 to 20:00 hr), in a vivarium maintained at a temperature of 24ºC. Water was continuously available in the cage. Approximately 10 days before the start of the experiment, food was limited to gradually reduce each rat's weight; rats were kept at 85% level of the ad libitum weight throughout the experiment.

Apparatus

Dominance pretests were carried out in the animal's home cage or in a similar but neutral cage. These metallic cages were 28 cm wide, 26 cm long, and 23 cm high, with bars of 0.1 cm in diameter and separated 1.5 cm apart. Consummatory training occurred in two conditioning boxes (MED Associates), each 29.2 cm long, 24.1 cm wide, and 21 cm high. The floor was made of aluminum bars measuring 0.4 cm in diameter and spaced apart 1.1 cm (from center to center). In the center of one of the lateral walls there was a hole measuring 5 cm in width, 5 cm in height, and 3.5 cm in depth, and located 10 cm above the floor. The sipper tube was inserted into this hole from the outside of the box, protruding approximately 2 cm inside the hole. A rat had to insert its head into the hole in order to reach the sipper tube located inside from which it could drink the solution by licking. The 32% sucrose solution (32 g of sucrose for every 68 ml of water) and water were presented through this tube. Each box was enclosed in a sound and light attenuating cubicle equipped with a source of white noise and diffuse house light (5 W). The conditioning boxes were also used during the final posttest of social interaction. These posttests were taped with a Panasonic camera. Behavioral patters were scored using Etho software.

Procedure

The entire experiment involved 5 phases of testing-training. In the *pretest*, 16 pairs were randomly established and observed in three 10-min sessions. In the first session, both animals were placed simultaneously in a new cage; in the second session, one animal was placed in the other's cage; and in the third session, the order was reversed. Thus each rat interacted with its pairmate in a neutral context, as a resident, and as an intruder. An observer recorded the occurrence of aggressive behavior (e.g., fights, attacks, bites) and submissive behavior (e.g., freezing, laying on back; see definitions below). These response categories were defined in Mustaca and Martinez (2000) and derived from prior research with aversive stimuli (e.g., Blanchard & Blanchard, 1977; Williams, 1982). Based on these three sessions, one pair member was classified as dominant and the other as nondominant. To qualify as dominant, a rat had to display at least dominant behavior as resident and absence of submissive behavior as intruder or in the neutral context. Dominant rats usually displayed aggressive behavior in all contexts. Dominance was not differential in one pair, thus both rats were eliminated from the study. The remaining 15 dominant subjects were randomly assigned to Groups 32-W ($n = 8$) and Group W-W ($n = 7$), whereas the 15 submissive subjects were used as intruders during the posttests. Intruders were kept at 85% deprivation level and handled daily to match the treatment given to dominant animals. However, intruders were not placed in the conditioning boxes.

In *preshift 1*, rats were placed in the conditioning boxes for a daily session of access to either a 32% sucrose solution or water. Prior to the first training session, rats in Group 32-W were given access to the sucrose solution in their home cage during two 20-min sessions to avoid taste neophobia during training. There were 7 preshift daily sessions. For the rats in Group 32-W, each session lasted 5 min since the occurrence of the first lick. For the rats in Group W-W, because their drinking was not consistent, session length was determined by the average duration of the session for all the subjects in Group 32-W (approximately 5 min).

In *postshift 1*, all rats received access to water in the conditioning box. This session lasted 5 min using the same criterion described above. The *posttest 1* began immediately at the end of the postshift session. Intruders were placed in the conditioning box during 5 min. Both the postshift and posttest session were taped for subsequent scoring (see Mustaca & Martínez, 2000). In order for the

observer to discriminate resident and intruder rats in the tape, residents were identified with black lines drawn on their head, back, and sides with a marker. Three behaviors were scored during the postshift and posttest sessions: Ambulation (animal moving all four legs, except when pursuing a conspecific), Sipper (head inserted in the sipper hole), and Rearing (standing on hind legs with fore legs on the air or touching a wall). Two additional behaviors were recorded during the posttest session: Attack (one animal pursuing and mounting a conspecific on its back, side, or ventrum), and Freezing (absence of motion standing on four legs or laying on the back).

