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Successive negative contrast after partial reinforcement in the consummatory behavior of rats☆

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Abstract

Rats given access to a 32% sucrose solution later reject a 4% solution significantly more than controls that have only received the 4% solution. In Experiment 1, this consummatory successive negative contrast (cSNC) effect was attenuated by previous exposure to 50% partial reinforcement. Furthermore, recovery from cSNC was also facilitated by partial reinforcement. In Experiment 2, the attenuating effects of partial reinforcement on cSNC were eliminated by administration of the benzodiazepine anxiolytic chlordiazepoxide (5 mg/kg) before nonreinforced trials. In Experiment 3, the attenuating effect of partial reinforcement was greater after a shift from 32 to 6% solution, than after a shift from 32 to 2% solution. The parallels between the effects of partial reinforcement on consummatory and instrumental behavior are discussed.

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When acquisition training involves widely spaced practice conditions (e.g., intertrial intervals greater than 1 h and spent outside the training context), responses paired with appetitive reinforcement on a random 50% of the trials are typically more persistent during extinction (i.e., when reinforcement is withheld) than responses acquired under a regimen of continuous reinforcement. This phenomenon, called the spaced-trial partial reinforcement extinction effect (PREE), has traditionally been shown in a variety of instrumental conditioning situations, including runway performance in both rats and pigeons (Thomas & Papini, 2003; Weinstock, 1954), lever pressing in rats (McNaughton, 1984), and key pecking in pigeons (Papini, Thomas, & McVicar, 2002). The PREE is not observed invariably, as shown by a variety of experiments in which partial reinforcement actually weakens persistence in extinction. Such spaced-trial reversed PREEs have been observed in within-group designs (see Papini et al., 2002), and in experiments involving fish, amphibians, and reptiles (see review in Papini, 2003).

Another example of a reversed PREE—and one directly relevant to the present paper—was reported in experiments assessing the consummatory behavior of adult rats, also under spaced training conditions. In one experiment (Mustaca, Freidin, & Papini, 2002), a group of rats received access to a 32% sucrose solution during 42 sessions (i.e., continuous reinforcement), followed by 12 extinction sessions in which the sipper tube was accessible, but the bottle was empty. The extinction performance of these animals was compared to that of a group that had access to the solution in 21 sessions and access to an empty bottle the remaining sessions, intermixed in a pseudorandom fashion (i.e., 50% partial reinforcement). Consummatory extinction was faster after partial reinforcement training, than after continuous reinforcement (i.e., a reversed PREE); this result contrasted with the conventional PREE obtained in experiments involving instrumental extinction.

Consummatory extinction is procedurally analogous to an experiment designed to study the consummatory successive negative contrast (cSNC) effect. The cSNC effect is defined as a temporary reduction in responding to a smaller reward by animals previously exposed to a larger reward, compared to the responding observed in a control group always exposed to the smaller reward. In both cases, the animals experience a downward shift in reinforcer magnitude, but whereas in consummatory extinction the shift is to nonreinforcement, in cSNC the shift is usually from a 32 to a 4% sucrose solution. Despite these procedural similarities, the actual outcomes obtained in consummatory extinction vs. cSNC situations seem to depend on different factors. For example, both cSNC and the conventional PREE obtained in instrumental situations can be reduced or eliminated by treatment with benzodiazepine anxiolytics, such as chlordiazepoxide (CDP; Flaherty, Grigson, & Rowan, 1986; McNaughton, 1984). Whereas the conventional PREE involves an affective reaction to surprising nonreward, much as cSNC does (see Amsel, 1992; Flaherty, 1996), the reversed PREE does not seem to involve any such affective response. In the case of a reversed PREE, animals register the change in the conditions of reinforcement after a shift to extinction, but responses decrease at the same rate in both groups. The reversed PREE could thus be described as reflecting a cognitive update of stimulus strength correlated with a change in reinforcement conditions (see Papini, 2003).

The present experiments further explored the effects of partial reinforcement on consummatory behavior. Unlike in Mustaca et al.'s (2002) experiments, the studies reported in this paper assessed the effects of partial reinforcement in the typical cSNC paradigm. The present experiments were designed to test the hypothesis that partial reinforcement training involves an affective response to surprising nonreward that modulates cSNC in the same direction as it does for instrumental extinction. Because partially reinforced instrumental responses are less prone to change in extinction, it was hypothesized that the partial reinforcement of consummatory behavior would also increase resistance to change and, therefore, reduce the size of the cSNC effect.

Experiment 1

Previous runway studies have shown that partial reinforcement training reduces the size of the SNC effect in instrumental situations (iSNC). For example, Mikulka, Lehr, and Pavlik (1967) found that 50% partial reinforcement eliminated iSNC after a shift from 10 pellets to 1 pellet. Similar attenuating effects on the iSNC effect were reported after training with variable reinforcer magnitudes (Ison, Glass, & Daly, 1969). In this case, the partial schedule involved a random sequence of trials reinforced with either 15 pellets or 1 pellet. A shift to continuous reinforcement for 1 pellet resulted in smaller iSNC than in a group that had received 15 pellets in all the preshift trials. The present experiment was planned to evaluate the effect of partial reinforcement on the cSNC effect using sucrose solutions as rewards and water as nonreward.

Method

Subjects

The subjects were 32 adult Wistar rats (*Rattus norvergicus*), 24 males and 8 females, all experimentally naïve and approximately 90 days old at the beginning of the experiment. The average ad libitum weight for the rats used in this experiment was 406.3 g. Ten days before the experiment, the subjects were transferred to individual plastic cages with water freely available. The daily amount of food was gradually reduced until their weights were lowered to a 80–85% of individual ad libitum weights. During training, the animals were fed daily 20 min after the training trial. The colony was under a 12:12 h cycle of light:darkness (lights on at 07:00 h). Temperature and humidity levels in the testing rooms and animal colony were kept relatively constant throughout the experiment.

