

Consequences of Surprising Reward Omissions

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A surprising reward omission (SRO) occurs when an appetitive reinforcer is not presented (or it is reduced in magnitude or quality) even though there are signals for its impending presentation. Evidence supporting the hypothesis that SROs produce an aversive emotional reaction with physiological and behavioral consequences is reviewed. SROs are followed by pituitary–adrenal activation; changes in immune function; odor emissions in rodents; distress vocalizations in rodents and primates; and increases in locomotion, aggressive behavior, drinking, and eating. SROs can support the acquisition of new escape responses and invigorate previously acquired responses. The review identifies common aspects of these phenomena and areas in which more research is needed.

One of Pavlov's (1927) most important discoveries was the "rapid and more or less smoothly progressive weakening of the reflex to a conditioned stimulus which is repeated a number of times without reinforcement. . ." (p. 49). He referred to this operation as *experimental extinction* and noticed that extinction applied to conditioned, rather than unconditioned, reflexes. Hull (1934) used a procedure he called *frustration* to study the elimination of blind alley entries during training in a maze. A well-trained rat was placed in the maze in which a physical barrier prevented the animal from entering the goal box. Hull argued that internal inhibition would develop in such a situation in a manner analogous to what happens during regular extinction, thus resulting in the elimination of the learned behavior. Whereas this response-decrement aspect of extinction continues to be a major topic of empirical and theoretical research, other consequences of extinction are less widely appreciated.

The purpose of this article is to review several independent lines of research on the effects of surprising reward omissions (SROs). The unexpected nature of these reward omissions results in a variety of effects that can collectively be referred to as *emotional* and *arousing*. Such

omission events are also named *frustrative nonreward* (Amsel, 1992) or *aversive nonreward* (Daly, 1974) within the framework of frustration theory, although the more neutral label adopted here (i.e., SROs) emphasizes common procedural aspects of a variety of psychological phenomena that have usually been considered independently for theoretical purposes. Although many of the papers reviewed here were published during the 1960s and 1970s, there have been no attempts at drawing parallels from these lines of research and, in many cases, theory has proceeded quite independently. As this review will illustrate, SROs are followed by a variety of physiological consequences, and result in the induction, maintenance, facilitation, and suppression of a variety of behaviors. The empirical links between these disparate phenomena suggest that a few theoretical principles may be needed to explain them.

In the studies reviewed here, omissions are "surprising" in the sense that they occur in the presence of stimuli that previously signaled the validity of a stimulus–outcome or a response–outcome contingency. The word *omission* is given a broader definition than is usually the case. Omissions may involve the complete elimination of the reward (e.g., extinction), an incomplete reduction in reward magnitude (e.g., magnitude contrast), a change from a more preferred to a less preferred reward (e.g., quality contrast), a reduction in the rate of reinforcement (e.g., a shift from a more to a less dense schedule of reinforcement), or the interpolation

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of a barrier between the subject and the reward (e.g., Hull's response frustration procedure).

Early Studies

Miller and Stevenson (1936) were among the first to notice that well-trained rats shifted to extinction exhibit a variety of responses that can be described as emotional. After training rats in a runway situation with food in the goal, they made behavioral observations during the course of several extinction trials. They recorded agitated behavior, defined as "vigorous, irregular motion. . . Bursts of speed followed by precipitous stops, rapid dashing to and fro, jerky tossing of the head up and back, and violent sniffing. . ." (p. 209). They found that just as latency of the running response increased during extinction (the response-decrement aspect alluded to previously), agitated behavior increased also gradually. They pointed out that responses such as sniffing, head movements, and grooming "frequently occurred in [an] almost explosive manner" (p. 227).

Skinner (1938) also described the course of extinction in rats, noticing that periods of lever-pressing were intermixed with periods of response suppression. He argued that behavior was being suppressed by an emotional state induced by the withholding of the reward. The same state was also described later in pigeons (Skinner, 1953) that were undergoing extinction of key-pecking responses: "A pigeon which has failed to receive reinforcement turns away from the key, cooing, flapping its wings, and engaging in other emotional behaviors" (p. 69).

Similar emotional responses have also been observed in contrast situations. For example, Tinklepaugh (1928) was using the delayed-response paradigm to study how monkeys form representations of stimuli. In some of his experiments, a monkey observed a piece of banana being placed under a cup and found, after a retention interval, that under that cup there was a piece of lettuce (the experimenter had made the shift during the retention interval, hidden from the monkey's view). Tinklepaugh found that monkeys would look at the lettuce but would not accept it, and instead would look "around the cup and behind the board [and] . . . on occasions turned toward observers present in the room and shrieked at them in apparent anger" (p. 224). Tinklepaugh pointed out that

monkeys would normally accept lettuce during training trials, indicating that the lettuce could be an effective reward.

Emotional reactions to the unexpected inaccessibility of a reward have been also described in human infants, whose crying responses clearly indicated the aversiveness of the manipulation. Sears and Sears (1940), for example, found a direct relationship between the amount of crying and the amount of milk received before feeding was abruptly interrupted. They concluded that "the strength of a frustration-reaction varies directly with the strength of instigation to the frustrated goal-response" (p. 300). More detailed observations suggested that such a drastic interruption of a feeding event leads to several behavioral changes in newborn infants, including increases in activity and goal-directed mouth activity, in addition to crying (Marquis, 1943).

These early studies show that an SRO is often accompanied by behavioral changes that most researchers have referred to as emotional and aversive. More recent research shows several features that support such claims. We begin our review by looking at indices of physiological activation in SRO situations and, whenever possible, make explicit reference to parallels between these experiments and those involving the presentation of more conventional aversive events, such as electric shock.

Physiological Consequences of SROs

A relatively direct approach to test the hypothesis that SROs are accompanied by the elicitation of aversive reactions is to measure physiological variables that are known to be affected in training situations involving aversive events. Aversive events produce a variety of physiological effects, some of which have been found in situations involving SROs, including changes in corticosteroid levels, immune activity, and autonomic nervous system activity.

Corticosteroid Release

Aversive events modulate the activation of the pituitary-adrenal axis, causing changes in corticosteroid levels in blood. Corticosteroids are known to increase after animals experience some type of stress, including pain, novelty, aggressive behavior, and signals of aversive stimuli (for a review, see Panksepp, 1993).

Corticosteroids prepare cells for a potentially aversive situation by affecting, among other things, muscle tone in the heart and blood vessels, and the release of nutrients into the blood.

Corticosterone levels in plasma were studied in a variety of tasks with rats as subjects. Coover, Goldman, and Levine (1971) found that a shift from acquisition to extinction of a water-reinforced lever-pressing response was followed by increases in corticosterone levels relative to the levels obtained in animals after reinforced sessions. Typically, blood samples were taken within 2 min of the end of the session. Analogous results were found in rats (Davis, Memmott, MacFadden, & Levine, 1976), pigs (Dantzer, Arnone, & Mormede, 1980), and Alpine goats (Carbonaro, Friend, Dellmeier, & Nuti, 1992) trained with solid food as the reward. Corticosterone also increased when rats were shifted from a fixed-ratio 20 to a fixed-ratio 40 schedule (Goldman, Coover, & Levine, 1973). Interestingly, Goldman et al. (1973) found that a shift to a condition of higher reward density actually led to a decrease in corticosterone levels; according to these authors, this suggests that the increased levels found in downward shifts in reward density are not caused by the novelty of the situation. Coe, Stanton, and Levine (1983) reported equivalent increases in corticosterone levels during extinction in a master group trained to lever press for water and in a yoked group in which water was delivered on a response-independent basis and at the same rate as for the masters. This result suggests that reward omissions are arousing whether the subject has been trained in an instrumental (master) or Pavlovian (yoked) situation. Moreover, Coe et al. found that corticosterone levels were more elevated after 20 min than after 5 min of the start of the extinction session.

