Apparent disinhibition of successive but not of simultaneous negative contrast

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In a series of three experiments, rats shifted from a 32% to a 4% sucrose solution, after 10 days' exposure to the 32% solution, exhibited a negative contrast effect in lick rate. In each experiment, shifted rats that received a novel stimulus (tone) during the postshift period exhibited a higher lick rate (smaller contrast effect) than shifted subjects not receiving the tone. This increase in lick rate resembles Pavlovian disinhibition and is interpreted as supporting an inhibitory view of successive negative contrast effects. Control conditions included in Experiments 2 and 3 favored the disinhibition interpretation of the effect of the tone, as opposed to a rate-dependency hypothesis or to the nonspecific energization of behavior. In Experiments 4-6, the tone was introduced coincident with the occurrence of a simultaneous negative contrast effect. Rather than disinhibition, a decrease in licking occurred. These results were discussed in terms of differences between successive and simultaneous contrast.

Rats exposed to one magnitude or quality of reward and then shifted to another will exhibit a different level of performance subsequent to the shift than rats exposed to only a single reward magnitude or quality. Whether a shifted group's performance is better or worse than an unshifted group's will depend on the direction of the shift. For example, rats shifted from a large to a small reward in a runway will exhibit poorer performance than nonshifted rats running for the smaller reward (e.g., Crespi, 1942; DiLollo & Beez, 1966). The poorer performance of this group has been termed a negative contrast effect. Positive contrast—better performance by animals shifted from a small to a large reward relative to animals always maintained on the large reward—has also been reported (Crespi, 1942; Mellgren, 1972).

Contrast effects, which occur in a wide variety of experimental situations, may be categorized into the following three classes.

Simultaneous contrast: Subjects receive two or more magnitudes or qualities of reward in some intermixed order throughout training. In the case of instrumental simultaneous contrast, these reward magnitudes are associated with different stimuli; for example, in a runway study, black and gray runways might be associated with large and small rewards, respectively.

Experiments 1-3 are based on a portion of the thesis submitted for the first author's Master of Science degree performed under the direction of the second author. We would like to thank Robert Blitzer for his assistance in conducting Experiment 4. This research was supported by a Biological Sciences support grant and a grant from the Rutgers University Research Council, both to the second author. Reprint requests should be addressed to Charles Flaherty, Psychology Department, Busch Campus, Rutgers University, New Brunswick, New Jersey 08903.

Successive contrast: Subjects are initially given consistent exposure to one level of reward and are subsequently shifted to a different level of reward in the same task. The new level of reward is then usually presented consistently and the performance of the shifted group typically recovers to that of the unshifted group.

Behavioral contrast: Subjects in a free-operant discrimination task receive two schedules of different reinforcement densities that alternate and are correlated with different external stimuli. Behavioral contrast is defined as an increase in responding to an S+ stimulus paired with the more dense reinforcement schedule over the rate maintained by that stimulus when both S+ and S- were associated with the same schedule.

In addition to the simultaneous, successive, and behavioral contrast effects found in instrumental behavior, simultaneous and successive contrast effects have also been found in consummatory responding. For example, rats shifted from a 32% sucrose solution to a 4% sucrose solution after 10 days' exposure to the sweeter solution will lick less for the 4% solution than rats that have been maintained on the 4% solution (Flaherty, Capobianco, & Hamilton, 1973; Vogel, Mikulka, & Spear, 1968); and when 32% and 4% solutions are alternately available for 1-min periods, both positive and negative simultaneous contrast effects occur in lick rate (Flaherty & Largent, 1975).

One major theoretical interpretation of contrast effects suggests that inhibition plays a major role in the phenomenon. Black (1968), for example, elaborated a theory based on Spence's (1956) model for discrimination learning. The model proposed by Spence assumes that effective excitatory potential

($\bar{E}$) is the result of the algebraic summation of excitation (E) and inhibition (I). Whenever a response is reinforced in the presence of a particular stimulus, an increment in E is said to occur, and whenever a response is not reinforced in the presence of a particular stimulus, the result is an increase in I. The strength of a response is, according to this model, equal to the algebraic summation of E and I ($\bar{E} = E + I$), where E and I are said to generalize along relevant stimulus dimensions.

Black expanded Spence's model by assuming that any reduction of reward from its average or expected value would also lead to an increment in inhibition, proportional to the size of the reduction. Hence, according to this model, during the preshift period neither group in a successive contrast experiment develops any inhibition, since both unshifted and to-be-shifted subjects experience only one level of reward. Following a reduction in the level of reward, the subjects experiencing the shift would develop inhibition, which would subtract from excitation and produce a negative contrast effect. According to Black, an increase in the level of reward would only entail a rise in excitation to the control level and no positive contrast effect is predicted.

Nevin (1973), however, in considering behavioral contrast experiments, suggested a model which may be adapted to explain positive contrast. Nevin's explanation of behavioral contrast suggests that the increment in responding that occurs during the S+ stimulus is the result of a postinhibitory rebound similar to that obtained with spinal preparations when removal of an external stimulus, which caused the cessation of reflexive swinging of the hind legs, leads to a resumption of swinging at a higher rate and greater amplitude. Nevin's model interprets the enhanced responding to S+ found in positive behavioral contrast as due to a rebound from response inhibition present during the S- component.

Since inhibition seems to provide a potentially fruitful theoretical approach to the phenomenon of contrast effects, it should prove valuable to have some method of independently assessing its involvement within this paradigm. The need for independent verification becomes even more important in view of the fact that the logical status of the concept of inhibition as a viable explanation in behavioral research has been questioned. Early criticism of the concept of inhibition came from Skinner (1936), who suggested that what had been termed inhibition was merely an observed decline in the strength of a response and could be more parsimoniously accounted for as a decrease in excitation. The only data that required the concept of inhibition, according to Skinner, were those defining the phenomenon of disinhibition.

Despite Skinner's (1936) early failure to obtain disinhibition in operant behavior, other investigations have found ample evidence supporting the concept of disinhibition in operant responding (Brimer, 1970a, 1970b; Hearst, Franklin, & Mueller, 1974; Hunter, 1935; Singh & Wickens, 1968; Winnick & Hunt, 1951; Yamaguchi & Ladioray, 1962).