Apparatus

Subjects received training in four identical conditioning chambers, each enclosed in a sound-attenuating cubicle. The internal dimensions of each chamber were 40 cm wide, 59 cm long, and 38 cm high. The floor of each chamber was made of stainless steel bars, 0.5 cm in diameter and spaced 1.7 cm apart, center to center. Located in the center of the front wall was a hole 1 cm in diameter 4 cm from the floor, through

which a stainless steel drinking spout (0.6 cm in diameter) could be inserted automatically. When fully inserted, the spout protruded 1.5 cm inside the chamber. A speaker and fan provided background white noise and ventilation, respectively. Training trials were conducted in the dark. A circuit connected the metallic bars in the box's floor with the sipper tube. Licking on the sipper tube closed the circuit, and this signal could be recorded by a computer located in an adjacent room. The main dependent variable in all the experiments reported in this article, labeled goal tracking time, was the time a rat spent in contact with the sipper tube during the trial. One count was recorded for every 20.4 ms of continuous contact.

The sucrose solutions (w/w) were prepared according to the following standard procedure. For the 32% solution, every 32 g of sucrose were mixed with 68 g of distilled water; for the 4% solution, every 4 g of sucrose were mixed with 96 g of distilled water. Solutions were prepared approximately 24 h before being used and were presented at room temperature.

Procedure

Rats were matched for sex and weight and randomly assigned to one of four groups ($n = 8$). Groups were labeled 32-4C, 32-4P, 4-4C, and 4-4P, depending on reinforcer magnitude (32 or 4%) received in each phase of the experiment (preshift or postshift) and the schedule of reinforcement (C for continuous and P for partial). A single trial per day was administered throughout the experiment.

The initial two trials were designed to habituate the rats to the conditioning chambers. Each habituation trial lasted for 5 min. During these trials, no event was scheduled (e.g., sucrose solution was not available).

Preshift started on the following day and lasted for 20 daily trials. In each of these trials, a rat was placed in the conditioning chamber and after a variable interval averaging 30 s (range: 15–45 s), the drinking tube was automatically inserted into the chamber. Each trial was 5-min long. This 5-min period started after the rat made contact with the drinking tube for a total of 5 s for every 30-s period. At the end of each trial, the drinking tube was automatically withdrawn and after a period averaging 30 s (range: 15–45 s) the animal was removed from the chamber. Groups 32-4C and 4-4C received access to 32 and 4% sucrose solution, respectively, in each of the 20 preshift trials. Groups 32-4P and 4-4P received access to their respective sucrose solution (32 or 4%) on half of the trials (reinforced trials, R); on the remaining half of the trials, these rats received access to distilled water (nonreinforced trials, N). Mustaca et al. (2002) used an empty sipper tube instead of distilled water for N trials. We chose to use distilled water on the basis of two assumptions: (1) sucrose, not water, is the reinforcing stimulus in food-deprived rats and (2) sucrose concentration is the variable manipulated in these experiments. The use of an empty tube in N trials adds a confounding—lack of sucrose and lack of fluid—which this procedure eliminates.

The sequence of R and N trials was the following for all rats in the partially reinforced groups: RNRRNNRNRNNRNRRNRNNR. There were 10 posthift trials. During postshift trials, all the rats received access to the 4% sucrose solution under the same conditions described above for Group 4-4C. The complete experiment took a total of 32 daily trials of training.

Animals were run in squads of four. The running order of the squads was randomized across days. Each box was cleaned with a damp paper towel after each training trial. Data were subjected to conventional analysis of variance (ANOVA). In all the statistical results reported in this paper, α was set at the .05 level.

Results and discussion

All animals consumed sucrose solution during the first trial, exhibiting no clear evidence of taste neophobia. They also consumed the solution delivered in all the trials of this experiment. The performance of the four groups during the entire experiment is shown in Fig. 1. Unfortunately, the data from the initial 4 trials of 18 rats (4 in Group 32-4C, 4 in Group 32-4P, 5 in Group 4-4C, and 5 in Group 4-4P) were lost due to computer malfunction. As a result, the means for trials 1–4 shown in the figure were computed with data from the remaining animals (n was reduced to 4, 4, 3, and 3, respectively, for Groups 32-4C, 32-4P, 4-4C, and 4-4P). Statistical analysis were performed only on the goal tracking times from trials 5 to 30, for which data from all animals were available ($n = 8$).

Preshift trials

Two aspects of the preshift performance plotted in Fig. 1 merit comments. First, the amount of goal tracking fell sharply during N trials, compared to R trials, and to a lower level in Group 32-4P than in Group 4-4P. This difference suggests that water may taste less palatable for an animal conditioned to expect a 32% solution than for one conditioned to a 4% solution. Second, the amount of goal tracking was also consistently lower for animals exposed to the 32% solution than for those exposed to the

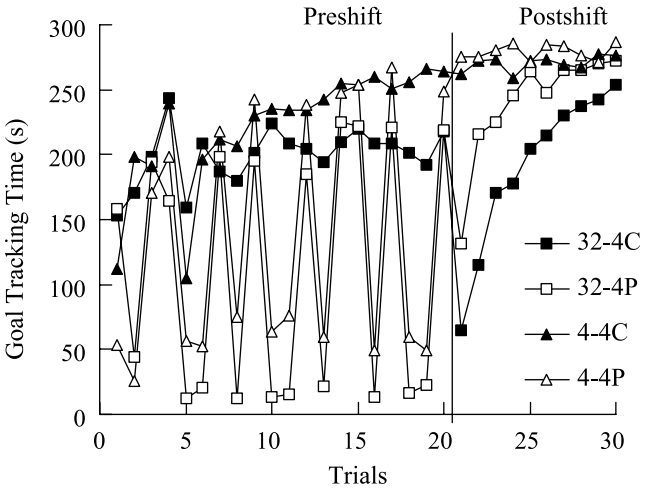

Fig. 1. Mean consummatory performance, measured in terms of goal tracking time, as a function of reinforcer magnitude (32 and 4%) and schedule of reinforcement (P, partial reinforcement and C, continuous reinforcement) during each preshift and postshift trial.

4% solution. A priori, one would have expected the opposite group order; the reasons for this result are discussed below.

A mixed-model ANOVA computed on the data from trials 5 to 20 with Sucrose (32, 4%), Schedule (P, C), and Trial (5–20) as factors (the latter as a repeated-measure factor), revealed the following effects. The partial groups performed significantly below the continuous groups, $F(1,28) = 65.77$; the 32% groups performed significantly below the 4% groups, $F(1,28) = 8.82$; and there was a significant acquisition effect, $F(15,420) = 90.84$. There were also significant interactions between sucrose and trial, $F(15,420) = 1.70$; schedule and trial, $F(15,420) = 65.61$; and sucrose, schedule, and trial, $F(15,420) = 2.34$. The interaction between sucrose and schedule was not significant.