Flaherty, Becker, and Pohorecky (1985) also found increased corticosterone levels in a consummatory contrast situation. After several sessions of access to a 32% sucrose solution, the rats shifted to a 4% solution rejected the 4% solution significantly more than control animals always given access to the 4% solution. Flaherty et al. reported that corticosterone increased in the second post-shift day, but not in the first. This result is not surprising given that consummatory training sessions were 5 min long and

that it takes time for the corticosteroids to reach measurable levels (Coe et al., 1983).

Activity of the Immune System

Aversive behavioral paradigms that suggest a relationship between stress and the activation of the pituitary-adrenal axis, such as learned helplessness and other situations involving exposure to a wide range of stressors, indicate that the immune system may be also compromised in these cases (for reviews, see Fabris, Jankovic, Markovic, & Spector, 1992; Maier, Laudenslager, & Ryan, 1985). Studies using several mammalian species show that an increase in corticosteroid levels has a suppressive effect on a variety of products from the immune system, including natural-killer cells and T-lymphocyte proliferation, and in the synthesis of antibodies, thus leading to increased health risk (Leventhal & Patrick-Miller, 1993). Because SROs activate the pituitary-adrenal axis and corticosteroid hormones have immunoregulatory functions, it follows that such reward inconsistencies should also affect the activity of the immune system. There is, however, relatively little information on this issue.

Suggestive evidence of a relationship between SROs and immune system activity is found in studies involving avian species. In birds, a type of phagocytic granulocyte cell called *heterophil*, which is part of the rapid reaction to bacterial infections, proliferates after exposure to a variety of stressors (Gross & Siegel, 1983; Mills, Jones, Faure, & Williams, 1993), to fasting (Maxwell, Hocking, & Robertson, 1992), or after corticosterone levels are experimentally raised (Jones, Beuving, & Blokhuis, 1988). Using a frustration-of-feeding situation in which food was visible but unavailable (analogous to Hull's response frustration procedure), Jones (1989) found increased levels of heterophils in domestic fowls assigned either to food deprivation or to fasting, compared to animals that had normal access to food. Similar results were obtained with hens (Beuving, Jones, & Blokhuis, 1989; Jones, 1990). It seems likely that other immunoregulatory influences should be obtained in extinction or contrast situations with mammals, although relevant information is not yet available.

Autonomic Responses

There is some information available on the effects of SROs on several autonomic responses, particularly in human subjects. The procedures used in most of the studies reviewed in this section differ markedly from those used in more conventional SRO experiments with nonhuman animals. However, the potential relevance of procedural parallels between these experiments may suggest extensions of this research into human behavior. One group of experiments measured changes in electrodermal activity while subjects were engaging in some task. Conventional aversive stimuli, such as electric shock, have been shown to affect electrodermal activity (for a review, see Andreassi, 1989), so the question is whether SROs also affect this autonomic response.

Otis and Ley (1993), for example, reinforced human participants with money for pressing a lever with a force greater than 1.5 kg but less than 3.0 kg. Participants were instructed to press a second lever to reset the reinforcing mechanism, but there was no force requirement on this second lever. After a shift from acquisition to extinction, participants showed both an increase in the force of the lever pressing response on the reset lever and an increase in the skin conductance response. A similar change in skin conductance was reported by Germana and Pavlik (1964) in a choice task in which the only reinforcement was the feedback from the experimenter about the participant's choice (i.e., whether it was "correct" or "incorrect"). After a shift in which all the responses were followed by an incorrect statement (called *extinction* by the authors), participants showed an increase in skin conductance that was directly related to the number of previous reinforcements. Interestingly, Germana and Pavlik (1964) also found that skin conductance increased during the initial acquisition trials and later decreased. Similar findings were reported by Pittenger and Pavlik (1989), who found an increase in skin conductance, both at the start of acquisition and at the start of extinction, in groups trained under either continuous reinforcement or 50% partial reinforcement. The fact that similar changes in electrodermal activity were observed at the beginning of acquisition suggests that it may not be the unexpected omission of the reward, but

the transition to a new phase of training that triggers an increase in skin conductance.

Changes in heart rate, which have also been typically observed following the presentation of aversive events (for a review, see Andreassi, 1989), may also occur after SROs. Elliott, Bankart, and Light (1970) found both a decrease in heart rate and an increase in electrodermal activity in the same participants as the complexity of a color-word interfering task (and therefore the number of nonrewarded responses) increased. When changes in heart rate are considered, however, it is important to be able to separate such changes from general changes in activity to determine the extent to which the cardiac response can be treated as a passive consequence of peripheral muscular activity. Cardiac-somatic uncoupling has been observed in some situations involving unexpected omissions of reward. Ehrlich and Malmö (1967), for example, trained rats in a lever-pressing situation and then shifted them to extinction while behavioral and physiological variables were being measured concurrently. An increase in the rate of lever-pressing responses was accompanied by a decrease in heart rate early in extinction.

Other experiments have shown that unexpected failures may be accompanied by significant increases in blood pressure. In one study, Gentry (1970) asked human participants to complete an intelligence test. While the participants were working, the experimenter interrupted their work, asked irrelevant questions, and eventually told them that they had failed the test. Such a situation led to significant increases in blood pressure relative to a control group that could complete the intelligence test successfully. Similar results were reported by Doob and Kirshenbaum (1973). An experimenter promised a group of participants a monetary reward for completing a task (counting by 2s to 100), but only if the experimenter judged the participants to be trying hard. The participants were interrupted several times and eventually told to stop at 80 because in the opinion of the experimenter they were not trying hard. Such a manipulation led to a significant raise in blood pressure in comparison to a control group that could finish the task without disruption.

Physiological Consequences: Conclusions

Of the physiological variables reviewed in this section, the change in corticosteroid level observed in situations involving SROs is the most reliable. There is sufficient evidence to conclude that corticosteroid levels are elevated after SROs, just as they are after the presentation of more conventional aversive stimuli, such as electric shocks. This similarity provides one source of evidence suggesting that SROs induce or elicit an aversive response or state. SROs also appear to affect the immune system, although the information in this case is much more restricted. The avian studies reviewed are interesting, but they involve somewhat atypical treatments relative to the procedures commonly used for studying SRO. These studies are also based on less conventional immunological measures, at least when contrasted with those used in research with mammals. For example, it would be interesting to determine if extinction or contrast procedures lead to immunosuppression, as it has been shown to occur with conventional stressors (see Fabris et al., 1992; Leventhal & Patrick-Miller, 1993; Maier et al., 1985).

Another area of potential interest is that involving autonomic variables, although the results are unfortunately inconclusive. For example, whereas skin conductance increases in several training situations involving SROs, the same change is obtained at the start of acquisition training (Germana & Pavlik, 1964; Pittenger & Pavlik, 1989). As previously discussed, the novelty of the situation, rather than surprising nonreward, may be what produces this change; novelty acts as a stressor (Panksepp, 1993), although it is clearly not an instance of SRO. To complicate things further, changes in some of these autonomic variables may be difficult to interpret. We already mentioned the possibility that changes in heart rate may be a by-product of changes at the behavioral level. In addition to the issue of cardiac-somatic uncoupling, heart rate measures may decrease or increase in aversive conditioning situations (Black, 1971), thus making it difficult to predict the direction of the change in SRO situations. Malmö (1963), for example, reported heart-rate acceleration, as well as increased lever-pressing rate, in extinction after

rats were trained with intracranial stimulation as the reinforcer. This result is contrary to that of Ehrlich and Malmö (1967) cited previously. The relationship between heart rate and blood pressure is also rather complex. Whereas they are usually inversely related, under certain circumstances (e.g., during the presentation of aversive stimuli) both measures may increase simultaneously (Andreassi, 1989). Therefore, the conclusion that extinction may be accompanied by increases in skin conductance, heart-rate deceleration, and a raise in blood pressure must be taken with caution until further research becomes available.