The purpose of the present investigation was to attempt to disinhibit the negative contrast effect that occurs in lick rate when rats are shifted from 32% to 4% sucrose solution and thereby provide an independent test of the role of inhibition in successive negative contrast. In the first three experiments, rats were given access to either a 32% or a 4% sucrose solution for 5 min per day for 10 days. Four days followed in which all subjects received 4% sucrose. In each experiment, half the rats shifted from 32% to 4% sucrose received a pulsing tone throughout the 4-day postshift period. In Experiments 2 and 3, control groups were included, the purpose of which was to interpret the apparent disinhibitory effects of the tone on negative contrast obtained in Experiment 1.

EXPERIMENT 1

Method

Subjects. Thirty naive male rats of the Holtzman strain served as subjects. The rats were individually housed and maintained at 80% of their free-feeding body weights via limiting daily food intake.

Apparatus. The apparatus consisted of three Plexiglas chambers, measuring 23 × 23 × 23 cm, which were housed in sound-attenuating boxes measuring 53 × 37 × 39 cm. In the center of the rear wall of the chamber was a 1.5-cm-diam hole, 4 cm above the floor. Outside the chamber, a graduated cylinder was mounted so that the orifice of a glass drinking spout was centered in the 1.5-cm hole, flush with the outside wall of the chamber. A wire was immersed in the solution contained in the cylinder and was connected to a drinkometer circuit that was completed through the grid floor of the apparatus each time an animal made contact with the solution.

Licks were recorded on a minute-by-minute basis for 5 min, starting with an animal's first lick. All recording was done via standard relay equipment located in an adjacent room. A CM 1819 bulb with 20 V applied was located in the center of the ceiling of the chamber and served as a houselight. A Sonalert tone generator (P. R. Mallory & Co., Model sc628-72081) was mounted next to the light.

Procedure. Rats were randomly assigned to one of three groups of 10 and then deprived to 80% of their free-feeding body weights. Water remained available at all times in the home cage. On the day prior to the first day of training, approximately 3 ml of sucrose solution was made available in the home cage in a petri dish. Each rat received the solution that was to be presented in the training situation, a procedure that gave the animals some experience with sucrose solution and thereby facilitated licking on the first day in the training apparatus. Training was conducted in the following manner. Two groups received a 32% sucrose solution (solute/solute + water) by weight. The remaining group received 4% sucrose solution and served as unshifted controls. Each animal was placed in a chamber with a graduated cylinder

in place containing the appropriate sucrose solution. Licks were recorded on a per-minute basis for 5 min, beginning with each animal's first lick. At the end of the 5-min period, the animals were removed from the chamber. The 4% solution group was randomly assigned to one of the three chambers, and subjects in this group were always run there. Subjects in the other two groups were randomly assigned to one of the remaining two chambers on an individual basis. The rats were run in the above manner every day for 10 days.

On the 11th day, the procedure changed as follows. One of the groups that had been receiving 32% sucrose was shifted to 4% (shifted no-tone group). The other group (shifted tone group) that had been receiving 32% sucrose was shifted to 4% but also received an "extra" stimulus in the form of a 4,500-Hz 90-dB tone that began 30 sec after their first lick and pulsed four times per second for the duration of the 5-min session. The unshifted control (no-tone) group was run as usual. The animals were tested in this manner over a 4-day postshift period.

The general running procedure during the postshift period was the same as during the preshift period, except that no animal in any other group was run simultaneously with those in the shifted tone groups to insure that animals in the other groups were not exposed to the tone.

Results

Since the tone began halfway through the first minute, only the data from the last 4 min of each daily session were considered in the present analysis. Terminal acquisition (Day 10) and daily postshift data for each group are presented in Figure 1. Analysis of the last preshift day revealed a significant group difference [$F(2,27) = 9.34, p < .01$]. Subsequent analysis using Fisher's lsd procedure (Federer, 1955) indicated a reliable difference only between the groups receiving 32% and the group receiving 4% ($p = .05$, two-tailed).

On the day following the shift, the lick rates of both shifted groups fell below the lick rate of the unshifted control groups, thus demonstrating a negative contrast effect. During the 4 postshift days, there was a tendency for the lick rates of both shifted groups to increase and approach the level of the unshifted control group. However, the group receiving the tone appears to have increased at a faster rate than the shifted no-tone group.

An analysis of variance performed on the postshift data provided statistical support for the above observations; a reliable Group effect [$F(2,27) = 9.77, p < .01$], Day effect [$F(3,81) = 10.09, p < .01$], and Group by Day interaction [$F(6,81) = 7.90, p < .01$] was obtained. Subsequent analysis of the Group by Day interaction using Fisher's lsd ($p = .05$, two-tailed) revealed the following: On Postshift Day 1, there was significant difference between the unshifted control group and both shifted groups but not between the two shifted groups. On Postshift Days 2 and 3, there were significant differences among all three groups: The shifted group that received the tone licked more than the shifted no-tone group, but less than the unshifted group. On Postshift Day 4, the shifted no-tone group still licked less than the unshifted group; however, the unshifted group and the shifted tone group did not differ.

Figure 1. Terminal preshift (Day 10) and mean daily postshift lick rates for the unshifted (4-4), shifted tone (32-4t), and shifted no-tone (32-4) groups in Experiment 1.

Discussion

The presentation of a tone reduced the magnitude of the negative contrast effect normally shown when rats are shifted from 32% to 4% sucrose. This effect of the tone on contrast could be interpreted as a disinhibitory effect and, therefore, the results of the present study lend support to the theoretical proposition that inhibition is involved in contrast effects (Black, 1968).

However, an alternative to the disinhibition explanation of the present data is that the tone somehow energized drinking in the shifted tone group. Therefore, a second experiment was conducted in an attempt to assess the possible energizing effects of the tone. To this end, an unshifted 4% group that received the tone in the postshift period was included.

EXPERIMENT 2

Method

Subjects. Forty naive male rats of the Sprague-Dawley strain purchased from Carworth Laboratories served as subjects. The animals were housed and maintained as in Experiment 1.

Apparatus. The apparatus was the same as that used in Experiment 1.