The following statistical procedure was implemented to determine the source of the complex effects described in the previous paragraph. A one-way ANOVA was computed across the four groups for each one of trials 5–20. This analysis was followed by pairwise LSD tests, which yielded the following results. The group effect was significant for trials 5, 6, 8, 10, 11, 13, 16, 17, 18, and 19, Fs$(3,10) > 8.72$. Except for trial 17, only N trials yielded evidence of significant group effects. First, a comparison of performance in days in which the partially reinforced group received an N trial (trials 5, 6, 8, 10, 11, 13, 16, 18, and 19) indicated a significantly higher level of goal tracking in Group 32-4C than in 32-4P for every trial. Group 4-4C also scored significantly above Group 4-4P in each of these trials, except for trial 5. Thus, nonreinforcement produced a significant drop in consummatory performance whether rats had access to the 32 or the 4% solution.

Second, the impression conveyed by Fig. 1 that nonreinforcement decreased consummatory performance more in Group 32-4P than in Group 4-4P was supported by the pairwise LSD tests, but only for trials 8, 10, and 11. Although small, this difference can be interpreted as higher suppression of responding in Group 32-4P than in Group 4-4P, probably due to a greater impact of a shift from 32% to water than of 4% to water (see Mustaca et al., 2002, Experiment 1). The overall mean goal tracking time in N trials for Group 32-4P was 17.58 s and for Group 4-4P was 60.85 s. A goal tracking time of 17.58 s might be considered to be just enough time for rats to taste which solution was presented on that trial (cf. Grigson, Spector, & Norgren, 1993). It is therefore possible that a floor effect diminished the observable differences between the groups. However, the main goal of the present experiment was to evaluate the effects of PR on SNC, and not to study the consummatory responding during the phase of PR. Therefore, appropriate control groups to evaluate the source of this difference were not included (e.g., a group receiving only N trials). Finally, the performance of Group 32-4C, was found to be significantly lower than that of Group 4-4C on trials 13, 16, 17, 18, and 19. In the final preshift trial, number 20, none of the groups differed from each other significantly.

The higher goal tracking scores in rats exposed to 4% solution than in those exposed to 32% solution is not the most typical outcome in experiments using the consummatory procedure, when the dependent variable is licking rate (see Flaherty, 1996). However, this has been a typical result in our lab, under conditions similar to those used in the present experiment. Although the reasons for this discrepancy

across experiments are not completely clear, an analysis of intratrial performance shows two features that contribute to a higher performance in the 4% condition than in the 32% condition. Fig. 2 shows the performance of the four groups in trial 20 (i.e., the last preshift trial) as a function of 5-s bins. Notice that the goal tracking times for all four groups start at a similar level (possibly reflecting a ceiling effect), but the 32% conditions show a decrease toward the end of the trial (possibly due to greater gustatory adaptation or satiation; see Smith, Davis, & O'Keefe, 1992). A Sucrose (32, 4%) × Schedule (partial, continuous) × 5-s Bin analysis indicated a significant interaction of sucrose and bin, $F(58, 1624) = 2.12$, capturing the greater reduction in goal tracking in the 32% groups than in the 4% groups toward the end of the trial. The main effect of bin was also significant, $F(58, 1624) = 5.38$. All other effects failed to reach significance. Despite the significant differences observed across the two reward magnitudes, terminal performance did not differ significantly on the last trial of the preshift phase. A Sucrose × Schedule analysis of trial 20 data (see Fig. 1) indicated that none of the main effects or the interaction was significant, Fs < 1. Whatever the reason for this within-trial decrease in consummatory performance, it does not affect the interpretation of the postshift results because all the groups were exposed to the same 4% solution.

Postshift trials

Fig. 1 also shows the results of the postshift phase of training. In these trials, all the groups received the same treatment: continuous reinforcement with a 4% solution. Starting with the first postshift trial, goal tracking times dropped substantially for the two groups switched from 32 to 4% solution. This cSNC effect was followed by recovery of performance; within 10 trials, the level of all the groups was approximately the same. Contrast was more pronounced, and recovery somewhat slower, in Group 32-4C than in 32-4P. A Contrast × Schedule × Trial ANOVA of postshift

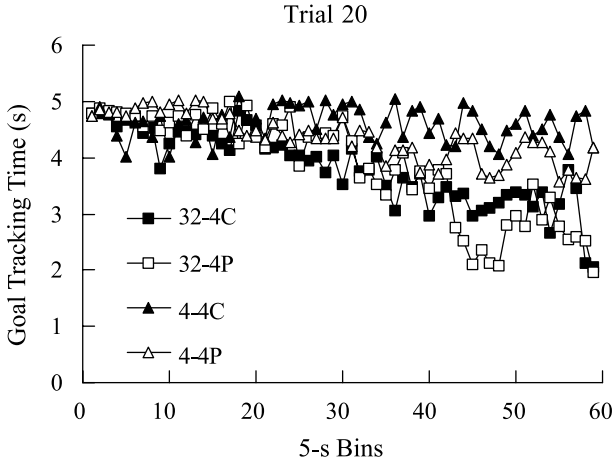

Fig. 2. Mean consummatory performance, measured in terms of goal tracking time, as a function of reinforcer magnitude (32 or 4% sucrose solutions), schedule of reinforcement (P, partial reinforcement and C, continuous reinforcement), and 5-s bin during preshift trial 20.

data revealed a pattern consistent with this description. There was a significant contrast effect, $F(1,28) = 43.66$, indicating that goal tracking scores were lower for groups shifted from 32 to 4% solution than for unshifted controls. Also significant were the main effects of schedule, $F(1,28) = 10.51$, and trial, $F(9,252) = 50.83$. More importantly, there was a significant contrast by schedule interaction, $F(1,28) = 5.11$, indicating that the contrast observed in Group 32-4P was smaller than the contrast observed in Group 32-4C. A differential recovery from contrast in both groups was detected by a significant triple interaction, $F(9,252) = 3.04$. The trial by contrast and trial by schedule interactions were also significant, $F(9,252) = 42.77$ and $F(9,252) = 3.42$, respectively. These effects reflect the decreasing differences between groups across postshift trials.