Behaviors Induced by SROs

The behaviors considered in this section appear to be simply induced by the surprising absence of a reward. Although there is no obvious reinforcement contingency underlying the maintenance of these behaviors, there is evidence suggesting that perhaps some responses may be maintained by *escape* (negative reinforcement) from the aversive state induced by unexpected nonreward.

Odor Emissions

In rats, SROs may lead to the emission of odors that can act as discriminative stimuli and control the instrumental behavior of other rats. This possibility was suggested independently by McHose and Ludvigson (1966) and by Spear and Spitzner (1966) after some incidental findings from experiments involving the adjustment of rats to different reward magnitudes. McHose and Ludvigson (1966) found discriminative performance in rats trained in a nondifferential situation but receiving training immediately after differentially rewarded rats. After dismissing several possibilities, McHose and Ludvigson concluded that the "most plausible explanation [was] that discrimination subjects exuded qualities or quantities of odor on S+ trials as opposed to S- trials, and that the odor trail left in the S- alley elicited the more competing responses in control subjects" (p. 486).

Although the actual compound responsible for this phenomenon has not yet been identified

(e.g., Eslinger, 1980), McHose and Ludvigson's remains as the most plausible hypothesis. For example, Seago, Ludvigson, and Remley (1970) found that the removal of the olfactory bulbs by aspiration eliminated differential performance based on odor emissions relative to sham-operated controls. As an additional control, bullectomized rats that solved the same problem but on the basis of visual signals developed discriminative performance, thus showing that the lesion produced its effect by affecting olfactory perception, rather than learning ability or performance per se. Moreover, Voorhees and Remley (1981) recorded mitral cell activity of curarized animals exposed to odors of floor paper samples from nonreinforced (N) and reinforced (R) trials, urine, and food pellets from donor animals. They found cells that responded exclusively to N odors by either increasing or decreasing their activity relative to a baseline level. There were also cells that responded exclusively to R odors.

Several studies show that the behavior of a test rat appears to be predominantly controlled by the donor rat's putative odor emission in N trials. Morrison and Ludvigson (1970) trained test rats in situations involving various combinations of R, N, and neutral putative odors and found that discriminative performance developed when N was present (e.g., N vs. R, N vs. neutral), but not when it was absent (e.g., R vs. neutral, neutral vs. neutral). Double alternation patterning (i.e., RRNNRRNN etc.) is also affected by the removal of N odors, but not by the removal of R odors (Taylor & Ludvigson, 1980). Rats prefer the side of a T-maze paired with a neutral odor relative to that paired with an N odor, but exhibit no clear preference between a neutral odor and an R odor (Collerain & Ludvigson, 1972). In this experiment, the neutral odor was obtained by placing a rat in a box in which a reward was never presented, whereas the N odor was obtained by placing a rat in a nonrewarded box previously paired with reward. Thus it is not just nonreward that causes the odor emission, but unexpected nonreward, or even the unexpected reduction of reward magnitude (Ludvigson, Mathis, & Choquette, 1985).

N odors can be used as stimuli signaling nonreinforcement, in which case they inhibit instrumental behavior, or as stimuli signaling reinforcement, in which case they facilitate

instrumental behavior (Eslinger & Ludvigson, 1980; Taylor & Ludvigson, 1987). There is also evidence that either R or N odors can be used as conditioned stimuli signaling toxicosis (Batsell & Ludvigson, 1989). Together, these results suggest that odors function as regular discriminative stimuli such as tones and lights. Other experiments suggest, however, that R and N odors from donor rats can also induce unconditioned approach and withdrawal in test rats (Collerain & Ludvigson, 1972; Mellgren, Fouts, & Martin, 1973; Wasserman & Jensen, 1969). Such tendencies develop in the absence of any specific reinforcement contingency on the test rats and are, therefore, appropriately described as unconditioned reactions to the odors. Rats can also acquire a hurdle-jump response to escape from a place where a donor animal received extinction trials or partial reinforcement training, although escape responses extinguish after repeated exposure to the N odor (Collerain & Ludvigson, 1977). As a whole, these experiments suggest that although the N odor may be unconditionally aversive to test rats, such aversiveness can be counterconditioned when the odor is used as a signal for reward.

Vocalizations

Another consequence of extinction is the emission of vocalizations. In rodents, ultrasound vocalizations (20–30 kHz) are emitted in aversive situations involving electric shock, vigorous handling, and in the presence of an aggressor or predator, among other aversive events (e.g., Brudzynski & Ociepa, 1992, and references therein). Cuomo et al. (1992) found, for example, that the rate of ultrasonic vocalizations gradually decreased from an initial frequency of about 20 vocalizations per minute, to approximately 3 vocalizations per minute, as rats were becoming more efficient in avoiding electric shocks in an active avoidance task. Bell (1974) suggested that one common element of situations inducing ultrasonic vocalizations in rodents is that they lead to increases in arousal. Ultrasonic vocalizations are also used to assess the stress response of infant rats (Mos & Olivier, 1989).

In line with these results, Amsel, Radek, Graham, and Letz (1977) reported that preweanling rats undergoing extinction of runway performance exhibited an increase in ultrasound

vocalizations (20–50 kHz) that paralleled the increase in running time of the instrumental response. The reinforcer was dry suckling from an anesthetized mother. In extinction trials, the anesthetized mother was visible but inaccessible to the infant in the goal box of the runway.

As mentioned in the Early Studies section, vocalizations have also been reported in human infants exposed to SRO. Such negative affective reactions have been found in infants of various ages exposed to several training situations including extinction, magnitude contrast, and frustration of an appetitive response. Lewis, Alessandri, and Sullivan (1990), for example, trained infants of 2, 4, 6, and 8 months of age to pull from a string for a reinforcer consisting of the presentation of a colored slide of a smiling baby and a record of the song "Sesame Street" sang by children for a period of 3 s. A control group received noncontingent presentations of the visual-auditory reward. Following a shift from acquisition to extinction, infants in the contingent condition showed an increase in crying and fussing vocalizations relative to those in the noncontingent condition. Vocalizations returned to nondifferential levels among the groups when the reinforcement contingency was reinstated in a third phase. Crying was also observed by Brackbill (1958) in a study in which 4-month-old infants were shifted to extinction after smiling had been socially reinforced (i.e., smiling responses were followed by smiling, soft talk, and physical contact from the experimenter for 30 s). One potential problem of interpretation with studies involving extinction is the confounding between reward omission and novelty. It is not clear whether infants vocalize because they treat the extinction situation as a new, unfamiliar one, or because the omission of a reward is unexpected. Evidence favoring the latter comes from studies involving contrast and response frustration manipulations although, as it will become apparent, the reactions to SROs and novelty are very similar.

Crying and fussing were reported in 3-month-old infants who experienced magnitude contrast (Mast, Fagen, Rovee-Collier, & Sullivan, 1980). The training situation involved mobiles with either 10-, 6-, or 2-colored wooden rods suspended above the infants' cribs and connected to their right ankle with a ribbon. The infant could make the mobile move by kicking.

After 2 days of training, the 10- and 6-rod groups were shifted to a 2-rod mobile, whereas the third group remained as the nonshifted control for 2 more days. Significantly more negative vocalizations were recorded in the shifted groups relative to the control condition in each of the two test sessions, thus suggesting that the shift was aversive. Although reward shifts induce crying in infants, only slightly more than half of all the infants tested actually cried. Fagen and Ohr (1985) found that those infants that reacted with crying to a downward shift in reward were rated by their mothers as significantly more active and more distressed in the presence of intense or novel stimuli compared to those that did not cry.