Procedure. In Experiment 2, four experimental groups were run. The unshifted no-tone, shifted tone, and shifted no-tone groups were similar to those in Experiment 1. In addition, an unshifted group that received the tone was included. Both unshifted groups (tone and no-tone) were assigned to one experimental chamber, and subjects in these groups were always run there. Subjects from the two shifted groups, however, were randomly assigned on an individual basis to one of the two remaining chambers. In Experiment 2, the tone began 10 sec after an animal's first lick rather than 30 sec as in Experiment 1. On the 4 postshift days, only one animal was run at a time to insure that subjects in the no-tone groups were not exposed to the tone. Except for the above-mentioned changes, the procedure and parameters were the same as in Experiment 1.

Results

Since the tone began 10 sec into the first minute, as in Experiment 1, only data for the last 4 min of each session were considered in the analysis. Terminal acquisition (Day 10) and daily postshift means for each group are presented in Figure 2. Analysis of the last preshift day revealed a significant Group difference [$F(3,36) = 4.52, p < .01$]. Subsequent analysis using Fisher's lsd procedure ($p = .05$, two-tailed) indicated that the difference was between the 32% and the 4% groups, but not between any of the groups receiving the same sucrose concentration.

Figure 2 shows that the relative lick rate of the unshifted no-tone and unshifted tone groups did not change after the introduction of the tone on the postshift days. As in Experiment 1, lick rates for both shifted groups fell below the rate exhibited by the unshifted groups. On the first day postshift, the mean of the shifted tone group was less than that of the shifted no-tone group's. On subsequent days, lick rates rose for both shifted groups and, after the first postshift day, the shifted tone group licked at a higher rate than the shifted no-tone group.

An analysis of variance performed on the postshift data showed significant Group [$F(3,35) = 11.02, p < .01$] and Day [$F(3,105) = 14.27, p < .01$] effects, as well as a significant Group by Day interaction [$F(9,105) = 5.14, p < .01$]. Subsequent tests using Fisher's lsd procedure ($p = .05$, one-tailed) revealed that the shifted tone group licked at a reliably higher rate than the shifted no-tone group on Day 2 and Day 4 postshift. At no time was there a significant difference between the unshifted tone and unshifted no-tone groups.

Discussion

The fact that the tone did not influence the 4% group indicates that nonspecific energizing properties of the tone are not responsible for the increase in lick rate seen in the shifted tone group, thus making the disinhibition hypothesis more attractive.

Another alternative hypothesis should, however, be examined before it is concluded that the observed effect is one of disinhibition. Several authors (Kelleher & Morse, 1968; McKearney, 1972) have suggested that the effect of a drug on a particular behavior will depend on the baseline rate of the behavior, a position that can be referred to as the rate dependency hypothesis. An extension of this hypothesis beyond the drug literature suggests that the effect of any manipulation on a particular behavior depends on that behavior's ongoing rate. In the present series of experiments, this raises the possibility that the effect of the tone may be dependent upon the lick rate occurring at the time of its presentation. Since the shifted groups exhibit a lick rate lower than that of the unshifted groups, this alone may be responsible

Figure 2. Terminal preshift (Day 10) and mean daily postshift lick rates for the unshifted no-tone (4-4), unshifted tone (4-4t), shifted tone (32-4t), and shifted no-tone (32-4) groups in Experiment 2.

for the differential effects of the tone on the shifted and unshifted groups. That is, the apparent disinhibitory effect may, in fact, be an energizing effect that occurs only in the shifted animals because they have a lower lick rate. The rate dependency hypothesis would predict that the effect of a tone on an unshifted group's responding at the same rate as a shifted group should be the same as the effect of the tone on the shifted group. The following experiment was conducted to examine this possibility by including an unshifted group whose lick rate was held at a lower level by maintenance on a less sweet solution.

Experiment 3 was similar in design to Experiment 1, except that two additional groups were included: One group received 4% sucrose throughout and the tone in the postshift phase; a second group received 2% sucrose throughout and the tone in the postshift phase. This latter group was included as a rate-dependency control.

EXPERIMENT 3

Method

Subjects. Forty naive male rats of the Sprague-Dawley strain purchased from Carworth Laboratories served as subjects. The subjects were housed and maintained as in Experiment 1.

Apparatus. The apparatus was the same as that used in Experiment 1, but with the following modification. An opaque black Plexiglas partition was inserted such that the test chamber was divided into two segments. One segment contained the hole in which the drinking tube was mounted and served as the test chamber for Experiment 3. The dimensions of the compartment formed in this manner were $23 \times 12 \times 23$ cm, and the drinking tube hole was 6 cm from the side wall and 4 cm from the partition.

Procedure. In Experiment 3, five groups were run with an unequal N in some groups in order to increase the number of subjects in the comparisons of interest. The groups were: unshifted no-tone ($N = 8$), unshifted tone ($N = 7$), shifted no-tone

($N = 10$), shifted tone ($N = 10$), and 2% tone ($N = 5$). The running and handling procedures in Experiment 3 were the same as in the previous experiments except that during the postshift period subjects that received the tone were run at the same time. In the preceding experiments, no subjects from any group were run simultaneously with a subject that received the tone to insure that subjects in the other chambers were not inadvertently exposed to the tone. However, it had been observed throughout the course of these experiments that subjects placed in their respective test chambers simultaneously start to lick immediately and therefore would experience tone onset at approximately the same time. Therefore, the procedure of testing subjects one at a time no longer seemed necessary.

Also, to avoid initial differences due to chance selection, group assignments were obtained by matching lick rate for the appropriate solution. Matching and group assignments were made on the day prior to the shift and were based on each subject's mean lick rates for Days 8, 9, and 10.

Tone onset occurred 30 sec after an animal's first lick, as in Experiment 1. The group that received the 2% sucrose solution was assigned to one experimental chamber, and the other groups were randomly assigned to one of the two remaining chambers on an individual basis.

Results

Figure 3 presents mean lick rate as a function of sucrose concentration and tone condition during both preshift and postshift. The data presented for preshift represent the mean of the last 3 preshift days, and the data presented for postshift represent the mean of all 4 postshift days.

An analysis of variance was performed on the preshift data after collapsing over the tone condition, which was a dummy variable at this point. The analysis reveals a significant Concentration effect [$F(2,37) = 20.12$, $p < .001$], and subsequent analysis with Fisher's *l*sd test ($p = .05$, one-tailed) showed reliable differences among all three concentration conditions; i.e., rats receiving 32% licked more than rats receiving 4%, which licked more than rats receiving 2%.