In *preshift 2*, the conditions were exactly as those in the previous preshift phase, except that only 3 daily sessions were run. In *postshift 2*, all rats received exposure to water in the conditioning box during two daily sessions. *Posttest 2* occurred at the end of the second postshift session and involved the same procedure describe for the first posttest session. There were two reasons to include this second series of phases, namely, to replicate the results of the initial tests and to determine whether the same behavioral effects could be obtained after two postshift sessions, rather than one. In the consummatory contrast situation, treatment with anxiolytic drugs (e.g., chlordiazepoxide) is effective after two 5-min postshift sessions, but not after one; similarly, plasma corticosterone levels are increased after two 5-min postshift sessions, but not after one (see Flaherty, 1996, for a review).

Behavioral scoring was performed on the postshift and posttest sessions. All the sessions were scored twice by the same observer, who was aware of the rat's status (i.e., resident vs. intruder), but not of the rat's training group (i.e., 32-W vs. W-W). The observer scored all the animals once and then scored the same sessions again. The duration of each response category was measured with Etho software. Agreement was defined as two duration measurements that differed in no more than 1 s. When two measurements differed by more than 1 s, the session was again scored twice until the criterion was met. The duration of each behavior was transformed into a percentage measure by dividing it by session length and multiplying it by 100. Drinking was measured in terms of the amount of fluid drank during the session. Mann-Whitney nonparametric tests were used to analyze the data given that often the level of behavior recorded in a particular condition was close to zero (e.g., unshifted controls drank very little water during training sessions). All the statistical results reported below are based on an alpha level set at 0.05 and on two-tailed distributions.

Results

During the pretest there were four fights initiated by the resident animal and two fights in the neutral arena. Four of the dominant rats attacked their pairmate even as intruders. During the last 3 sessions of the preshift 1 phase the average fluid consumption was 8.63 ml for Group 32-W and 0.03 ml for Group W-W, a difference that reached statistical significance [$U(8, 7) = 0$; $p < 0.01$]. Consumption was also significantly higher in Group 32-W (mean = 0.625 ml) than in Group W-W (mean = 0 ml) during the postshift 1 session [$U(8, 7) = 0$; $p < 0.01$]. Notice that whereas the amount consumed by rats exposed to a downward shift was drastically reduced, it was still above that of the unshifted controls; under the present conditions, cSNC is prevented by a floor effect given that W-W subjects consumed little or nothing during the training sessions. Behavioral observations indicated that 32-W rats approached the sipper tube significantly more than W-W rats [$U(8, 7) = 1$; $p < 0.01$], but these conditions generated amounts of rearing [$U(8, 7) = 28$] and ambulation [$U(8, 7) = 22$] that were not significantly different.

Immediately after this postshift 1 session, intruders were placed in the conditioning box for 5 min. The five behavioral patterns scored in both residents and intruders indicated generally similar levels, except for attack behavior (see Table 1, posttest 1, and Figure 1). Rats exposed to a shift

from 32% sucrose solution to water displayed a significantly reduced level of attack behavior relative to W-W unshifted controls. This difference was statistically significant [$U(8, 7) = 0$; $p < 0.01$]. The frequency of attacks among intruder rats exposed to rats in each of the two conditions was not significantly different [$U(8, 7) = 21$]. Downshifted rats did not differ significantly in the level of attack responses relative to their intruders [$U(8, 7) = 23$], but unshifted controls attacked more than their respective intruders [$U(8, 7) = 0$; $p < 0.01$]. All other responses yielded nonsignificant results.