Another situation that leads to crying responses is a variation of Hull's response frustration procedure in which a barrier is interpolated between the infant and the rewarding object. In one study (Kramer & Rosenblum, 1970), 1-year-old infants were shown a brightly colored object while the experimenter was holding a transparent glass screen as a barrier. Approximately 36% of these infants exhibited some type of negative affective response including crying, withdrawal postures, and signs of distress.

Locomotor Activity

In the first demonstration of the successive negative contrast effect, Elliott (1928) found poorer maze performance after a shift from a more preferred to a less preferred type of food than in a control group always trained with the less preferred food. Performance was poorer because shifted animals kept entering blind alleys. Elliott considered two possible explanations: Contrast was either caused by "an emotional upset of some sort" (p. 28), or because the rats "were searching for the accustomed (and more desirable) food" (p. 29). Although Elliott favored the second alternative, more recent work suggests that increases in several types of locomotor activity may be related to emotionality. For example, Royce, Poley, and Yeudall (1973) took several measures of activity in mice that were exposed to a variety of novel situations (e.g., open field, runway), and found, after factor analysis, that several of such measures made up a factor they named *motor discharge*. Because the situations were

novel, motor discharge was characterized as motor reactivity to stress. A shift in reward conditions may thus induce increased motor reactivity as an emotional reaction to the unexpected change.

Flaherty, Blitzer, and Collier (1978) tested Elliott's two hypotheses in a consummatory contrast situation with rats. After having access to a 32% sugar solution in one tube located in an open field, rats were shifted to a 4% solution. The shift was accompanied by the introduction of four new drinking tubes, also containing the 4% solution. The authors reasoned that if Elliott's exploratory hypothesis was correct, shifted rats should show higher levels of approach to the new tubes than nonshifted controls because the SRO should induce exploration of the environment. By contrast, they found that shifted rats were significantly less likely to sample from a new drinking tube than nonshifted controls. Shifted rats also exhibited significant increases in locomotor activity and rearing responses relative to controls (see also Flaherty, Troncoso, & Dreschu, 1979). A similar increase in activity after the 32%-to-4% shift was also reported in an 8-arm radial maze situation by Flaherty, Krauss, Rowan, and Grigson (1994). The study, however, failed to find any evidence of greater activity levels in a strain of rats artificially selected for large consummatory contrast than in a small contrast strain.

General activity also increases after the omission of a food pellet in a variety of training situations. Gallup and Altomari (1969) trained rats on a partial reinforcement schedule and, after 30 s in the goal box, they transferred them immediately to an open field where activity and rearing responses were measured. They found significantly more activity and rearing after nonrewarded trials than after rewarded trials. Such a comparison is not very informative because the behavioral differences may be caused by transient changes in hunger motivation after food consumption rather than by the surprising omission of food. One possibility is to compare activity levels after a nonrewarded trial in groups trained either under partial reinforcement (for which nonreward was presumably unexpected), or under continuous nonreinforcement in that goal box. Such a comparison has also led to increased activity in partial reinforcement animals than in control animals, whether

the experiment involves runway performance (Dunlap, Hughes, Dachowski, & O'Brien, 1974; Dunlap, Hughes, O'Brien, Lewis, & Dachowski, 1971) or Pavlovian conditioning procedures (Wookey & Strongman, 1974). Wookey and Strongman, for example, administered a single 300-mg pellet at the onset of a 60-s long stimulus and measured activity during the stimulus period and during a similar period before stimulus onset. When the pellet was omitted in some test trials, activity from the prestimulus to the stimulus period increased significantly above the level of a control group that had never received pellets during the stimulus period, and that showed no change in activity from the prestimulus to the stimulus period.

The Elliott (1928) study described at the beginning of this section is different from the others in one important respect. Elliott's experiment involved a single trial per day, and activity increased in the postshift phase before the rat actually arrived in the goal box (i.e., increased activity preceded the goal event). In the other studies, increases in activity actually occurred after a change in reward conditions (i.e., activity followed the goal event). Increased activity may thus be viewed as both the unconditioned and the conditioned or anticipatory reaction to SRO.

Aggressive Behavior

Aversive stimulation has long been known to induce aggressive behavior in rats and other mammals (Azrin, Hutchinson, & Hake, 1963; O'Kelly & Steckle, 1939; Ulrich & Azrin, 1962). Similar responses also have been described in the appetitive literature in cases in which animals have been exposed to SROs. Indeed, it was Dollard, Miller, Doob, Mowrer, and Sears (1939) who first made extensive theoretical use of the relationship between SROs and aggressive behavior in their frustration-aggression theory; the available experimental evidence was, however, very slim. Skinner (1953) mentioned the emotional behavior of pigeons exposed to extinction, and Terrace (1972) later documented the wing flapping and withdrawal responses that occur during the initial sessions of training in an A+/B- successive discrimination, immediately after the onset of the B- cue. Terrace found that, as discrimination training progressed, the emo-

tional behavior decreased in frequency until it "gradually disappeared following extended exposure to S—" (Terrace, 1972, p. 202).

Azrin, Hutchinson, and Hake (1966) exposed pigeons to successive periods of acquisition and extinction of key-pecking reinforced with access to grain. While one pigeon was being trained, a second one (either a live or a stuffed pigeon) was present in the Skinner box during training sessions. The experimenters found that a shift from reinforcement to extinction was accompanied by an increase in the frequency and duration of attack responses. Aggressive attacks were confined mostly to the initial portion of extinction, increased monotonically with the number of prior reinforcements, and developed even in pigeons raised in social isolation; attacks during extinction sessions were reduced by free food in the cage. Similarly, Thompson and Bloom (1966) observed an increase in the amount of aggressive behavior of rats shifted from acquisition to extinction, and Dantzer, Arnone, and Mormede (1980) reported an increase of aggressive fighting in pigs during the extinction of a panel-pressing response previously reinforced with food. Rats would also bite a plastic target during the extinction periods of a multiple variable-time extinction schedule (Tomie, Carelli, & Wagner, 1993). Several studies show that aggressive responses are observed under analogous conditions in children and adults (see Frederiksen & Peterson, 1977).

Aggressive behavior has also been observed in a variety of appetitive training procedures that could be considered as variations of extinction. For example, food-deprived fowls that can see the food but cannot reach it (frustration-of-feeding situation), display significantly more aggressive responses (including threats, pecks, grips, and chases) than fowls that cannot see their food (Duncan & Wood-Gusch, 1971). Gallup (1965) trained pairs of rats in parallel runways on a 50% partial reinforcement schedule and released them on a common arena after 30 s of confinement in the goal box. Gallup recorded the aggressive responses of these rats during the following 60 s as a function of whether the trial had been reinforced or nonreinforced. He found that aggressive behavior was four times greater after an N trial than after an R trial.

Azrin et al. (1966) argued that any situation

involving substantial periods without food delivery can be thought of as extinction. Most schedules of intermittent reinforcement work in precisely that fashion; rewards are spaced apart and there are relatively long periods during which contextual stimuli remain constant and no food is delivered. Interval, ratio, time, and differential reinforcement of low rates (DRL) schedules have all been found to promote aggressive behavior if an appropriate target is available (Frederiksen & Peterson, 1977; Roper, 1981; Staddon, 1977). More importantly, such aggressive responses are usually limited to the period immediately following the termination of the feeding episode, over a wide range of interreinforcement intervals (Campagnoni, Lawler, & Cohen, 1986). Following Azrin et al.'s (1966) point, if the termination of a feeding episode (e.g., after the rat eats the food pellet or the pigeon's hopper is lowered) is aversive, then its behavioral effects should be similar to those observed when rewards are unexpectedly omitted. This point is further elaborated in connection to polydipsia in the next section.