During the postshift period, an analysis of variance revealed a significant Group effect [$F(4,35) = 2.72$, $p < .05$] and subsequent analysis with Fisher's *l*sd revealed the following: Group 32-4 licked reliably less than Group 4-4 (a negative contrast effect). Group 32-4t, however, did not lick reliably less than Group 4-4 or Group 4-4t and therefore did not exhibit a reliable negative contrast effect. The *l*sd test also revealed that the 32-4t group licked at a reliably higher rate than the 32-4 group. Thus, the effect of tone presentation on the shifted group was to decrease negative contrast.

Presentation of the tone to the unshifted groups did not increase lick rate, as would be predicted from the hypothesis that the tone's effect on the shifted group was due to its nonspecific energizing properties. The 4-4t group showed no increase in licking when the tone was presented during the postshift period, and their lick rate was numerically below that of the 4-4 group. A separate analysis of variance comparing

Figure 3. Mean preshift (Days 8-10) and postshift (Days 11-14) lick rates for the unshifted no-tone (4-4), unshifted tone (4-4t), shifted tone (32-4t), shifted no-tone (32-4), and 2% tone (2-2t) groups in Experiment 3.

the preshift (Days 8, 9, 10) and postshift lick rates of the 2-2t group showed that their lick rate was significantly suppressed during the postshift period when the tone was presented [$F(1,4) = 48.92$, $p < .01$]. There was, therefore, no evidence of an energization or rate-dependent energization effect of the tone.

Discussion

The higher lick rate exhibited by the shifted tone group generally replicated the effect of the tone on shifted subjects observed in the previous experiments. Again, in Experiment 3, the groups that received the tone but were not subjected to a shift to a less concentrated solution did not show increases in lick rate, an observation that supports the disinhibition interpretation of the effects of tone presentation during the postshift period. In fact, whenever a trend could be detected for these groups, it was towards a lower rate rather than the higher rate that would be predicted by the hypothesis that the tone non-selectively energized behavior or that subjects exhibiting a low rate of licking would respond to the tone with an increase in lick rate no matter how that lower rate was engendered.

The results of Experiments 1-3, in addition to supporting Black's (1968) speculations concerning the role of inhibition in successive negative contrast, also have implications for other theoretical interpretations of incentive contrast. For example, a number of investigators (Capaldi & Lynch, 1967; Mackintosh, 1974; Spear & Spitzner, 1966) have argued that successive negative contrast may be due

to generalization decrement. That is, the shift in reward is assumed to be analogous to a change in any other stimulus attribute of the test situation, a change which generally leads to a decrement in performance. Application of this interpretation to the present data would suggest that a generalization decrement resulting from the shift from 32% to 4% sucrose accounts for the occurrence of contrast. However, the tone which should have added more generalization decrement to the shift produced an increase in licking, an effect which seems to be at variance with predictions made from generalization decrement theory.

These data, along with recent data obtained by E. D. Capaldi, Smith, and White (1977), which showed that shifts in deprivation concurrent with shifts in reward reduced negative contrast, and recent data obtained by Shanab, Kong, and Domino (1977), showing that negative contrast could be obtained with repeated shifts in reward, would appear to be substantial evidence against the hypothesis of Capaldi and Lynch (1967) that generalization decrement provides a complete account of successive negative contrast.

However, it should be noted that the disinhibitory effect, although statistically reliable, did not completely eliminate contrast. The effect of the tone tended to be somewhat greater on the second post-shift day than on the first day, and even then did not remove all evidence of contrast. This partial effect of the tone may indicate that there are multiple causes of the successive negative contrast effect obtained in the present paradigm, only some of which were influenced by the tone. One possibility for another causative agent is emotion-related behaviors, the presumed role of which has been stressed by many investigators (Cleland, Williams, & DiLollo, 1969; Crespi, 1944; Spence, 1956). How emotional responses might actually produce contrast effects is not clear. Many investigators (e.g., Bower, 1961) have mentioned the possibility that responses that compete with an ongoing instrumental response are a component of the emotional response and that it is these competing responses that actually produce the contrast effect.

In the light of the pattern of disinhibition obtained in the present experiments, the following sequence of events is suggested. The initial reaction to the changed sucrose solution is, in part, a response to novelty, and as such could be termed either generalization decrement or neophobia. Over time, during the post-shift period, an approach-avoidance conflict develops in regard to the postshift solution (a 4% solution does have potent reinforcing properties, as demonstrated by the unshifted animals). It is during this approach-avoidance period that there is an active inhibitory component in the animal's behavior, and it is during this time that the disinhibitory stimulus is effective.

EXPERIMENT 4

Thus far, we have presented evidence concerning the effects of a disinhibitory stimulus in a successive negative contrast paradigm. Negative contrast effects are also obtained in situations in which an animal is repeatedly switched between two levels of reward with each reward correlated with the occurrence of a distinctive stimulus (e.g., Bower, 1961). This type of contrast, termed a simultaneous contrast effect, has often been assumed to be caused by different factors than the apparently similar successive negative contrast. For example, Mackintosh (1974, p. 397), in considering instrumental contrast data, argues that inhibitory factors may play a more important role in simultaneous contrast than in successive contrast. A fourth experiment was conducted in order to investigate the effect of a disinhibitory stimulus in a consummatory response version of the simultaneous contrast paradigm.

Simultaneous positive and negative contrast effects are readily obtained when rats are allowed alternating periods of 1-min access to two drinking tubes containing different concentrations of sucrose solutions. With different sucrose solutions in the two tubes, the rats lick more for the high concentration than they do when both tubes contain only the higher concentration (a positive contrast effect); they lick less for the lower concentration than when both tubes contain only the lower concentration (a negative contrast effect). These bidirectional contrast effects occur when the same animals serve under both contrast and control conditions and when separate groups of animals serve as controls for positive and negative contrast (Flaherty & Avdzej, 1974; Flaherty & Largent, 1975).

In Experiment 4, the same subjects were exposed to five 4-day cycles of alternating sucrose solution. Within each cycle, a random order of one of the following sucrose concentrations was presented on each training day: 32% on the right with 4% on the left; 4% with 32%, 4% with 4%; and 32% with 32%. During Cycle 4, a tone was presented throughout the last minute of access on the left, and during Cycle 5, a tone was presented throughout the last minute on the right, thus allowing the assessment of the tone's effect on both contrast and control conditions.