To further evaluate the differential recovery of Group 32-4C vs. Group 32-4P, a Schedule × Trial ANOVA was computed on their postshift data. This analysis indicated a significant schedule effect, $F(1,14) = 9.47$, a significant trial effect, $F(9,126) = 67.20$, and a significant schedule by trial interaction, $F(9,126) = 4.16$. These results support the conclusion that contrast was more pronounced, and recovery somewhat slower, in Group 32-4C than in Group 32-4P.

Separate one-way analyses followed by LSD pairwise tests were computed on each postshift trial to pinpoint the source of the major effects. The group effect was significant for all postshift trials, except trials 28 and 29, Fs$(3,28) > 3.41$. There were four pairwise comparisons of importance for the present analyses and the LSD results were the following. First, the conventional cSNC effect, Groups 32-4C vs. 4-4C, was significant for postshift trials 21–27, 29, and 30, but not for trial 28. Second, a significant cSNC effect was also found among the partially reinforced groups, Groups 32-4P vs. 4-4P, and it was significant only for trials 21–23 and trial 26. Third, the two unshifted controls, Groups 4-4C vs. 4-4P, were never statistically different from each other. Finally, and most importantly, a direct comparison between partially and continuously reinforced groups indicated significantly higher performance in Group 32-4P than in Group 32-4C in trials 21–26, but not for trials 27–30.

These results support the hypothesis that partial reinforcement training generates persistent consummatory behavior that immunizes the animal against the suppressive effects of surprising downshifts in reward magnitude. In a direct comparison of the cSNC effects generated by continuous reinforcement (the conventional treatment) and partial reinforcement, partial reinforcement shortened the cSNC effect by two trials. In a direct comparison between the two shifted groups, partial reinforcement attenuated consummatory suppression during the initial five postshift trials. These effects were, thus, quite robust. The following experiment was designed to evaluate the role of affective reactions to nonreinforcement during preshift trials.

Experiment 2

There are three major accounts of results such as those obtained in Experiment 1. First, the attenuating effects of partial reinforcement on cSNC may be the result of

the development of tolerance to the disruptive affective effects of surprising nonreward. According to frustration theory (Amsel, 1992), tolerance to frustration arises through counterconditioning resulting from the occasional pairings between secondary frustration and reinforcement during preshift R trials. Such pairings may endow secondary frustration with the ability to control approach (rather than withdrawal) tendencies toward the goal object. Thus, frustration theory suggests that the effect of partial reinforcement is to reduce the size of the contrast effect by increasing consummatory persistence after the shift. Second, the apparent persistence of consummatory behavior observed in Experiment 1 may be the result of differential amounts of reinforcement in the partial and continuous reinforcement groups. Group 32-4C received twice the number of rewarded preshift trials than Group 32-4P (i.e., 20 vs. 10 R trials, respectively) and, according to this hypothesis, should show the strongest contrast effect not because of tolerance in the partial group, but because of greater contrast in the continuously reinforced group. Finally, incentive averaging theory (Flaherty, 1996), suggests that partial reinforcement attenuates contrast because animals compare the 4% postshift solution with an average of the 32 and 0% solutions received, respectively, in R and N trials. As a result, the reference magnitude is lower in the partially reinforced animals than it is in the continuously reinforced animals, and contrast is thus reduced.

These alternative hypotheses were tested by treating rats with the benzodiazepine anxiolytic chlordiazepoxide (CDP) before N trials. There is extensive evidence that CDP attenuates anticipatory affective states induced by prior exposure to surprising nonreward. In the cSNC situation, CDP attenuates response suppression only after the animal has had some experience with the downshifted solution. For example, CDP decreases contrast in the second postshift trial, but not in the first (Flaherty et al., 1986), but it attenuates contrast in the first trial if the animal has been downshifted repeatedly (Flaherty, Clarke, & Coppotelli, 1996). Furthermore, first-trial contrast is not affected when the trial is 5-min long, but contrast is reduced when trial duration is increased (Flaherty et al., 1986). Similar effects were obtained in mice treated with the benzodiazepine diazepam and given 60-min long sessions (Mustaca, Bentosela, & Papini, 2000). CDP also reduces the iSNC effect (Rosen & Tessell, 1970) and the spaced-trial PREE (McNaughton, 1984).

These results suggest that CDP can be a useful tool to isolate the affective effects of partial reinforcement from the incentive averaging effects. In the present experiment, one group of rats received CDP administration only before N preshift trials. If CDP attenuated the affective reaction to nonreward, then the immunizing effects of partial reinforcement on cSNC should be reduced or eliminated, thus increasing the size of the cSNC effect. However, if the attenuating effects of partial reinforcement on contrast are caused by different amounts of reinforcement or by incentive averaging, then CDP treatment should not affect the degree of consummatory suppression after the downshift. The performance of a CDP-treated group was compared to that of partially and continuously reinforced groups given saline injections before the same trials. CDP was administered only before N trials to avoid excessive drug administration and also to determine whether it is just the effect of CDP on N trials that modulates the effects of partial reinforcement on cSNC (see Weiner, Feldon, & Bercovitz,

1987; for a similar treatment using amphetamine). Unshifted controls were not included because the main goal of this experiment was to evaluate the extent to which CDP was able to affect the degree of consummatory suppression after the downshift. Notice that CDP was not administered during the postshift trials and, in fact, was last injected 48 h before the first postshift trial.

Method

Subjects and apparatus

The subjects were 24 adult Wistar rats, 12 male and 12 female, with a mean ad libitum weight of 360.7 g. Assignment of the subjects to the groups, maintenance conditions, and training chambers were as described in Experiment 1.

Procedure

Rats were matched for sex and weight and randomly assigned to one of three groups ($n = 8$). Groups were labeled C/Sal, P/Sal, and P/CDP depending on the schedule of reinforcement (continuous or partial) and on the injection treatment (CDP 5 mg/kg or saline). Injections were administered ip, approximately 30 min before the start of N trials in the partially reinforced group, or before the equivalent trial for the continuously reinforced rats.

All animals received two context-habituation trials similar to those described in Experiment 1. The training parameters used in preshift trials for partial and continuous reinforcement conditions were, respectively, those used in Experiment 1 for Groups 32-4C and 32-4P. None of the rats was injected before R trials or during postshift trials.

