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PRIMARY FRUSTRATION IN THE RED OPOSSUM (LUTREOLINA CRASSICAUDATA)

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ABSTRACT: Red opossums (*Lutreolina crassicaudata*) were trained in a Y-maze to locate a piece of food (the initial response, Ri) and afterwards to run back to the start box (the final response, Rf) where no reward was available immediately although a new trial was scheduled after a 30-s intertrial interval. Omission of food in some of the training sessions (Sessions 2, 10, 20, and 30) led to a decrement in latencies of the Rf, but only in Sessions 10 and 20, which was interpreted as evidence that primary frustration elicited by omission of an expected reward increases the vigor of ongoing instrumental behavior. The absence of this effect in the first and last extinction sessions ruled out an account based on post-ingestion factors, such as transitory satiation. The results are discussed in relation to vertebrate research on learning phenomena thought to depend on the frustrative consequences of nonreward.

Didelphid marsupials reject a low concentration sugar solution significantly more if they have been preexposed to a high concentration solution in that environment, a phenomenon named successive negative contrast (SNC; Papini, Mustaca, & Bitterman, 1988). This effect has long been known to occur in other mammalian species which are shifted from a high to a low magnitude of reward or from a preferred to a less preferred food item (Cowles & Nissen, 1937; Crespi, 1942; Elliott, 1928; Flaherty, Becker, & Cheeke, 1983; Tinklepaugh, 1928).

The explanation of SNC offered by frustration theory (Amsel, 1958, 1962) is based on the notion that the discrepancy between the expected and the actual amount of food generates primary frustration, an aversive emotional response which disrupts the actual consumption of less preferred food. Frustration is also conditioned to the apparatus cues so that in subsequent trials both approach and consumption can be disrupted by anticipatory frustration (Flaherty, 1982). Primary frustration is also assumed to energize ongoing instrumental responses, an effect first reported by Amsel and Roussel (1952). In their experiment, rats were exposed to a double-alley run-

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way in which the omission of an expected reward in the first goal box led to an increase in the speed of running in the second alley.

Although post-ingestion factors play some role (Seward, Pereboom, Butler, & Jones, 1957), they cannot account for the results of other experiments suggesting that it is the omission of an expected reward that energizes behavior, whether this is produced by summation of frustration and hunger (Amsel, 1958, 1962; Spence, 1960) or by escape from frustration (Daly & Daly, 1982). The effect, for instance, does not appear in a group never rewarded in the first goal box (Wagner, 1959), and is directly related to the number of rewarded trials before omission (Hug, 1970a; Stimmel & Adams, 1969; Yelen, 1969), and to the amount of reinforcement in the first goal box in a within-subject experiment (Peckham & Amsel, 1967). Particularly important are experiments showing that the magnitude of the frustration effect changes during training, a result difficult to account for by post-ingestion factors such as temporary satiation which should permanently affect performance (Amsel & Ward, 1965; Hug, 1970b). In Hug's experiment, for instance, reinforced and nonreinforced trials alternated in the first alley and the frustration effect in the second alley increased and later disappeared as alternation patterning developed in the first alley.

In the course of experiments on the acquisition of behavioral sequences in marsupials (Papini, Hermitte, Mustaca, & Haut, 1989), we gathered information on primary frustration in red opossums. Animals were trained in a Y-maze task to run in each trial to one of the arms where food was accessible and, after its consumption, to run back to the start box where food was never available. Trials were separated by a fixed intertrial interval. In this situation, unlike the double runway experiments, only one reinforcer was delivered per trial, although two responses were required to collect it: running from the start box to the baited arm (the initial response, Ri) and running back to the start box (the final response, Rf) after consumption of the food. Interspersed among training sessions were four extinction sessions in which no food was available in the previously baited arm. The main questions were whether the Rf latencies would decrease below the level observed in trials with reward available, and whether this would occur only after some training but not initially, a pattern necessary to discard post-ingestion factors in this situation.

METHOD

Animals

Four, 42-week old red opossums, three males and one female, with free-food weight between 360 g and 600 g, served as subjects.