Method

Subjects. The subjects were six male rats of the Sprague-Dawley strain purchased from Carworth Laboratories. They were housed and maintained as in the previous experiments.

Apparatus. Testing was conducted in a Plexiglas chamber measuring 30 × 25 × 25 cm, with a Sonalert tone generator mounted in the center of the ceiling. On one side of the chamber there were two centrally located 1.5-cm-diam holes spaced 21.7 cm apart and 4 cm above the wire-mesh floor. Two graduated cylinders, located outside the chamber, were programmed so that either cylinder could automatically be moved into a drinking position in which the orifice of the drinking spout was centered in the 1.5-cm hole, flush with the outside wall of the chamber. Pilot

lights, mounted on either side of the chamber close to the drinking access holes, were illuminated whenever the cylinder in closest proximity to that light was in the drinking position. A contact relay circuit was used to measure the licking response.

Procedure. On each test day, the rat was placed in the apparatus with only the left tube in the drinking position; it remained available for a 1-min period, starting from the time of the first lick. At the termination of this period, the left tube retracted and the right tube moved in for a 1-min period starting with the first lick. The left tube then retracted and the right tube again became available. This procedure continued for a total of three presentations of each tube.

The sucrose solutions contained in the drinking bottles were varied over five 4-day cycles. On 2 days of each cycle, both bottles contained the same solution, 32% on one day and 4% on the other. On the remaining 2 days, one bottle contained the 32% solution and the other contained the 4% solution. On one of these days the 32% solution was in the left bottle, and on the other day it was in the right bottle. Five cycles were presented with a 3-day break between each cycle. Within each 4-day cycle, the actual sequence of sucrose conditions was randomized. On each day of the fourth and fifth cycles, a pulsating tone similar to that used in the previous experiments was presented. During Cycle 4 the tone was present throughout the last minute on the left, while during Cycle 5 the tone was present throughout the last minute on the right. Tone onset occurred concurrently with the introduction of the tube containing the 4% solution.

Data recorded included (1) the number of licks made during each 1-min period, and (2) the latency of the first lick when the bottles were changed. Only the last 2 min of each session will be reported. The conditions of interest are comparisons of lick rates when (1) both bottles contained 32% (32-32), (2) both bottles contained 4% (4-4), and (3) one bottle contained 32% solution and one bottle contained the 4% solution. The data for the latter condition were obtained by averaging across positions (and therefore days) to obtain lick rate for 32% when the alternative bottle contained 4% (32-4) and lick rate for 4% when the alternative bottle contained 32% (4-32).

In addition, after the above lick rates were obtained, the data was averaged over cycles. Since during Cycle 4 the tone was presented on the left and during Cycle 5 the tone was presented on the right, averaging over these cycles with respect to solution condition and tone condition yielded a measure of the tone's effect independent of its position. Averaging over Cycles 2 and 3 was also conducted to obtain similar measures prior to tone presentation.

Results

Figure 4 presents the mean lick rate as a function of sucrose conditions during the last 2 min of each daily session averaged over Cycles 2 and 3. The rats licked more for 32% sucrose solution when the other tube contained 4% than when the other tube contained 32% [$F(1,5) = 7.19, p < .05$], and they licked less for 4% [$F(1,5) = 90.64, p < .01$] under 4-32 than under 4-4 conditions. Thus both positive and negative contrast effects occurred in Cycles 2 and 3.

Similar data obtained for Cycles 4 and 5 are presented in Figure 5. In this figure, the effect of the tone on each condition is also presented. It is clear that, as in Cycles 2 and 3, both positive and negative contrast effects occurred. An analysis of variance performed on the 32-4 and 32-32 data for Cycles 4 and 5 revealed a significant positive contrast effect [$F(1,5) = 9.16, p < .01$] but no effect of the tone

Figure 4. Mean lick rate as a function of sucrose concentration condition during the last 2 min of each daily session averaged over Cycles 2 and 3. (32-4 refers to lick rate for 32% when the alternative bottle contains 4%, etc.)

($F < 1$) or the Tone by Condition interaction ($F < 1$). A similar analysis performed on the 4-4 and 4-32 data revealed a significant *reduction* in lick rate during tone presentation [$F(1,5) = 40.48, p < .01$].

Similar analysis of the log latency data showed a reliable negative contrast effect, i.e., longer latency to start licking for 4% when switching from 32% to 4% than when switching from 4% to 4%. This effect was statistically reliable for Cycles 2 and 3 [$F(1,5) = 115.06, p < .01$] and Cycles 4 and 5 [$F(1,15) = 35.13, p < .01$].

Positive contrast, i.e., shorter latency to lick on 32% when switching from 4% than when switching from 32%, although numerically present was not statistically reliable for the latency data in either Cycles 2 and 3 or Cycles 4 and 5.

Figure 5. Mean lick rate as a function of sucrose concentration condition and tone condition during Cycles 4 and 5. (32-4 refers to lick rate for 32% when the alternative bottle contains 4%, etc.)

No effect of tone presentation was obtained in the latency measure ($F < 1.00$ in all cases).

Discussion

In this experiment, as in previous experiments using this paradigm (Flaherty & Avdzej, 1974; Flaherty & Largent, 1975), both positive and negative simultaneous contrast effects were obtained. However, unlike the results obtained with the successive contrast paradigm in the first three experiments, the novel stimulus was found to have no disinhibitory effect. When the tone was presented under negative contrast conditions (4-32), there was no increase in lick rate to the 4% solution, relative to the no-tone condition. In fact, there was a reliable decrease in lick rate correlated with tone presentation, both under contrast (4-32) and control (4-4) conditions, a result that could be termed either generalization decrement or external inhibition. The tone had no effect when the animals were licking for the 32% solution, under both contrast (32-4) and control (32-32) conditions. The latency to switch tubes proved to be sensitive to the negative contrast conditions (the animals switched more slowly going from 32% to 4% than between 4% solutions) but was not sensitive enough to reflect the reliable positive contrast effects obtained in lick rate. The latency measure was also uninfluenced by presentation of the tone, under both contrast and control conditions.