Drinking

The relationship between aversive stimuli and drinking is complex (see Dess, 1992). In some cases, prior experience with shock may suppress drinking, particularly if the animal is exposed to a stimulus previously paired with shock (i.e., conditioned licking suppression). In other cases, exposure to shock actually facilitates drinking. For example, rats drink more water when drinking sessions are preceded by the delivery of electric shocks in a different context (Amsel & Maltzman, 1950; Siegel & Siegel, 1949), and squirrel monkeys exhibit increased drinking following the administration of electric shocks (Hutchinson, 1977). Similar drinking also occurs when rats are exposed to schedules of periodic food delivery (Falk, 1961). Because drinking does not seem to be maintained by the schedule of food reinforcement and consumption quantity usually exceeds normal levels of fluid intake, such drinking is referred to as *schedule-induced polydipsia*. Interestingly, even schedule-induced polydipsia may be enhanced by prior exposure to unsignaled shocks in the same context (King, 1974).

It is clear that conventional SRO procedures do not increase drinking. For example, a shift

from acquisition to extinction suppresses drinking, even when polydipsia has already been established (Freed, Carpenter, & Hymowitz, 1970). Food omission is followed by the immediate increase of responses such as approach to the goal site and exploratory behavior (sniffing, climbing, rearing), which may interfere with drinking (Iversen, 1977). The connection between polydipsia and the other behaviors induced by SROs reviewed previously lies in the sensitivity of polydipsia to three critical aspects of the training situation. First, the appetitive reinforcer needs to be of relatively high incentive value for polydipsia to develop. Second, the context in which reinforcers are presented needs to be relatively excitatory, thus providing the ground for reward omission to increase emotional arousal. Third, polydipsia develops when there are periods of nonreward within a session in which reward is presented periodically. These three points are reviewed subsequently. Notice, however, that acknowledging the equivalence between conventional SRO procedures (e.g., extinction, contrast, reduction in reward density, and response frustration) and Azrin et al.'s (1966) notion that long interreinforcement periods are analogous to extinction, provides a rationale for a common theoretical treatment of these phenomena.

The first point was that polydipsia is facilitated when the instrumental reinforcer has a relatively high incentive value. Whereas there are several possible ways to increase the incentive value of a reward, perhaps the simplest one is to expose independent groups to the periodic administration of rewards differing in magnitude. In general, polydipsia develops faster with larger reward magnitudes in the intermittent schedule. Flory (1971) found that the rate of drinking increased when two pellets per cycle were delivered, rather than one; moreover, the effect of reward magnitude on drinking increased with increases in the interreinforcement interval. Reid and Dale (1983) also found more drinking in rats that were exposed to a fixed-time 60-s schedule which delivered four pellets per cycle, than in a previous and following phase of training with a similar schedule, but delivering one pellet per cycle. Using a within-group design, Rosellini and Burdette (1980) found a similar reward magnitude effect on polydipsia using pellets of different size (45, 190, and 500 mg). Moreover,

rats exposed to the largest magnitude showed drinking at interreinforcement intervals of up to 12 min, a value that yielded almost no drinking with the smallest magnitude. It should be noted, however, that this direct relationship between reward magnitude and amount of drinking has not always been found (e.g., Falk, 1967; Freed & Hymowitz, 1972). In some cases, the difference may be related to the number of drinking opportunities. When the total number of rewards per session is held constant, rats receiving two pellets per cycle have half the number of opportunities to drink compared to rats receiving one pellet per cycle. Hawkins, Everett, Githens, and Schrot (1970) reanalyzed Falk's (1967) data with the number of drinking opportunities equated across conditions and found that drinking rate was generally higher in the two-pellet condition than in the one-pellet condition. Another complication that arises when rats are given different amounts of food is that food itself can induce differential drinking even in the absence of periodic reward presentations. For example, Rosellini and Lashley (1982) reported significantly more drinking in rats exposed en masse (the so-called *baseline condition*) to 190-mg pellets, than in groups exposed to 45-mg pellets.

Manipulations of reward quality, which do not present the problems associated with reward magnitude, show that polydipsia emerges faster when rats are exposed to a more preferred reward. Rosellini and Lashley (1982) first gave rats a choice between three different types of pellets—regular, peanut flavored, and quinine flavored—and found their preferences to be ranked in that order. When independent groups of rats were exposed to a fixed-time 120-s schedule based on each of these rewards, polydipsia developed faster and to a higher asymptote as a direct function of pellet preference. Rosellini and Lashley (1982) showed that this increase in drinking was not caused by the rewards themselves, because the amount of water drunk during baseline sessions in which all the pellets were presented simultaneously was equivalent across groups. Another manipulation that increases the incentive value of a reward is the subject's level of food deprivation. Roper and Nieto (1979) exposed rats to a fixed-time 60-s schedule and found that the amount of polydipsia decreased as rats were shifted from restricted access to food (80% and

90% of the free-food weight), to ad libitum food access. Similar results were reported by Freed and Hymowitz (1972) who used independent groups of rats deprived at 60, 70, 80, or 90% of their ad libitum weight. Shifts in reward magnitude may also affect the amount of water intake in the training situation. For example, Thomka and Rosellini (1975) trained groups of rats under fixed-time 30-s schedules for either six or two pellets per delivery. Polydipsia developed at about the same rate during an initial phase of training; but when the group exposed to six pellets was shifted to two pellets, the amount of water intake increased significantly above that of the control group always trained with two pellets.

The second point was that polydipsia develops in an excitatory context. The main evidence suggesting this generalization is the well-established relationship between the development of polydipsia and the length of the interreinforcement interval in the schedule of food delivery. Drinking is minimal when all the pellets to be consumed are immediately available (the en masse condition often used as a baseline control), then increases as the interreinforcement interval lengthens to a point, and then decreases (e.g., Falk, 1966a). This later decrease of drinking at longer interfood intervals can be attenuated by the use of large rewards, as already noted (Flory, 1971; Rosellini & Burdette, 1980). These two determinants of polydipsia—the interreinforcement interval and reward magnitude—suggest that the termination of a meal is particularly aversive when the training context has acquired some minimum appetitive value and when there is a relatively long period of food omission after a reward. Contextual value has been independently shown to be an inverse function of the interreinforcement interval in appetitive situations (Mustaca, Gabelli, Papini, & Balsam, 1991; Papini, 1995). Therefore, very long interreinforcement intervals may not sustain enough contextual value for polydipsia to develop. Pavlovian conditioning experiments show that contextual value can also be decreased by the addition of a signal before the reinforcer (see Durlach, 1989). Consistent with this, Lashley and Rosellini (1980) reported that signaling each reward in a random-time schedule increased drinking, compared to the same random-time schedule without the signal. Even the presence of a very brief signal (150 sec) may

allow for the development of polydipsia in random-time schedules (Rosellini, 1985).

The third point was that polydipsia develops when there are periods of reward omission during the session. Typically, periodic schedules of food reinforcement are characterized by the fact that food is followed by a period in which another delivery of food does not occur. This can be manipulated by delivering food at a constant probability within the interfood interval and, when this is done, food termination may no longer be followed by food omission. For example, Millenson, Allen, and Pinker (1977) reported that drinking was readily acquired in variable-interval schedules (which involve a minimum postreinforcement interval when food is never available), but considerably reduced in random-interval schedules (which involve a constant probability of food delivery throughout the interval). However, polydipsia developed in random-time schedules (constant probability of response-independent reinforcement) with increases in the schedule value and the minimum postreinforcement interval during which food is never presented (Shurtleff, Delamater, & Riley, 1983). Of course, these two changes will tend to make random-time and variable-time schedules more alike by introducing a period of nonreinforcement after food presentation.