An error in the video-taping process caused the loss of data for several rats in each group, reducing the sample size to 5 animals per group. During the 3 sessions of the preshift 2 phase, the average consumption was 9 ml for Group 32-W and 0 ml for Group W-W. This difference was significant [$U(5, 5) = 0$; $p < 0.01$]. Consumption was also higher in Group 32-W than in Group W-W during the two postshift 2 sessions, although the difference was significant only for the first session. The values for these two groups were, respectively, 1 ml and 0 ml in the first session [$U(5, 5) = 0$; $p < 0.01$] and 1.8 ml and 0 ml for the second session [$U(5, 5) = 10$]. Postshift 2 data also indicate a significantly higher approach to the sipper tube in Group 32-W than in Group W-W for the second postshift session [$U(5, 5) = 0$; $p < 0.01$], but not for the first [$U(5, 5) = 3$; $p < 0.06$]. Unlike it was the case in postshift 1, 32-W rats reared significantly less than W-W rats in both postshift 2 sessions [$Us(5, 5) = 0$; $p < 0.01$]. There were no reliable group differences in terms of ambulation [$U(5, 5) = 10$].

Table 1 also shows the results of the behavioral observations during the 5-min-long posttest 2 scheduled immediately after the second postshift 2 session. As in the previous equivalent posttest session, the only group differences were observed in connection with attack responses (Figure 1). Group 32-W displayed significantly less attack than Group W-W [$U(5, 5) = 0$; $p < 0.01$] and about the same level as their intruders [$U(5, 5) = 11$]. By contrast, the unshifted controls displayed significantly more attack behavior than their respective intruders [$U(5, 5) = 0$; $p < 0.01$]. Levels of attack behavior were not different across intruder groups [$U(5, 5) = 12$].

Discussion

The unexpected shift from a highly valued 32% sucrose solution to the less valued water inhibits aggressive behavior in rats previously rated as dominant. This result is similar to that observed under more typical cSNC conditions, i.e., when the magnitude of the sucrose solution is shifted from 32% to 2% (Mustaca & Martínez, 2000). Several potential accounts of the present results can be safely eliminated. First, it is possible that the reduction in aggressive attacks reflects an increase in a competing response. In the present experiment, surprising nonreward was accompanied by an

Table 1
Behavioral Observations During Posttest Sessions

Group	Rats	Ambulation	Sipper	Rearing	Attack	Freezing
			Posttest 1			
32-W	Residents	10.0	7.0	11.5	7.9	9.6
	Intruders	10.8	4.5	15.2	7.4	6.5
W-W	Residents	7.6	1.7	6.4	42.8	0.5
	Intruders	14.3	3.5	17.3	5.1	6.0
			Posttest 2			
32-W	Residents	10.7	17.8	9.6	8.7	0
	Intruders	11.0	15.5	13.1	6.6	10.4
W-W	Residents	6.9	2.7	14.7	36.4	0.6
	Intruders	14.3	4.9	16.2	3.9	12.9