Results and discussion

All animals consumed the solution delivered in all the trials of this experiment. The results of this experiment are plotted in Fig. 3. These results may be summarized in two major points. First, the drastic drop of performance during N trials observed in the previous experiment was replicated. Furthermore, such performance was not obviously affected by CDP. Second, the most noticeable group differences occurred during the initial three postshift trials; afterward, the groups converged, with the average goal tracking time of Group C/Sal staying consistently below the scores of the other two groups. The attenuating effect of partial reinforcement on postshift consummatory performance (also observed in Experiment 1) was particularly strong in trials 21–23. In addition, previous administration of CDP during preshift N trials seemed to result in a performance very similar to that of Group C/Sal during trials 21 and 22, but more like that of Group P/Sal in the remaining postshift trials. Statistical analyses confirmed these conclusions.

Preshift trials

A Group (C/Sal, P/Sal, P/CDP) × Trial ANOVA of the preshift data yielded significant effects for group, $F(2, 21) = 75.07$; trial, $F(19, 399) = 70.04$; and their

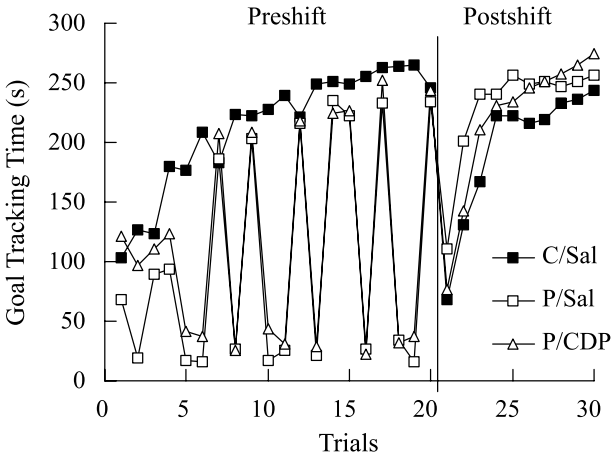

Fig. 3. Mean consummatory performance, measured in terms of goal tracking time, as a function of schedule of reinforcement (P, partial reinforcement and C, continuous reinforcement) and drug treatment (Sal: saline and CDP: chlordiazepoxide, 5 mg/kg) during each preshift and postshift trial.

interaction, $F(38, 399) = 18.57$. The source of this interaction was examined using the same statistical approach as in the previous experiment, namely, one-way ANOVAs for each trial with LSD pairwise tests. The group effect was significant for trials 2, 5, 6, 8, 10, 11, 13, 16, 18, and 19, all corresponding to N trials in the two groups receiving partial reinforcement training, Fs$(2, 21) > 8.49$. LSD pairwise tests indicated that Group C/Sal was significantly different from both P/Sal and P/CDP in all these trials, except for trial 2, in which C/Sal differed significantly from P/Sal and P/Sal differed from P/CDP. None of the other pairwise comparisons reached significance. Finally, groups were not significantly different on trial 20, the last preshift trial ($F < 1$).

Postshift trials

A Group × Trial analysis of the postshift performance depicted in Fig. 3 indicated the following effects. The difference between groups fell short of statistical significance, $F(2, 21) = 3.41$, $p < .06$; however, there were significant effects for trials, $F(9, 189) = 104.47$, and for the group × trial interaction, $F(18, 189) = 2.45$. One-way analyses of variance for each postshift trial indicated a marginally significant effect for trial 21, $F(2, 21) = 3.29$, $p = .057$, and significant effects for trials 22 and 23, Fs$(2, 21) > 3.92$. The following comparisons are important in this experiment. First, LSD pairwise tests indicated that Group C/Sal performed significantly below Group P/Sal in trials 21–23, thus replicating the results of Experiment 1. Second, LSD pairwise tests indicated that Group P/CDP performed significantly below Group P/Sal on trial 22. Third, Group C/Sal was not significantly different from P/CDP in trials 21 and 22, which indicates that CDP abolished the decremental effects of partial reinforcement on suppression after a downward shift in the magnitude of the sucrose solution. The effect of CDP was weaker on trial 23; in fact, the performance of Group P/CDP in trial 23 was significantly above that of Group C/Sal, while the difference

between Group P/Sal and P/CDP was still significant. Group effects were not significant on trials 24–30. This would seem to indicate that, under the present parameters, CDP masked the effects of exposure to N trials on consummatory responding without completely eliminating them.

Experiment 3

Experiments 1 and 2 together show that the attenuating effect of partial reinforcement on consummatory behavior after a downshift in reward magnitude is mediated by an aversive affective reaction induced by nonreinforcement. According to frustration theory (Amsel, 1992), partial reinforcement can achieve such an attenuating effect through the counterconditioning of secondary frustration induced by the occasional pairings between this aversive anticipatory state and reinforcement. Frustration theory also predicts that the cSNC effect should be more attenuated the smaller the preshift–postshift discrepancy. In the present experiments, groups of rats received partial or continuous reinforcement training with the 32% solution during preshift trials and were subsequently shifted to either 6 or 2% solution. Given that these groups did not differ in terms of their partial reinforcement training during preshift trials, they should develop counterconditioning to an equal strength. Frustration theory predicts that equal amounts of counterconditioning across groups will counteract more successfully the relatively mild frustration induced by a shift to 6% solution than that induced by a shift to 2% solution. Notice that according to frustration theory, conterconditioning is not specific to a particular amount of frustration experienced during surprising reward downshift; as a result, an analysis in terms of generalization decrement (i.e., that the 32-water shifts during the preshift trials are more similar to the 32–2 shift than to the 32–6 shift in postshift trials) does not apply in this case (Amsel, 1992). Furthermore, the difference in the postshift solution, 6% vs. 2%, was aimed at inducing weaker vs. stronger cSNC effects, respectively. Frustration theory then predicts that the attenuating effect of partial reinforcement on the cSNC effect should be greater in the 32–6 condition than in the 32–2 condition. The key comparisons are, therefore, between shifted and nonshifted groups that received partial reinforcement training.

Method

Subjects and apparatus

The subjects were 32 adult Wistar rats, 16 male and 16 female, with a mean ad libitum weight of 338.1 g. Assignment of animals to groups, maintenance conditions, and the conditioning boxes used during training were as described in Experiment 1.