In summary, optimum conditions for polydipsia involve a highly preferred reward (whether in terms of magnitude, quality, or immediacy), presented in an excitatory context, and omitted during some portion of the interreinforcement interval.

Eating

There is experimental evidence that aversive stimuli including electric shock and tail pinch may induce eating in rats, although as Greeno and Wing (1994) pointed out in their extensive review of the evidence, the effects may not be long lasting. Other, less studied stressors involve swimming in cold water, handling, housing conditions, and defeat in fighting (Greeno & Wing, 1994). Comparatively less is known about the induction of eating, including nonregulatory eating in sated animals, in conditions of surprising nonreward. In an experiment summarized by Cantor and Wilson (1985), male rats were placed in a chamber in which there was an anestrous female for 10 min. Immedi-

ately following that session, the rats were transferred to an adjacent chamber where they had access to wet mash. In other sessions, either before or after having been exposed to anestrus females, the same male rats were allowed to interact with a receptive female for as many as three mounts, including intromission, which is known to be short of the 7 to 15 mounts necessary for a complete copulation. The male rats ate more after such "sexual frustration" (p. 303) than after exposure to the anestrus females. In a less direct demonstration, doves previously trained to drink from a bowl displayed increased pecks at the floor (similar to the pecking behavior elicited in a feeding context) when the bowl was dry or blocked by a glass screen (McFarland, 1965).

Nonregulatory eating can be induced by conditions similar to those involved in the polydipsia phenomenon, that is, a schedule of periodic reward delivery. Wilson and Cantor (1987), for example, implanted electrodes in the medial forebrain bundle of rats and trained them under several conditions, including fixed-interval schedules, with intracranial stimulation as the reward. Rats consumed more wet mash in these sessions of intermittent reward delivery than in control sessions with massed delivery of intracranial stimulation, or after several sessions of extinction. Control conditions showed that eating was not being induced by intracranial stimulation per se. In another experiment, Wetherington and Brownstein (1979) found that rats exposed to fixed-time schedules of water delivery learned to press a lever for food pellets during the interwater interval. Lever-pressing and eating increased after a water delivery event and decreased gradually during the second half of the interval, across a wide range of fixed-time values. Although eating was far from excessive in these cases, the temporal organization suggests parallels with polydipsia. It should be noted, however, that schedule-induced eating is not a very reliable phenomenon, and it fails to appear under many of the conditions that are known to promote polydipsia (e.g., Campbell & Oei, 1986).

Induced Behaviors: Conclusions

The surprising omission of many different appetitive events may induce a variety of behaviors that appear to be limited mainly by

the nature of the training environment. There are at least two problems that are suggested by the evidence reviewed in this section. First, these results generally suggest that, to the extent that the omission of the reward occurs in a situation that has otherwise been paired with the presentation of that reward, the behavioral consequences are more or less permanent. However, nonreinforcement has to remain surprising, as in partial reinforcement training. For example, Ludvigson, McNeese, and Collerain (1979) found that donor rats continue to produce an odor with essentially constant properties even after more than 500 placements in a box in which the reward was unexpectedly omitted. They noticed that the animal's reaction to the experience of nonreward showed no evidence of habituation. Similarly, responses induced by schedules of intermittent food delivery appeared to be chronic, occurring in an undiminished fashion after hundreds of reinforcements. To the extent that these behaviors reflect an underlying aversive state, such a state appears to be quite stable.

A second question relates to the function of these induced behaviors. The recognition that there is an aversive state induced by SROs suggests that these behaviors could be less reflexive than has generally been assumed, and perhaps more analogous to instrumental responses. If vigorous responding could interfere, reduce, or even eliminate the aversive state induced by an SRO, then such responding would be negatively reinforced. Negative reinforcement usually involves the elimination of an external source of aversive stimulation (e.g., the escape or avoidance learning that results in the elimination of electric shock), but there is no reason why the source of reinforcement could not be internal. Obviously, the physical features of the environment in which the reward omission takes place provide support only for certain behaviors (i.e., polydipsia develops only if there is fluid available for drinking in the training box). Once these responses are elicited, however, the termination or reduction of the aversive state induced by unexpected nonreward provides a source of reinforcement for the further increase in strength of that behavior.

There is evidence that some of the behaviors induced by SROs do in fact reduce arousal levels. Levine, Weinberg, and Brett (1979) reviewed several relevant experiments. In one of

them, rats exposed to a novel situation that activated the pituitary–adrenal axis showed reduced levels of plasma corticosterone if drinking was allowed in that environment. More specifically, plasma levels of corticosterone increased during exposure to intermittent food schedules, but corticosterone was reduced when the animal could drink from a tube. Interestingly, plasma levels of the adrenocorticotropic hormone (a pituitary hormone that also increases under stress) were also reduced by aggressive behavior in a situation in which rats were exposed to unsignaled shocks. Rats exposed to extinction also show a negative correlation between plasma corticosterone level and frequency of biting responses (Osborne, Sivakumaran, & Black, 1979), and pigs exposed to an intermittent reward schedule showed reduced levels of cortisol when they could chew nonnutritional material during the session (Dantzer, Gonyou, Curtis, & Kelley, 1987; Dantzer & Mormede, 1981). Furthermore, Devenport (1978) reported a positive correlation between the size of the adrenal gland and the tendency to develop polydipsia in rats. The aversive internal state induced by periodic food delivery and assessed in terms of pituitary–adrenal activation is significantly reduced when animals can engage in some type of consummatory response.

The motivational strength of this aversive state is illustrated by a casual observation reported by Freed and Hymowitz (1969). After observing a disruption of polydipsia, it was found that the rats had managed to pull the cellulose sheets that lined the excreta tray located underneath the grid floor, and were chewing and shredding that material. The environment suddenly supported chewing as a schedule-induced behavior. Polydipsia resumed when the sheets were removed and chewing was no longer possible. In a more technical demonstration of the motivational strength of the state induced by periodic food delivery, Falk (1966b) showed that rats exposed to a variable interval schedule of lever pressing for pellets would also learn a concurrent fixed-ratio schedule for water. The level of polydipsia developed by these rats was equivalent to that found in the regular procedure in which water was freely available.

It is not clear, however, whether nonconsummatory behaviors such as odor emissions, locomotor activity, or vocalizations have motiva-

tional consequences analogous to those of consummatory responses described previously. The present review certainly encourages integrative questions. For example, it may be worth studying the potential relationships between the responses reviewed in this section, the extent to which they would be suppressed by concurrent access to consummatory responses, or the extent to which they are correlated with physiological indices of stress (e.g., corticosteroid levels).

Behaviors Facilitated by SROs

Direct evidence suggesting that the state induced by SROs has motivational properties is provided by the “escape-from-frustration” phenomenon. In addition, SROs can also facilitate responses that have their own reinforcement contingencies.

Escape From Surprising Nonreward

There is substantial evidence that Pavlovian stimuli paired with the absence of an otherwise present appetitive event tend to control withdrawal responses (Papini, 1988; Papini & White, 1994; Wasserman, Franklin, & Hearst, 1974). In runway situations, rats shifted from acquisition to extinction show a direct relationship between the speed of retracing from the empty food cup in the goal box and the magnitude of the reward experienced during acquisition (Jones, 1970). Withdrawal and retracing responses suggest that the stimulus or place in which a reward has failed to occur may become at least temporarily aversive. In fact, there is compelling evidence of the aversiveness of SROs in the ability of animals to learn a response that allows them to escape from the place in which such omissions have occurred. This is obviously analogous to the more typical escape conditioning situation in which a response terminates some aversive event, such as electric shock.