Note. All measurements expressed as percentage of the session. See *Procedure* for a description of scored behaviors.
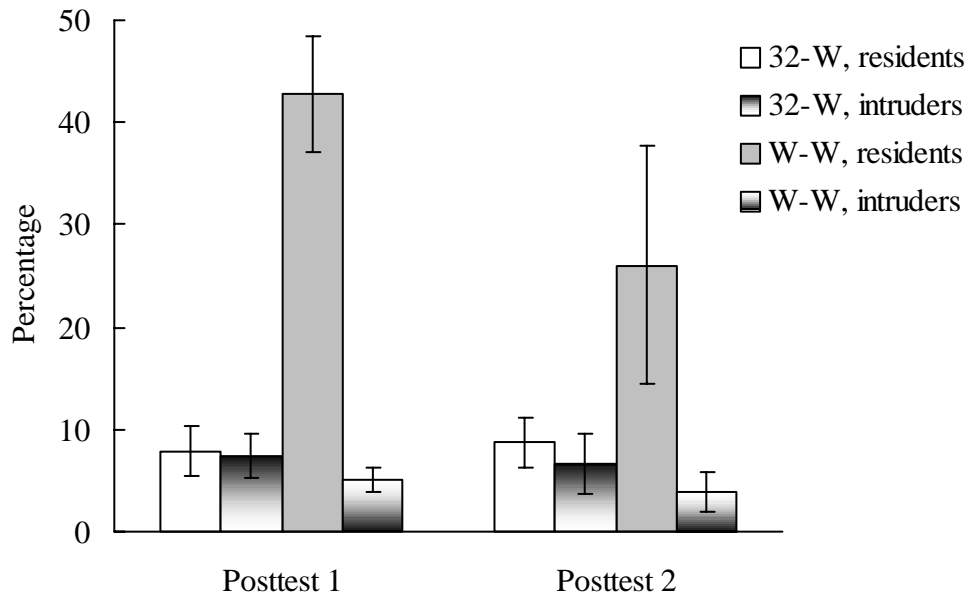

Figure 1. Frequency (in percentage) of attacks during the posttest 1 (immediately after a single postshift session) and posttest 2 (immediately after two postshift sessions). "Residents" refers to animals exposed to the shift from a 32% solution to water (32-W) or unshifted controls always exposed to water (W-W). Residents had been selected on the basis of their dominance in pretests. "Intruders" refers to pairmates that behaved submissively during the pretests. Intruders were matched for handling experience during the experiment, but were never exposed to the conditioning boxes or to the sucrose solution.

increase in sipper approach during the postshift session, when resident rats were alone in the conditioning box (see also Pellegrini & Mustaca, 2000). However, sipper approach was not different across groups during the post-tests, when resident animals were interacting with the intruders. Further-more, the levels of ambulation, rearing, and freezing, three other potentially competing responses, were all nondifferential across groups during the posttests. While it is still possible that some unidentified response induced by the treatment may have successfully interfered with the expression of attack responses in shifted rats, direct observation of posttest sessions pro-vided no hint as to the nature of that putative response. Therefore, a re-sponse competition account of the present results seems unlikely.

Second, similarly unlikely, and for the same general reasons, seems an account of the present results based on the possibility that the group dif-ferences in attack behavior may have been the result of differential behavior of the intruders, rather than of the resident rats. Direct observation of post-test sessions provided neither concrete evidence for this hypothesis (tests of various behaviors were all nonsignificant across groups), nor a hint as to how these intruders might have differed behaviorally.

A potential problem with the present results is the inequality in the consumption of sucrose solutions across groups and the potential effect this may have upon aggressive behavior. Evidence on the possible relationship between sucrose consumption and aggressive behavior is inconclusive. For example, some experiments show that rats given a regular diet exhibit more aggressive behavior toward intruders than rats given the same diet with the addition of sucrose (Lore, Gottdiener, & Delahunty, 1986). However, rats made obese by providing access to a diet high in sucrose (as well as fat and protein) actually exhibited greater levels of aggressive behavior than rats fed on regular chow food (Schultz & Lore, 1987). In the present experi-ment, both the deprivation level and the weight of all the rats were kept constant. Thus, any inhibitory effects on aggressive behavior derived from access to sucrose consumption in the experimental animals cannot be attrib-uted to these variables. However, future experiments should equate access to sucrose solution across groups by providing the 32% solution to the un-shifted controls (and water to the shifted rats) in a different context.

The present results are at variance with those of a variety of experi-ments showing that extinction of appetitive responses is accompanied by an increase in aggressive attacks, provided there is an adequate target for this behavior (e.g., Haskell et al., 2000; Lyons et al., 2000). Indeed, Weinstein (1982) even suggested that iSNC observed in a lever-pressing situation and with a shift from a 16% to a 4% sucrose solution, could be entirely ac-counted for in terms of an increase in aggressive behavior (defined as bites directed at the sipper tube). According to Weinstein (1982), the suppression of lever pressing after the shift from 16% to 4% solution was unrelated to an emotional state of frustration, but rather it reflected response competition

from biting responses. It seems plausible, however, that changes in agonistic behavior reflect the activation of a state of frustration caused by the surprising reduction in reinforcer magnitude (Papini & Dudley, 1997).