The animals were from the same litter, born in the laboratory. They were deprived to 80% of their ad lib weight. Each animal was housed individually with water continuously available. These animals had received prior training in this task under the same conditions used in the rewarded sessions of the present experiment. That training ended 15 weeks before the start of the present experiment and the results were reported separately (Papini et al., 1989). During the interval between experiments animals had free access to water and food (Ladrina(R) dog chow supplemented with eggs and vitamins).

Apparatus

Training was carried out in a Y-maze with a start box separated from the rest by a guillotine door. The maze was built with wood, fully lined with plastic, and covered by transparent lids with the exception of the start box which had a wooden lid. The walls of the start box were black, whereas the rest of the maze had white walls. The floor of the maze was light blue. At the end of each arm there was a container with food which was accessible only in the correct arm. The maze was illuminated by three lamps (7 W) placed above each food container and in the start box, 15 cm from the floor. The maze was 60 cm high, 40 cm wide, 95 cm long in the central alley, 79 cm long in each arm, and 40 cm long in the start box. It was located in a sound-attenuated room where temperature varied between 20° and 27° C.

Procedure

Animals received 10 trials per day during 30 daily sessions in a spatial discrimination task. In each session, the subject was brought to the maze room in its cage and gently transfered to the start box where it remained for 30 s. The guillotine door was raised after that interval and at the same time a digital timer was manually started. The introduction of the animal's nose into the container was the criterion to stop the timer which was counting the Ri latency. Each trial was rewarded with a 2 g ball of crude meat. The food was eaten immediately and subsequently the animal usually licked the container and left the place, the whole sequence lasting 10-20 s. The final time the animal moved its nose away from the food container was the criterion to initiate a second timer which recorded the Rf latency, or the time required to go from the food container back to the start box. Once the animal entered the start box, the guillotine door was lowered and the Rf timer was stopped. A new trial started after an intertrial interval of 30 s. After the last trial, the animal was kept in the start box for 30 s and then gently placed back in its cage and carried to the colony room, where 30 min later received access to food for 45 min (this was enough to maintain deprivation level constant during training). Water was continuously available in the cage.

Sessions 2, 10, 20, and 30 were extinction sessions. The initial 2 trials of these sessions were rewarded but reward was withheld during the last 8 trials of the session. The inaccessible food placed in the wrong arm was also withdrawn.

RESULTS

Despite prior training in this situation, latencies (transformed to the $\log_{10}$ for the purpose of statistical analyses) were relatively high initially in training, and gradually decreased during training. A test on the first two trials of each session, which were always rewarded, indicated a significant latency decrement for both Ri ($F(29,87) = 2.35$, $p < .025$) and Rf ($F(29,87) = 3.82$, $p < .001$).

The effect of extinction was analyzed by comparing the latencies obtained in trials 3-10 of the four extinction sessions (2, 10, 20, and 30) with those obtained in the corresponding trials of the immediately preceding session. The Ri latencies were slightly increased by extinction but not enough to yield a significant difference between the comparable pre-extinction and the extinction sessions. There was a tendency toward the end of the extinction sessions for subjects to run more slowly from the start box to the previously baited arm, reflected in a significant Session by Trial interaction for the first, second, and third tests ($F\text{s}(7,21) > 2.60$, $p\text{s} < .05$); the effect disappeared in the last extinction session.

The results for the Rf latencies are depicted in Figure 1 for each of the test sessions separately. Here extinction produced the opposite effect: it decreased the Rf latencies below those obtained in the pre-extinction session, although the size of the effect varied across tests. The statistical analyses showed that latencies did not differ during the first extinction session (none of the factors reached a significant level); the lower latencies in Session 2 than in Session 1 were caused by one animal which ran consistently faster than in the first session. Latencies during extinction were significantly decreased in Session 10 ($F(1,3) = 151.62$, $p < .005$) and Session 20 ($F(1,3) = 19.48$, $p < .025$). The last extinction test (Session 30) yielded non-significant differences, which may be a consequence either of a floor effect (i.e., an efficient performance of the Rf in the pre-extinction session), or of higher latencies in the extinction session (i.e., anticipation of extinction may have diminished the frustrative effects of reward omission). Simple analyses of the pre-extinction (Sessions 19 vs. 29) and extinction (Sessions 20 vs. 30) sessions failed to detect any significant difference.