Procedure

The groups of this experiment were labeled 32-2C, 32-2P, 32-6C, 32-6P, 2-2C, 2-2P, 6-6C, and 6-6P, depending on the schedule of reinforcement (continuous, partial) and the concentration of the sucrose solution received in preshift and postshift trials

(32, 6, and 2%). All other training parameters were the same as those used in the previous experiments.

Results and discussion

All animals consumed the solution delivered in all the trials of this experiment. The main results are plotted in Fig. 4. As in the previous experiments, nonreinforcement during preshift trials caused a drastic reduction in consummatory behavior. There was also evidence of cSNC with shifts from 32% solution to both 2 and 6%. Importantly, the size of the cSNC effect was a direct function of the size of the discrepancy between preshift and postshift solutions. The recovery was also slower in the 32–2 case than in the 32–6 case. Finally, partial reinforcement attenuated cSNC in both conditions, but it seems to have had a greater impact in the 32–6 case than in the 32–2 case, at least when the performance in the first postshift trial is considered. Statistical analyses provided support for these conclusions.

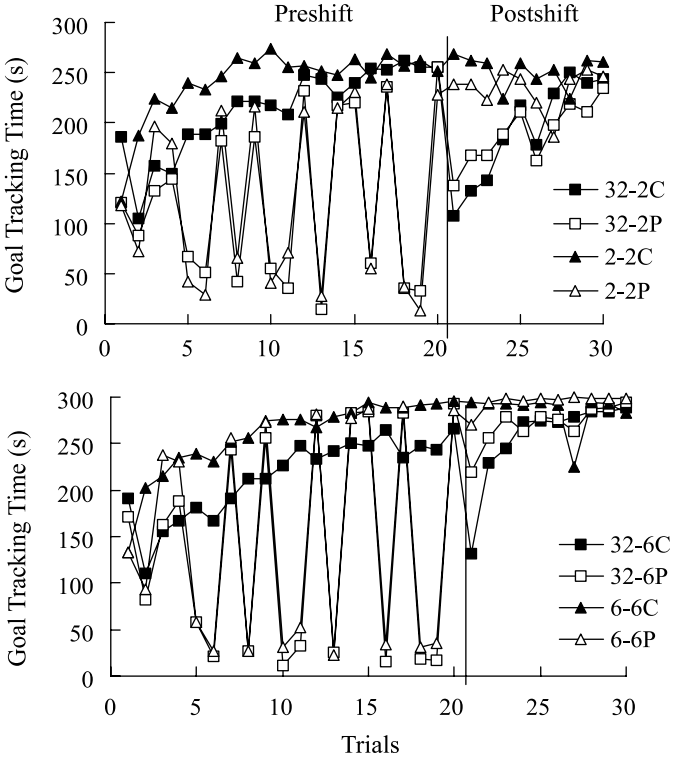

Fig. 4. Mean consummatory performance, measured in terms of goal tracking time, as a function of reinforcer magnitude (32, 6, or 2% sucrose solutions) and schedule of reinforcement (P, partial reinforcement and C, continuous reinforcement) during each preshift and postshift trial.

Preshift trials

A Sucrose (2, 6%) × Schedule (C, P) × Trial ANOVA of performance during preshift trials revealed the following effects. There were significant main effects of sucrose, $F(2, 57) = 7.80$; schedule, $F(1, 57) = 408.11$; and trial, $F(19, 1083) = 108.76$. Moreover, there were also significant interactions for sucrose and trial, $F(38, 1083) = 3.35$; schedule and trial, $F(19, 1083) = 103.64$; and sucrose, schedule, and trial, $F(38, 1083) = 1.86$. Other effects failed to achieve significance. The triple interaction supports the conclusion that groups with access to the 6% solution responded more than groups with access to 2% solution and 32% sucrose, and that the continuously reinforced groups responded more than the partially reinforced groups.

The same statistical approach used in previous experiments was implemented for the current data. One-way analysis of variance tests were performed for the eight groups and for each trial, followed by LSD pairwise tests. Only some pairwise tests are of interest, however. First, performance in days in which the partially reinforced groups received an N trial (trials 2, 5, 6, 8, 10, 11, 13, 16, 18, and 19) indicated the following results. A comparison of Groups 32-2C vs. 32-2P and of Groups 32-6C vs. 32-6P indicated that nonreinforcement significantly suppressed drinking in all N trials. A similar comparison of Groups 2-2C vs. 2-2P and of Groups 6-6C vs. 6-6P indicated a significant decrease in all N trials in the partial groups relative to the continuous groups. Thus, nonreinforcement significantly suppressed consummatory behavior in all sucrose magnitude conditions.

Second, the performance of groups receiving partial reinforcement training was compared also on N trials (32-2P vs. 2-2P and 32-6P vs. 6-6P). Except for trial 11, in which Group 32-2P differed from Group 2-2P, goal tracking was not different in any of these two comparisons, in any of the preshift trials. Goal tracking times in N trials did not seem to relate to the concentration received in R trials. Third, performance was also assessed as a function of sucrose concentration. Comparisons of 32-2C vs. 2-2C yielded significant differences only for trial 3; and comparisons of 32-6C vs. 6-6C yielded significant differences for trials 4, 5, 6, 9, 10, 13, 15, and 17. Finally, on trial 20, Group 2-2P scored significantly below all the other groups, whereas Group 6-6C scored significantly above Groups 2-2C and 32-2P. None of the other groups differed from each other significantly in the final preshift trial.

Postshift trials

A Contrast (shifted, nonshifted) × Schedule (continuous, partial) × Sucrose (2, 6%) × Trial ANOVA was computed on the data obtained in postshift trials. This analysis yielded significant main effects for contrast, $F(1, 55) = 26.24$; sucrose, $F(1, 55) = 68.26$; and trial, $F(9, 495) = 29.79$. The schedule effect was nonsignificant. There were also some two-factor significant interactions, including the ones between sucrose and trial, $F(9, 495) = 4.20$; contrast and trial, $F(9, 495) = 27.91$; and contrast and sucrose, $F(1, 55) = 8.79$. No other two-factor interaction was significant, Fs < 3.30. More important for the present experiment, there was a significant triple interaction for contrast, schedule, and trial, $F(9, 495) = 2.84$, indicating that the downshifted, partially reinforced groups consumed more than the downshifted, continuously reinforced groups. Also relevant was the significant triple interaction

between contrast, sucrose, and trial, $F(9,495) = 3.56$, indicating a larger contrast effect in the groups shifted to 2% solution than in those shifted to 6% solution. No other three-factor interaction was significant; the four-factor interaction was also nonsignificant.