EXPERIMENT 5

Clear evidence of an apparent disinhibitory effect of a novel stimulus was obtained in three experiments involving a successive negative contrast paradigm, but no such effect was obtained when the tone was superimposed on a simultaneous negative contrast effect in Experiment 4.

One reason for this difference may lie in the fact that in the simultaneous study the subject received extensive exposure to the disparate sucrose concentrations prior to receiving the tone, whereas, in the successive experiment, the tone was presented on the first day of exposure to the lower concentration. Given these procedural differences, it seems possible that "active" inhibition may have been present early during the exposure to the disparate sucrose concentrations but was replaced by a more passive mechanism which mediated the negative contrast effect after extended training. The early stages of simultaneous contrast, therefore, may be subject to disinhibition while the latter stages are not. In any event, it appeared to us that simultaneous contrast may, in the initial sessions, be more like successive contrast than it is after extended training has occurred. In order to test this possibility, an experiment was conducted that was similar to Experiment 4, but in

which one group of subjects received the tone "early" in training and another group received the tone "late." Also, in contrast to Experiment 4, in the present experiment concentration conditions were varied between, rather than within subjects. That is, some subjects received 32% with 4% while others received only 4%. The 32% with 32% condition was eliminated, since the assessment of positive contrast was not necessary.

A final difference between the present experiment and Experiment 4 was that tone onset occurred simultaneously with the initiation of drinking during the third minute of access to the 4% solution rather than with the availability of the tube.

Method

Subjects. Thirty-six naive male albino rats of the Sprague-Dawley strain served as subjects. The subjects were housed and maintained as in Experiment 1.

Apparatus. The apparatus was the same as that employed in Experiment 4.

Procedure. The subjects were assigned to one of the following six groups ($N = 6$ in each group) by matching on 80% body weight: (1) The 32-4t early group received both 32% and 4% sucrose solutions and also received a tone during their last minute of access to 4% on Days 1 and 2 of testing; (2) the 32-4t late group received both 32% and 4% on all 4 test days, but received a tone only during their last minute of access to 4% on Days 3 and 4 of testing; (3) the 32-4 group received both 32% and 4% on all 4 days of testing but were not exposed to the tone; (4) the 4-4t early group received 4% in both bottles and were exposed to the tone on Days 1 and 2 of testing in the same minute of access as the subjects in the 32-4t early group; (5) the 4-4t late group received 4% in both bottles on all 4 days of testing and were exposed to the tone on Days 3 and 4 of testing in the same minute of access as the subjects in the 32-4t late group; (6) the 4-4 group received 4% in both bottles on all 4 days of testing but were not exposed to the tone. The position (right or left) in which the different sucrose concentration conditions and tone presentations occurred was counterbalanced in all groups. Each group was given 1 day of pretraining and 4 days of testing, except for Groups 32-4t early and 4-4t early, which were run only on the first 2 days of testing.

On the day prior to pretraining, subjects received approximately 3 ml of sucrose solution in a petri dish in their home cage. Subjects that were to receive 4% during testing were given 4% and subjects that were to receive both 32% and 4% were given 3 ml of a mixture of half 32% and half 4%. On the pretraining day, the subjects were run in the apparatus with the sucrose solution they had received on the previous day. Testing was conducted on the next 4 consecutive days, during which the running procedure was similar to that of Experiment 4. As in Experiment 4, the 1-min access periods were timed starting with the first lick, and all training sessions began with the left tube in the drinking position and the right tube retracted. The tone started with the animal's first lick during the minute in which it was scheduled and continued throughout that minute. The parameters of the tone were the same as those employed in Experiment 4.

Results

Mean licks per minute for the 4% solution as a function of minute of access and group is presented in Figure 6. Data for the groups that received the tone early during testing (Days 1 + 2) are presented

Figure 6. Mean licks per minute as a function of group and minutes of access to the 4% solution. Each panel represents 1 day of testing. Groups 32-4t and 4-4t received the tone in Minute 3 only.

in the two top panels, and data for the groups that received the tone late in testing (Days 3 + 4) are presented in the two bottom panels. Two subjects in the 4-4t early group made less than 20 licks on Day 1 of testing, and their data were therefore dropped from the analysis and presentation of results. Separate analyses of variance were performed on each day of testing.

An examination of the figure indicates that, at all stages of testing, the effect of the tone was to produce a decrement in lick rate; there was no evidence of disinhibition. The results for each panel of the figure will be considered in detail below.

On Day 1, there was a substantial negative contrast effect: the lick rates of the animals receiving both 4% and 32% were reliably lower for the 4% solution than animals that received 4% in both tubes [$F(1,18) = 32.19$, $p < .01$]. The effect of the tone can be seen by comparing the lick rates of the 4-4t early and 32-4t early groups with that of the 4-4 and 32-4 groups in Minute 3. All four groups exhibited a significant decline in lick rate from Minute 2 to Minute 3 [$F(1,18) = 10.10$, $p < .01$] with an apparently larger decline exhibited by the groups that received the tone; this decline, however, was not statistically reliable (Tone Condition by Minute interaction, $F < 1$).

Thus, the effect of the tone on the early animals, both contrast and control, was to produce a nonsignificant decline in lick rate, rather than an increase that would be expected if disinhibition had occurred.

The degree of contrast demonstrated by the tone groups (32-4t vs. 4-4t) was less than that demonstrated by the no-tone animals in Minute 3 (Scheffé test; Federer, 1955; $t_{\text{obs}} = 4.46 > t_{\text{crit}} = 2.47$, $p < .05$). However, this difference was clearly not related to an effect of the tone on the shifted animals; rather, it was related to the generalization decrement-like effects of the tone superimposed on a *pretone* (Minute 2) difference in the lick rates of the control groups (Group 4-4t < Group 4-4, in Minute 2 by Scheffé test).

The results obtained on the second day of testing were similar to, but clearer than, those obtained on Day 1.

On Day 2, a negative contrast effect was again obtained [$F(1,18) = 48.74$, $p < .001$], and the effect of introducing the tone in Minute 3 was again one of lowering lick rate, both in contrast and control animals. However, this effect of the tone was not statistically reliable (Tone Condition by Minute interaction, $F < 1$).