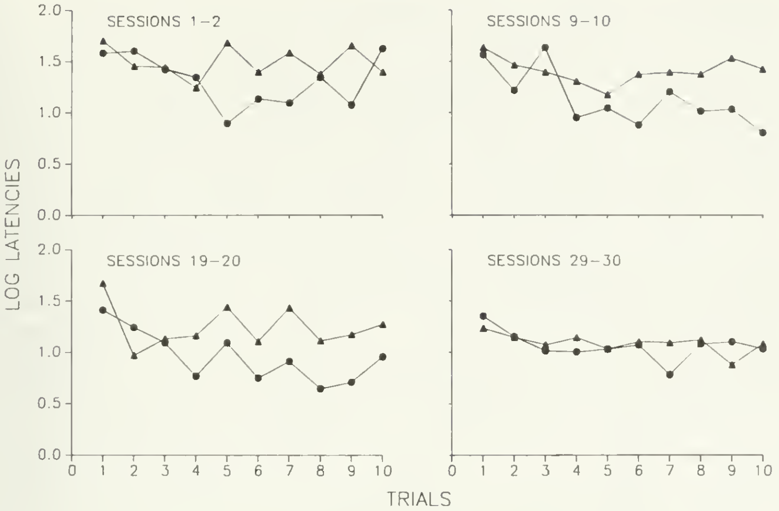

FIGURE 1. Final response (Rf) latencies during pre-extinction (triangles) and extinction (circles) sessions. There were four extinction sessions (2, 10, 20, and 30). Trials 1 and 2 were rewarded in all cases.

DISCUSSION

Omission of food decreased the latency to return to the start box only in Sessions 10 and 20 but not in Session 2. The effect was also absent in Session 30 but the reason for this seems different. The absence of the effect in Session 2—which contradicts an account based, for instance, on temporary satiation—can be interpreted in terms of frustration theory as produced by an incomplete acquisition which attenuated the otherwise frustrative effects of reward omission. On the other hand, the absence of the effect in Session 30 may reflect either a floor effect produced by low latencies during the pre-test session, or the absence of the energizing effect of reward omission during the test session.

A clear frustration effect emerged in Sessions 10 and 20, when latencies during the pre-test sessions were not yet asymptotic. The effect was relatively strong, appearing after a single exposure to reward omission, and remaining strong for the rest of the session. Particularly interesting is the fact that extinction caused not only a decrement in Rf latencies but also an increment in Ri latencies toward the end of the session. This pattern suggests that, whereas the omission of food facilitated subsequent responding, (i.e., Rf), it extinguished antecedent responses (i.e., Ri). Evidence that reinforcement plays both a retroactive and a proactive role in the acquisition of this response sequence was also found in rats (Papini & Silingardi, 1989).

The present results are analogous to what others found in rats (see Introduction) and complement a previous experiment in which evidence of SNC was found in these marsupials (Papini et al., 1988). Together they suggest that primary and anticipatory frustration controls instrumental behavior in didelphid marsupials in the same way that it does in rats. It remains to be determined whether frustration can be counterconditioned in marsupials, a mechanism assumed to underlie the partial reinforcement extinction effect in rats (Amsel, 1958, 1962). This communality in learning processes between rats and opossums is important because some of the effects thought to reflect the operation of frustration mechanisms, such as the SNC and the partial reinforcement extinction effect, have failed to appear in teleost fish (Couvillon & Bitterman, 1985; Gonzalez, Potts, Pitcoff & Bitterman, 1972; Longo & Bitterman, 1960; Lowes & Bitterman, 1967; Mackintosh, 1971; Schutz & Bitterman, 1969), toads (*Bufo arenarum*, Schmajuk, Segura, & Ruidiaz, 1981), and turtles (*Chrysemys picta*, Pert & Bitterman, 1970; Pert & Gonzalez, 1974). Further comparative studies should show the extent to which frustration theory applies to the instrumental learning of species other than mammals and birds (Roberts, Bullock, & Bitterman, 1963).

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