The initial reaction to a downward shift in reward magnitude in the contrast situation can be ascribed to either an affective response (e.g., Amsel, 1992) or to the invigoration of searching responses (e.g., Flaherty, 1996). The fact that changes in agonistic behavior were observed after the first postshift session is consistent with the affective hypothesis, to the extent that the inhibition of aggressive attacks can be interpreted as involving affective content. However, Amsel's (1992) theory does not provide for any mechanism that would lead one to predict submissive, rather than aggressive, behaviors under the present conditions. These results appear to be less consistent with Flaherty's (1996) multistage model of cSNC. According to this model, the first postshift day reflects behavioral disruption caused by the activation of searching behavior, whereas affective modulation of drinking requires some experience with the shifted solution. Consistent with this model, several anxiolytic drugs (e.g., chlordiazepoxide) that attenuate cSNC on the second postshift session, have no detectable effects on the first postshift session. There are at least two ways to reconcile the multistage model with the present findings. First, it could be argued that enough experience with the shifted solution has accumulated by the end of the first postshift session to induce a negative affective state that may trigger changes in agonistic behavior. Second, it could be argued that both the initial and the anticipatory responses to surprising nonreward are both affective in content (e.g., Amsel, 1992), but they are mediated by different neural and neurochemical pathways (e.g., Henke, 1977). Such a dissociation would be consistent with the differential effects of anxiolytics on the first vs. second postshift sessions, as mentioned above.

The results reported here suggest that the distinction between consummatory and instrumental responses may be important to understand differences in social interactions that occur following downward shifts in reward value. Rats that experience a shift from 32% to 4% sucrose solution in a runway situation do not exhibit negative contrast in terms of running latency (an instrumental response), but do show this effect in terms of licking rate in the goal box (a consummatory response; e.g., Flaherty & Caprio, 1976). Such a dissociation of cSNC and iSNC effects suggests these response systems are differentially sensitive to the effects of surprising reward shifts. Similarly, whereas surprising reward omissions induce aggressive interactions when animals have been trained in an instrumental situation, the same manipulations inhibit aggressive behavior when the training was consummatory. In fact, the present results in the consummatory situation resemble those obtained when social interactions are preceded by exposure to inescapable electric shock. For example, Williams (1982; Williams & Lierle, 1986) reported that rats first rated as dominant and subsequently

subjected to inescapable shocks exhibit significant reductions in dominance in a posttraining social test. Exposure to inescapable shock is known to impair subsequent avoidance behavior (Overmier & Seligman, 1967) and cause a variety of physiological effects (Maier & Jackson, 1979) collectively referred to as learned helplessness (Overmier & LoLordo, 1997). Interestingly, exposure to electric shock in a situation involving the instrumental reinforcement of concurrent responses may actually increase the frequency of aggressive responses (e.g., Azrin, Hutchinson, & Hake, 1963). Thus there is a parallel between the effects of pain-fear and frustration in the agonistic behavior of rats. Instrumental training involving either appetitive or aversive reinforcers tends to induce aggressive behavior; however, consummatory training (as in the cSNC situation) and Pavlovian training (as in the induction phase of a learned helplessness experiment) seem to increase submissive behavior in rats. The functional similarity between the effects of fear and frustration has been known for a long time (e.g., Brown & Wagner, 1964) and has prompted some to suggest that the underlying brain mechanisms must share important components (e.g., Gray & McNaughton, 2000). Exactly how consummatory contrast influences aggressive behavior in rats remains to be determined.

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