The data for the late animals (tone presented on Days 3 and 4 of testing) are presented in the bottom two panels of Figure 6. Analysis of Day 3 data revealed a reliable negative contrast effect [$F(1,20) = 20.66$, $p < .001$], and a significant Tone Condition by Minute by Sucrose Condition interaction [$F(1,20) = 7.83$, $p < .05$]. Subsequent analysis of this term using Scheffé's procedure showed that, in Minute 3, the lick rate of the 4-4t group was lower than the lick rate of the 4-4 group ($t_{\text{obs}} = 3.08 > t_{\text{crit}} = 2.08$); in Minute 2, however, no reliable differences existed between these two groups ($t_{\text{obs}} = 1.13 < t_{\text{crit}} = 2.08$), indicating that the tone produced a reliable reduction in licking. The results of Day 4 of testing were similar to those obtained on Day 3. A significant depression in lick rate was obtained in the group receiving 4% with 32% compared to the groups receiving only 4% [$F(1,20) = 47.09$, $p < .001$]. Again, a reliable Tone by Minute by Sucrose Condition interaction was obtained [$F(1,20) = 6.98$, $p < .05$]. Subsequent analysis with the Scheffé procedure again revealed a lower lick rate in the 4-4t group when compared to the 4-4 group ($t_{\text{obs}} = 3.43 > t_{\text{crit}} = 2.08$) in Minute 3, a difference that did not exist in Minute 2 ($t_{\text{obs}} = .55 < t_{\text{crit}} = 2.08$). As on Day 3, no significant effects of the tone were obtained in the 32-4t group.

Discussion

Experiment 5, like Experiment 4, showed that the presentation of a novel stimulus during the occurrence of a simultaneous negative contrast effect does not lead to a reduction in that contrast effect. In fact, any effect that the tone did have was to produce

a generalization decrement-like effect of lowering lick rate, a result that was particularly apparent in the control animals.

This experiment also indicated that the effects of presenting the tone early during simultaneous contrast training are substantially the same as presenting the tone after extended training. This result renders it unlikely that the failure to obtain disinhibition in Experiment 4 was due to the contrast animals' extended experience with the 4% solution. In addition, this experiment indicates that the failure to find disinhibition of simultaneous negative contrast in Experiment 4 was not due to the within-subjects nature of the design used in that experiment, nor was it due to the fact that tone onset occurred prior to the initiation of drinking.

Another possible reason for the different effects obtained with the tone in the two contrast paradigms might relate to procedural differences in tone presentation rather than to any fundamental differences in the contrast paradigms per se. For example, in Experiments 1-3, the tone was presented some time after the animals began to drink (either 10 or 30 sec) and remained on for the duration of the 5-min session. In Experiments 4 and 5, however, tone onset occurred either before licking was initiated or simultaneously with the onset of licking in the third minute of access to the 4% solution. This difference in procedure was dictated, to a large extent, by differences in the nature of the contrast paradigms themselves and by our desire to present the tone at a time when a contrast effect (and possibly inhibition) would be present. Observations we have made in previous successive contrast experiments indicated that rats did not demonstrate any apparent contrast when first exposed to the 4% solution. Instead, the rats tend to drink steadily for some 20-30 sec before the first pause. From this point on, licking tends to be at a declining or low level, reflecting the contrast. Hence, the introduction of the tone in the successive experiments was delayed, so that tone onset would occur at a time when contrast was being demonstrated.

When the simultaneous procedure is used, the contrast is usually clear by the third minute of access to the less preferred solution (Flaherty & Lagen, 1975). Hence, the tone was introduced coincident with the availability of the less preferred solution during the third minute of access (when a contrast effect would be present).

It has been suggested (Mellgren, Note 1) that the pattern of results obtained in these experiments might occur if the tone produced a generalization decrement effect during the first minute in which it was applied and a disinhibitory effect thereafter (only the successive groups received the tone "thereafter"). Examination of the minute-by-minute lick rates obtained from the successive contrast ani-

mals in Experiments 1-3 was somewhat compatible with Mellgren's suggestion. In Experiments 1 and 3, the tone groups tended to show clear disinhibitory effects from Minute 2 through Minute 5 on Day 1 postshift and in all 5 min of Day 2 postshift. In the first minute of Day 1 in these two experiments, there was a slight, nonreliable, decrement in lick rate in the animals that received the tone. In Experiment 2, the animals that received the tone licked at a lower rate than the nontone animals throughout the first day and in the first minute of the second day. Thereafter, they licked at a higher rate.

In order to investigate the possibility that disinhibitory effects might be obtained in the simultaneous paradigm if the tone was presented for a longer period of time, a sixth experiment was conducted.

EXPERIMENT 6

While in Experiments 4 and 5 the tone was presented only during the third minute of access to the 4% solution, in the present experiment the tone was presented during the second half of the first minute of access and throughout the second and third minutes. This extended presentation of the tone was thought to be sufficient to answer the question of whether or not disinhibitory effects would be obtained in the simultaneous paradigm if the tone was presented for a longer period of time. Since we were primarily interested in the effect of the tone on licking for the 4% solution when the other tube contained 32%, and since presenting 4% in conjunction with 32% has always resulted in a large simultaneous negative contrast (Flaherty & Avdzej, 1974; Flaherty & Lagen, 1975; Flaherty, Lombardi, Kapust, & D'Amato, 1977), a contrast control group that received only 4% was not included in the present experiment.

Thus there were two groups of animals in this experiment; those that received a tone during exposure to the 4% tube but not during access to the 32% tube, and those that received the same sucrose conditions but no tone. All animals were trained for 2 days without the tone and then tested for an additional 2 days during which the tone conditions were imposed.

Method

Subjects. The subjects were 10 male Sprague-Dawley rats purchased from Blue Spruce Animal Farms. They were housed and maintained as in Experiment 5.

Apparatus. The apparatus was the same as that employed in Experiment 5.

Procedure. On the day prior to the first training day, all subjects were given 3 ml of a mixture of half 4% and half 32% sucrose solution in a petri dish in their home cage. All subjects were then given 2 days of training with 32% in the left tube and 4% in the right tube. The left tube was always in the drinking position at the start of each rat's daily session, and each session allowed the rat three alternating periods of 1-min access to the

left and right tubes, with each minute of access being timed from the rat's first lick on that tube. Licks during each minute were recorded as in Experiments 4 and 5.