One problem with these interaction effects is the relatively large number of trials during which the performance was essentially recovered from the downshift, particularly in the 6% groups (see Fig. 4). These scores thus may obscure any effects observed early in the postshift trials. The same statistical approach of the previous experiments was used on these data, namely, one-way analyses at each postshift trial followed by LSD pairwise tests. The main effect of groups was significant in all postshift trials, Fs$(7,55) > 2.71$. There are four key comparisons, each with two pairwise tests of interest. First, were there conventional cSNC effects in the continuous groups? A comparison of Groups 32-2C vs. 2-2C indicated significant differences for trials 21–26, 29, and 30, whereas a comparison of Groups 32-6C vs. 6-6C indicated a significant difference only for trials 21 and 22. In all other trials, group differences were not significant. Thus, the cSNC was more prolonged after a $32 \rightarrow 2$ shift, than after a $32 \rightarrow 6$ shift. Second, were there cSNC effects in the partial groups? Groups 32-2P and 2-2P only differed significantly in trials 21-24, whereas Groups 32-6P and 6-6P reached statistical significance only on trial 21. Partial reinforcement reduced the length of the cSNC in the 2% condition and it completely eliminated it in the 6% condition. Third, was the performance of unshifted controls receiving 2 or 6% sucrose solution different? Pairwise comparisons indicated that Group 6-6C scored significantly above Group 2-2C in trials 24–28. Moreover, Group 6-6P scored significant above Groups 2-2P on postshift trials 22–30. Finally, were there effects of partial reinforcement in the 2 and 6% conditions? The pairwise comparisons between Groups 32-2C vs. 32-2P yielded significant effects on trials 22–25. However, only trial 21 reached significance for pairwise comparisons between Groups 32-6C vs. 32-6P.

An additional analysis was calculated to further assess the cSNC effects in the 2% vs. 6% conditions in relative terms. Separate Contrast $\times$ Schedule ANOVAs were computed for each postshift trial and solution concentration. Particularly important for the present purpose are the results of the contrast by schedule interactions, since they indicate the presence of a significantly larger cSNC effect in the continuous groups than in the partial groups. For the groups shifted to 6% solution, this interaction was significant only on trial 21, $F(1,28) = 7.34$. In contrast, for the groups shifted to 2%, the contrast by schedule interaction was significant on trials 21–23, Fs$(1,27) > 4.71$. Importantly, the same analyses indicated that the 6% groups showed significant main effects for contrast on trials 21–22, Fs$(1,28) > 10.31$. This implies that although contrast was still detectable after a downshift to 6% in trial 22, the beneficial effect of partial reinforcement training was by then no longer evident. As for the 2% groups, there were significant contrast effects on trials 21–26, Fs$(1,27) > 9.75$.

The interactions described in the previous paragraph might have been in part determined by the differential performance of the control groups (2-2C vs. 2-2P and 6-6C vs. 6-6P). Thus, additional analyses were computed on these data to directly test the differences between Groups 32-2C vs. 32-2P, and Groups 32-6C vs. 32-6P. These analyses were followed by separate ANOVAs for each trial, as required. Because

counterconditioning is assumed to counteract more effectively a shift to 6% than a shift to 2%, it was predicted that the groups shifted to 6% would show significant differences for a greater number of trials than the groups shifted to 2%. This was confirmed by the analyses. The comparison between Groups 32-2C vs. 32-2P show only a significant effect of trials, $F(9,117) = 29.34$, while the comparison between Groups 32-6C vs. 32-6P revealed a significant trial effect, $F(9,126) = 27.22$, as well as a significant trial × group interaction, $F(9,126) = 4.29$. No other effect was significant. Further analyses indicated that the significant interaction was due to a higher performance of Group 32-6P than of Group 32-6C on trial 21, $F(1,14) = 4.72$; these groups did not differ significantly in any other trial. In conclusion, these analyses indicate that group differences, although small, went in the direction predicted by frustration theory.

All together, these results confirmed that partial reinforcement attenuates the cSNC effect, as shown in Experiment 1, and provided support for the prediction that this attenuating effect is an inverse function of the size of the incentive discrepancy between the preshift and postshift solutions.

General discussion

The results of these three consummatory response experiments demonstrate that partial reinforcement training attenuates the size of the cSNC effect. This effect is consistent with similar results obtained in more traditional learning preparations, such as those involving runway and lever-pressing performance (i.e., iSNC effects; see Introduction for references). In the present case, partial reinforcement was implemented by exposing rats to an unpredictable sequence of trials involving access to a sucrose solution (reinforced trials) and access to distilled water (nonreinforced trials). Because sucrose was defined as the reinforcer, nonreinforced trials contained only the vehicle in which the sucrose was dissolved. Furthermore, the results of Experiment 1 indicated that partial reinforcement also increased the speed of recovery from cSNC; Experiment 2 provided evidence that the effect of partial reinforcement on consummatory suppression is significantly reduced by the administration of CDP, a benzodiazepine anxiolytic, prior to nonreinforced preshift trials; and Experiment 3 indicated that the effects of partial reinforcement on cSNC were more prolonged with a relatively large reward discrepancy (i.e., 32% → 2%, rather than 32% → 6%).

These experiments were designed to shed light on the role of frustration in consummatory situations. Frustration is implicated when a less preferred appetitive reinforcer occurs in the presence of cues previously paired with a more preferred one. Previous results indicated that, unlike in instrumental extinction, the extinction of consummatory behavior does not seem to require the involvement of an affective response of frustration (Mustaca et al., 2002). Thus, consummatory extinction is characterized by a reversed PREE after partial reinforcement training and by a reversed magnitude of reinforcement extinction effect after training with different reward magnitudes. Such reversed effects are consistent with a simple learning principle known as the strengthening–weakening rule (see Papini, 2003), according to which the strength of a response (or of the controlling stimulus) is a direct function of

the frequency with which it has been reinforced and nonreinforced, and of the magnitude of the appetitive reinforcer. In contrast, the results reported in this paper support the hypothesis that affective responses of frustration are indeed induced by partial reinforcement training in the consummatory preparation and that their consequences parallel those observed in instrumental situations.