Rohrer (1949) was among the first to entertain the idea that extinction leads to a “frustration drive which when reduced by [responses] other than the blocked [response], leads to the development of habitual reactions to frustration such as aggression, withdrawal, etc.” (p. 476). Maatsch (1954) also suggested that the response frustration procedure, that is, the physical interruption of acquired performance, is reinforc-

ing, and on the basis of this notion later developed the escape-from-frustration procedure (Adelman & Maatch, 1955, 1956). In one experiment (Adelman & Maatch, 1956), a group of rats trained to traverse a runway for a food reward was given the opportunity to escape from the goal box during extinction trials by jumping to a platform located 25 cm above the floor of the goal box. These animals learned the jumping response just as fast as rats that were rewarded with food for jumping, and faster than a group of rats exposed to the jumping procedure without ever receiving reward, either in the goal box or on the platform. Interestingly, the jumping response quickly extinguished when the reward was withheld in the group reinforced for jumping; by contrast, the rats in the extinction condition exhibited an undiminished jumping response.

This basic result was greatly extended in a series of experiments reviewed by Daly (1974). In Daly's experiments, rats learned to escape from a goal box (by jumping over a 5-cm high hurdle) during extinction (following acquisition trials in a runway, goal-box reinforced placements, and after trials rewarded with food pellets or a 20% sucrose solution). Rats also learned to escape after a shift from a larger to a smaller (but nonzero) reward magnitude, and after the introduction of a 15-s delay of reinforcement. Daly also showed that responses other than hurdle-jumping could be developed during extinction. In one experiment, rats shifted from acquisition to extinction in a placement procedure were lifted from the conditioning box after pressing a lever. Shifted animals exhibited a significantly higher level of lever-pressing than a control group that had never been rewarded in the conditioning box. This result may be important given that SROs also tend to increase general activity, as discussed previously. Although increases in activity may account for the acquisition of jumping and shuttling responses, it would be hard to explain the development of lever pressing on this basis alone. This result should, however, be interpreted with caution because rats also learn to press a lever during extinction (and after rewarded placements in a box) when the only consequence is that the lever, but not the animal, is removed from the conditioning box (Senkowski & Denny, 1977). According to Senkowski and Denny, the lever functions as a

target for aggressive responses induced by an extinction-dependent state of frustration.

Animals can also learn to escape from cues paired with SROs. For example, Wagner (1963) reported that rats trained in a runway with a partial reinforcement schedule and exposed to a noise-light compound stimulus during the nonrewarded trials were later faster at escaping from that stimulus than yoked controls that had received the same exposure to the compound stimulus in a retaining cage. Using basically the same procedure, Daly (1974) reported that rats learned to escape from a stimulus that had previously served as the negative stimulus in an A+/B- discrimination procedure (white vs. black goal boxes). It is interesting, in relation to the stability of reactions induced and maintained by SROs, that escape from the B- stimulus of a discrimination was significantly attenuated after extended discrimination training. Presumably, reward omission in B- trials is no longer unexpected after extended training. Finally, escape from cues previously paired with SROs was also demonstrated in a key-pecking situation with pigeons (Rilling, Askew, Ahlskog, & Kramer, 1969; Terrace, 1971). Terrace (1971) further found extinction of key-pecking when the response no longer terminated the B- stimulus, thus showing that the response was a simple consequence not of increased activity levels, but of a reinforcement contingency.

It is interesting to note that the acquisition of escape responses can be used to identify the aversive properties of situations that do not appear aversive at first glance. For example, Azrin (1961) trained pigeons on a ratio schedule on one key; responding to a second key was maintained even though the only consequence was to terminate the ratio schedule currently enforced in the first key. Such escape responding on the second key increased as the ratio requirement on the first key also increased. Escape responses also developed during the postreinforcement pause period of fixed-interval schedules (Brown & Flory, 1972). Thompson (1964) found a similar effect in rats. He observed that escape lever-pressing responses were more frequent during the postreinforcement pause of fixed-ratio schedules. Interestingly, if rats were trained on a mixed fixed-ratio fixed-ratio schedule, escape responses tended to peak at a point corresponding to reward presentation for the schedule with the lower

ratio requirement. Apparently, then, animals find the termination of a feeding episode aversive, a result that agrees in general terms with the research on polydipsia and other adjunctive behaviors reviewed.

The Frustration Effect

Amsel and Roussel (1952) first reported that rats run faster in a runway immediately after a nonrewarded trial than after a rewarded trial in a partial reinforcement schedule, and labeled this the *frustration effect* (FE). Similar FEs have been reported in a variety of training situations and species (Davenport, Flaherty, & Dyrud, 1966; Gonzalez & Champlin, 1974; Papini & Ramallo, 1990; Ryan & Watson, 1968; Scobie, Gold, & Fallon, 1974). Amsel and Roussel explained the FE assuming that the increase in vigor of the instrumental response was caused by an emotional reaction to the unexpected omission. Such emotional reaction, eventually labeled *primary frustration*, was postulated to have aversive hedonic value, to induce increments in drive, and to have stimulus feedback properties that could support behavior (Amsel, 1992).

There are, however, several alternative explanations of the FE not based on the emotional consequences of unexpected nonreward. For example, the FE may arise not because animals run faster after a nonrewarded trial, but because they run slower after a rewarded trial; slow running may be a consequence of a transient decrease in motivation after eating. They may run faster because of an undiminished reward expectancy after nonreward, because of the decrement in generalization of inhibitory tendencies, or because of postconsummatory competing responses after a rewarded trial (Amsel, 1992; Dickinson & Scull, 1975; Hamm & Zimmerman, 1967; Scull, 1973; Wagner, 1959). There is, however, evidence inconsistent with these alternatives, and also evidence suggesting that the FE depends on an emotional reaction to surprising nonreward.

One relevant set of experiments involves manipulations that result in dynamic changes in performance across sessions. For example, Amsel and Ward (1965) trained rats in a successive visual discrimination in the first of two runways arranged in tandem and measured performance in the second runway under

continuous reinforcement. Second-runway performance was initially nondifferential after the S+ or S- trial in the first runway, but soon an FE developed that lasted until about the time when performance to the S+ and S- of the first runway became differential. In an analogous experiment, Hug (1970) found an FE in the second runway until differential performance developed in the first one, where a single-alternation problem was enforced. The conditions of training did not change in the course of these studies; only the rat's experience with the discriminative problem changed. When nonreward became more predictable in the visual or alternating discriminative problems, it was no longer surprising and therefore frustrating.

A second line of evidence is particularly troublesome for alternative hypotheses of the FE based on demotivation and competing postfeeding responses: The FE also occurs under conditions in which the experimental and control groups are matched in the amount and frequency of reinforcement. Dudley and Papini (1995) used a completely Pavlovian procedure to achieve such a matching of reward parameters. Rats exposed to light-food pairings pressed a lever (in an autoshaping procedure) at higher rates immediately after a light-alone trial than after a light-food trial; rats also pressed more than a control group exposed to the same pellet presentations and omissions but in an un signaled fashion. The similar omission of a sugar solution, or a decrease from five pellets to one, also produced an enhancement of lever pressing.

A final line of evidence from lesion studies suggests that emotional arousal is a critical component of the FE. The FE is eliminated by bilateral lesions of the *amygdala*, a complex structure implicated in nonspecific arousal (Kapp, Whalen, Supple, & Pascoe, 1992) and fear conditioning (Davis, 1992). Henke, for example, reported that amygdalotomized rats showed no evidence of the enhancing effect of unexpected nonreward on runway performance in the double-alley situation (Henke, 1977; Henke & Maxwell, 1973), as well as in a Skinner-box situation in which unexpected omissions occurred in the course of fixed-interval or fixed-ratio schedules (Henke, 1973).

These three independent lines of evidence are consistent with the hypothesis that it is the surprising nature of the reward omission and the

emotional reaction it elicits that facilitates performance and leads to the FE.