After 2 days of training, the rats were divided into two groups ($N = 5$ each) matched on lick rate for the 4% solution on the second training day. On Days 3 and 4, one of these groups (Group 32-4t) received a tone of the same intensity parameters employed in the previous experiments. The tone began halfway through the first minute of access to the 4% solution and continued until that tube was withdrawn. The tone was also presented for the second and third minutes of access to 4%, but during these minutes the tone began with the rat's first lick and continued until the tube was withdrawn. The remaining group (Group 32-4) received no tone on Days 3 and 4.

Results

Table 1 presents mean lick rate for Groups 32-4 and 32-4t as a function of minutes of access for Days 2, 3, and 4 of training.

An analysis of variance performed on the data from Day 2 revealed a significant concentration effect [$F(1,8) = 147.13, p < .001$], which is apparent in Table 1. Group, which was a pseudovariable at this point, was not significant ($F < 1$), nor were there any significant interactions between group and concentration or minute.

On Day 3 of testing, Group 32-4t received the tone for the first time, but, as can be seen in Table 1, there was no increase in lick rate when the tone was presented in any of the access periods. The only place where there is an apparent difference between the groups is in Minute 1, where the lick rate of Group 32-4t seems lower than that of Group 32-4; however, an analysis of variance performed on data from Day 2 did not find any statistically reliable differences between the two groups. A significant Concentration [$F(1,8) = 142.28, p < .001$], Minute [$F(2,16) = 14.33, p < .001$], and Concentration by Minute interaction [$F(2,16) = 12.43, p < .001$] was revealed by the analyses; however, none of these effects interacted with group.

The results of Day 4 were similar to those of Day 3; again, no change in lick rate was found when the rats in Group 32-4t were exposed to the tone ($F < 1$).

GENERAL DISCUSSION

Experiments 1-3 demonstrated that the presentation of a tone during the occurrence of a successive negative contrast effect in lick rate led to a reduction in contrast. Various control procedures indicated that the rise in lick rate (i.e., reduction in contrast) produced by the tone was not due to an energizing effect, or to a rate-dependent energizing effect, of the tone. This pattern of results is consistent with Brimer's conclusion, derived from his operant studies, that "disinhibition will be manifested only when a response which was once at a higher level of probability has been reduced to some critical lower level of probability" (Brimer, 1972, p. 224).

Experiments 4-6 demonstrated that the presentation of the same tone during the occurrence of simultaneous negative contrast did not have a disinhibitory effect. In fact, any effect that the tone did have in this paradigm was one of reducing lick rates in both contrast and control animals, a result that could be termed either generalization decrement or external inhibition. In addition, these experiments indicated that the failure to find disinhibition in the simultaneous task was not related to the amount of experience that the animals had in the task prior to the presentation of the tone, nor, apparently, to duration of tone presentation.

We should now consider possible reasons for the different effects of the tone obtained in the two contrast paradigms. Simultaneous and successive contrast paradigms are different in a number of procedural dimensions. In the simultaneous paradigm, there are multiple shifts, with a short time period between each shift, and there are differential stimuli correlated with the two levels of reward. In comparison, the successive paradigm typically involves a single shift, usually with a relatively long time period between exposures to the two levels of reward, and there are no differential cues correlated with the two levels of reward.

In addition to the different effects of the tone on the two paradigms in the present series of experi-

Table 1
Mean Licks per Minute of Access to 32% or 4% Sucrose Solution for Groups 32-4 and 32-4t on Days 2, 3, and 4 of Experiment 6

Group	Concentration	Day 2			Day 3			Day 4		
		Minute			Minute			Minute		
		1	2	3	1	2	3	1	2	3
32-4	32%	285	275	269	252	313	336	349	309	298
	4%	27	25	20	42	23	4	30	23	15
32-4t	32%	302	340	233	229	324	341	317	363	367
	4%	31	19	22	27	23	5	28	4	14

Note—Group 32-4 received the tone for half of Minute 1 and throughout Minutes 2 and 3 starting on Day 3 of training.

ments, other studies have also indicated functional differences between the two contrast paradigms. For example, a number of studies have indicated that simultaneous (and behavioral) contrast are more likely to occur in fish and turtles than is successive negative contrast, which apparently has not been demonstrated in members of these classes (Burns, Woodard, Henderson, & Bitterman, 1974; Cochrane, Scobie, & Fallon, 1973; Gonzales, Ferry, & Powers, 1974; Gonzales & Powers, 1973; Pert & Gonzales, 1974).

Whether the contrast effects obtained with these two procedures are due to different causative mechanisms has been a matter of some speculation. For example, both Bitterman (1976) and Spear (Note 2) have argued that the opportunity for multiple comparisons, and the short time period between comparison, available in the simultaneous paradigm might enhance the contribution of sensory-perceptual factors relative to the successive paradigm. While there is no direct evidence relevant to a sensory-perceptual interpretation of simultaneous contrast, the failure to obtain disinhibition of simultaneous negative contrast in Experiments 4, 5, and 6 would be compatible with such a notion. In other words, the response to the 4% solution may simply involve a hedonic shift; it tastes less sweet to the comparison animals than to the control animals, and the lowered response rate indicative of contrast reflects this hedonic difference and does not involve an active inhibition of behavior on the part of the contrast animals.

However, the failure to obtain disinhibition of simultaneous contrast could also be related to Brimer's empirical generalization mentioned earlier. That is, Brimer found that disinhibition of a low response rate is obtained only when that response had previously occurred at a high rate (Brimer, 1972). The data obtained in the present experiments are clearly consistent with this generalization; the lick-rate response disinhibited in Experiments 1-3 was a low-rate response that had previously been at a high rate. The various low-rate control groups used in these experiments had not previously been responding at a high rate and were not subject to apparent disinhibition. In the last three experiments, where disinhibition was not obtained, the lick rate for the 4% solution when presented in conjunction with the 32% solution was never at a high rate.

Thus, the results obtained in the six experiments presented here are consistent with the possibility that successive negative contrast involves the active inhibition of the licking response on the part of the shifted animals, but that a simultaneous negative contrast does not involve such active inhibition.

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(Received for publication June 3, 1977;
revision accepted September 14, 1977.)