Based on the results of analogous instrumental reinforcement experiments involving partial reinforcement and contrast, it was hypothesized that the partial reinforcement of consummatory behavior would also increase resistance to change and, therefore, reduce the size of the cSNC effect. Although the results of each of the present experiments can be explained in terms of alternative hypotheses, all together they are consistent with frustration theory. For example, the attenuating effects of partial reinforcement on cSNC observed in Experiments 1 and 3 could be explained in terms of differential amount of reinforcement across groups. The groups exposed to partial reinforcement received half the number of reinforced trials received by the groups exposed to continuous reinforcement. As a result, the consummatory response of partial rats would be relatively weaker than that of continuous rats and this would lead to a smaller cSNC effect when magnitude is downshifted. There is some suggestion in the literature that increasing the amount of preshift training augments contrast size with human subjects (Weinstein, 1972); however, there is also evidence that rats minimally exposed to the 32% sucrose solution (e.g., one or two 5-min trials) still show evidence of cSNC (Flaherty, Becker, & Checke, 1983a). Whatever the case, the amount-of-training hypothesis cannot account for the small—but significant—effects of CDP reported in Experiment 2 because the number of reinforced and nonreinforced trials in Groups P/CDP and P/Sal was equal.

A second alternative explanation suggests that the attenuating effects of partial reinforcement on SNC are the result of incentive averaging. In one set of experiments (Peters & McHose, 1974), rats that had received preshift training in a runway with either 20 or 4 pellets (i.e., randomly intermixed trials, Group 20/4), or consistent reinforcement with 7 pellets (i.e., Group 7), subsequently exhibited iSNC effects of similar size when shifted to 1 pellet. Presumably, the $7 \rightarrow 1$ downshift experienced by Group 7 was equivalent to that experienced by Group 20/4. The choice of these particular magnitudes was based on a calculation of incentive value derived from previous research (see McHose, 1970; McHose, Maxwell, & McHewitt, 1971). Accordingly, the incentive values derived by Peters and McHose (1974, see Eqs. 1 & 2) were equal to 1, 0.8, and 0.6, for magnitudes of 20, 7, and 4 pellets. The average incentive value for Group 20/4 was then calculated as the sum of the two incentive values weighted by the proportion of trials in which each magnitude was presented: $0.5(0.6) + 0.5(1) = 0.8$. Similarly, for Group 7, the incentive average was equal to: $1(0.8) = 0.8$. Thus, these two groups were matched in terms of average incentive value and should have experienced the same degree of contrast.

A straightforward application of the same metric to the conditions of Experiment 1 yields partially correct predictions. According to the formula used by Peters and McHose (1974, Eq. 2), 32, 4, and 0% sucrose solutions were equal to incentive values of 1, 0.6, and 0, respectively, yielding average incentive values of 1, 0.5, 0.6, and 0.3 for Group 32-4C, 32-4P, 4-4C, and 4-4P, respectively. Whereas the size of the

discrepancy is larger for 32-4C vs. 4-4C ($1 - 0.6 = 0.4$) than it is for 32-4P vs. 4-4P ($0.5 - 0.3 = 0.2$), thus agreeing with the main results of Experiment 1, these values incorrectly predict the performance of the unshifted controls. These groups failed to differ in their performance, even though the incentive value for 4-4C is twice the size of that for 4-4P (0.6 and 0.3).

Other researchers concerned with the application of incentive averaging theory to cSNC experiments using sucrose solutions as incentives suggested that, under such conditions, the arithmetic mean of the incentive magnitudes without any scalar transformation might lead to more accurate predictions (Flaherty, Becker, & Osborne, 1983b). If an arithmetic mean is computed for the parameters of Experiment 1, then the downshift experienced by the rats in Group 32-4C is greater than that experienced by the rats in Group 32-4P, which, in turn, would be equivalent to a $16 \rightarrow 4$ downshift: $1(32) = 32 > 0.5(32) + 0.5(0) = 16$. This method for computing incentive averages predicts a larger cSNC effect in Group 32-4C than in Group 32-4P, a result confirmed by Experiment 1. Thus, incentive averaging suggests that the effects of partial reinforcement on cSNC are analogous to the effects of reducing the discrepancy between the preshift and postshift solutions, for which there is abundant confirmatory evidence (see review in Flaherty, 1996). Unless some ad hoc assumption is postulated, incentive averaging cannot account for the effects of CDP on consummatory suppression reported in Experiment 2. One example of an ad hoc assumption would rely on the mechanisms by which CDP affects behavior. It could be argued that the effect of CDP is to reduce the weight of N trials from the computation of the average incentive value during preshift trials. If CDP eliminates or reduces the aftereffects of nonreinforcement, then incentive value would be computed predominantly on the basis of reinforced trials, and the partial schedule would approximate a continuously reinforced schedule. Incentive averaging implies that any treatment that interferes with the memory of nonreward should attenuate the effects of partial reinforcement on cSNC (e.g., posttrial administration of GABAergic agonists; see Salinas & McGaugh, 1996). A test of this possibility awaits further research.

As pointed out previously, the present results are consistent with frustration theory. The effects of partial reinforcement on the size of cSNC and the speed of recovery are explained in terms of a hypothetical process of counterconditioning of frustration developing during preshift trials (see Amsel, 1992). Such counterconditioning reduces the suppressive effects of anticipatory frustration on consummatory behavior thus promoting a milder cSNC effect and a faster recovery (Experiment 1). Moreover, CDP is assumed to reduce the aversive emotional impact of surprising nonreward experienced during nonrewarded preshift trials, thus effectively disrupting counterconditioning and reinstating a normal-size cSNC effect (Experiment 2). Finally, counterconditioning should be particularly effective in a situation involving a relatively mild frustrative response (Experiment 3). An outstanding problem remains, namely, if frustration theory accounts reasonably well for a set of effects involving partial reinforcement, why does consummatory behavior exhibit a reversed PREE in extinction (Mustaca et al., 2000)? The critical comparison between contrast and extinction procedures has not been done within a single experiment and, therefore, any answer to this question would be tentative and premature.

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