Behavioral Facilitation: Conclusions

The aversiveness of the state induced by SROs is clearly indicated by the escape-from-frustration phenomenon. This phenomenon is not only important in its own right, but also because of its implications for the development of other behaviors (see previous discussion of induced behaviors). One implication of this phenomenon is relevant to the FE. Although the drive-inducing properties of SROs were emphasized, it has long been recognized that performance in the second runway may be also the result of escape from frustration. The increase in running speed in the second runway after nonreinforcement in the first, may result from the sum of an approach tendency to the second goal plus a withdrawal tendency from the first goal, where the rat has just been frustrated (Leitenberg, 1965). Such an interpretation appears to break down in Skinner-box situations, where withdrawal from the food cup area usually implies also withdrawal from the lever area (Scull, 1973). It is possible, however, that intense responding successfully interferes with that aversive state; if this is the case, the animal may be able to escape in a nonspatial sense (Dudley & Papini, 1995). A similar escape mechanism was previously suggested for the case of some induced behaviors (e.g., aggressive responses, polydipsia). For example, vigorous drinking behavior (or other schedule-induced behaviors), at a moment when food reinforcement has decreased drastically, may allow the rat to reduce the aversive emotional state generated by reward omission.

It is still unclear whether SROs invigorate behavior via increased arousal, or through some form of escape from frustration. The arousal explanation is central to frustration theory (Amsel, 1992), and it has received some support from an independent line of evidence. Wagner (1963) found, for example, that the presentation of a stimulus previously associated with SROs potentiated the startle reflex elicited by a loud noise in rats. This observation is clearly more congenial to a drive-inducing hypothesis than it is to an escape-from-frustration hypothesis. It is interesting to note that a similar potentiation of the startle reflex occurs when the loud noise is

preceded by a signal for shock (Davis, 1992), another piece of evidence pointing to the parallels between surprising nonreward and aversive conditioning.

General Conclusions

The present review of empirical evidence on the behavioral and physiological consequences of SROs suggests that such events have a powerful impact on the organism, involving the activation of physiological systems that also respond to more typical kinds of stressors. Such a parallel between the emotional reaction to unexpected nonreward and to painful stimuli has traditionally been recognized in the field of animal learning (Wagner, 1969). Despite its volume and generality, however, the evidence is less than sufficient in some critical areas, both physiological and behavioral. For example, a greater understanding of the impact of SRO events on autonomic variables and on immune activity is needed. Little is known about the neurochemical systems that mediate the emotional reaction to unexpected nonreward and the critical brain areas that participate in the various behavioral effects we described. The problems posed by the wide range of consequences of SROs for research are enormous, but recognizing their communalities is one major first step. In this vein, one may ask about other psychological phenomena that may relate to the basic body of evidence described in this article.

Flaherty and his associates have developed a consummatory contrast situation in the rat that has a clear relevance in the present context, as pointed out in the sections on corticosteroids and locomotor activity. In the typical experiment, a group of rats is given access to a 32% sucrose solution for a number of sessions until eventually the animals are shifted to a 4% solution. Their intake of this 4% solution is compared to that of control rats that have always received the 4% solution. Sessions usually last about 5 min. After a 32%-to-4% shift, the 32% animals reject the 4% solution during a few initial sessions, but with a sufficient number of sessions they drink just as much of the 4% solution as controls—the successive negative contrast effect (Flaherty, 1982). The first post-shift session clearly fits the definition of a SRO event. After the first session, subsequent ones could reflect a mixture of the reaction to the

SRO itself and the anticipated version of that reaction. In terms of frustration theory (Amsel, 1992), the rat's consummatory behavior may be heavily influenced by primary frustration in the first postshift day, but by a mixture of primary and anticipatory frustration in the subsequent postshift days. This issue could be clarified by simply measuring the latency to the first lick, in addition to liquid intake. In sessions subsequent to the first, not only should rats drink less of the 4% solution, but the latency to begin licking should increase also. Such a latency increase would reflect anticipatory frustration. Interestingly, a variety of drugs modulate the successive negative contrast effect from the second postshift day forward (Flaherty, 1991), but very few drugs capable of eliminating or reducing contrast in the first postshift day are known (Grigson & Flaherty, 1991). A similar dissociation occurs in the effects of antianxiety drugs on the FE and on the partial reinforcement extinction effect thought to involve anticipatory frustration (Gray, 1969). This is, therefore, one suitable animal model to study the neurochemical basis of the initial reaction to an SRO event.

Although the emphasis in this review has been on the surprise caused by the unexpected omission of a reward, this notion is clearly related to the concept of surprisingness suggested by Kamin (1969). In his initial report of the blocking effect, in which an otherwise viable stimulus fails to condition when it is reinforced in compound with a previously trained stimulus, Kamin suggested that acquisition may depend on the surprise caused by the presentation of an unexpected reinforcer. According to Kamin, blocking occurs because the previously trained stimulus makes the reinforcer unsurprising. Such a notion led to experiments in which surprisingness was assessed through its effects on the learning of stimuli presented before the unexpected event. For example, the surprising omission, as well as addition, of a reinforcer can disrupt blocking, that is, enhance acquisition to an otherwise blocked stimulus (e.g., Dickinson & Mackintosh, 1979). This effect is, of course, superficially similar to the effects reviewed in this article, all of which occur after the unexpected event. It is interesting to note that there is some evidence, though not entirely convincing, that the surprising presentation of a reward may have activating effects on the

response that follows that event; such enhancing effects of surprising reward presentations have been referred to as the *elation effect* (Meyer & McHose, 1968). Moreover, it was mentioned previously that a shift toward a condition of higher reward density in an operant situation is followed by a decrease in plasma corticosterone in rats (Goldman et al., 1973). Unexpected reward presentations can also have physiological consequences, although in this case, the consequences seem to be opposite to those of unexpected omissions. The relations between these lines of evidence, which proceed from independent theoretical frameworks, certainly merit attention.

There are also interesting parallels between the consequences of SROs and of mother-infant separation. The mother of a newborn mammal provides a considerable amount of appetitive reinforcement in the form of milk, warmth, tactile comfort, and familiar olfactory cues. Mother-infant separation may then be viewed as a special case of SRO in the sense that a source of appetitive reinforcement is removed from the infant's immediate, familiar environment. Glucocorticoid levels increase in infants after separation from their mothers in a variety of mammalian species (Coe, Wiener, Rosenberg, & Levine, 1985; Reite & Capitanio, 1985; Suomi, 1991). Separation is also followed by vocalizations and changes in activity, but unlike plasma cortisol, which does not seem to habituate (Jordan, Coe, Patterson, & Levine, 1984), these behaviors tend to decrease in an extinction-like fashion. In humans, separation or loss of a loved one may have a variety of consequences including severe depression (so-called anaclytic depression in infants deprived of appropriate care) and other affective disorders, disruption of autonomic functions, changes in appetite, disruption of sleep, general deterioration of health, suppression of immune activity, and increased mortality (Bartrop, Luckhurst, Lazarus, Kiloh, & Penny, 1977; Reite & Capitanio, 1985; Schleifer, Keller, Camerino, Thornton, & Stein, 1983; Stein & Trestman, 1990).

Although much work remains to be done in this area, the broad data base, the wide range of documented effects, and the possibility that a relatively simple manipulation involving the unexpected removal of an appetitive event underlies all of these effects are encouraging. The actual physiological mechanisms by which

the emotional reaction is translated into physiological and behavioral changes obviously needs to be worked out more explicitly. From the theoretical point of view, these effects powerfully demonstrate that the surprising omission of a reward not only results in the classic and perhaps more popular phenomenon of extinction, but also in an emotional reaction with potentially far reaching consequences.

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