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Can contextual cues control consummatory successive negative contrast? ☆

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Abstract

Rats exposed to incentive downshift show behavioral deterioration. This phenomenon, called successive negative contrast (SNC), occurs in instrumental and consummatory responses (iSNC, cSNC). Whereas iSNC is related to the violation of reward expectancies retrieved in anticipation of the goal (cued-recall), cSNC involves reward rejection and may require only recognition memory retrieved at consumption. The three within-subject experiments reported here suggest that cued-recall memory can also operate in cSNC under some conditions. A small but significant cSNC effect was obtained when animals were exposed to the conditioning context during an average 90-s interval before the introduction of the incentive (either 16% or 2% sucrose solutions), rather than being given immediate access to the sucrose upon entry into the context (Experiment 1). Neither simultaneous contrast (Experiment 2) nor simple sequential effects (Experiment 3) contribute to this within-subject version of cSNC. These results suggest that cSNC can be shifted to a cued-recall mode with appropriate training parameters.

Keywords: Incentive contrast; Contextual conditioning; Cued-recall memory; Rats

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Rats rapidly learn to locate and consume a reward that is highly preferred because of its quality or quantity. After such experience, a downshift in incentive value typically leads to a deterioration of behavior beyond the level of a control condition in which rats have received the downgraded reward in all trials. This phenomenon is called instrumental successive negative contrast (iSNC) when it occurs in anticipatory instrumental situations (Crespi, 1942; Elliott, 1928) and consummatory successive negative contrast (cSNC) when it occurs as a result of direct contact with the reward (Vogel, Mikulka, & Spear, 1968). These two procedures usually respond in similar manner to a variety of behavioral and physiological manipulations (see Flaherty, 1996). However, several lines of research show that they engage different mechanisms. For example, whereas iSNC does not occur in the runway when incentive downshift involves a change in the concentration of sucrose solutions, cSNC can be readily obtained in the same animals in terms of licking responses in the goal box (Flaherty & Caprio, 1976; Sastre, Lin, & Reilly, 2005). Furthermore, damage to several brain areas, including the hippocampus, septum, enthorinal cortex, and nucleus accumbens, disrupts iSNC after a downshift in the number of food pellets, but does not affect cSNC after a downshift in sucrose concentration (e.g., Flaherty, Coppotelli, Hsu, & Otto, 1998; Leszczuk & Flaherty, 2000). In general, experiments that illustrate this dissociation suggest that cSNC is more readily obtained than iSNC.

An obvious procedural difference suggests a possible source for the dissociation between iSNC and cSNC. In a typical iSNC experiment, rats receive a single trial per day in a runway apparatus and the speed of running is the main dependent variable (for an example of multiple trials per day, see Flaherty et al., 1998). Thus, evidence of iSNC comes entirely from the animal's ability to anticipate the properties of the reward as it runs toward the goal box. This anticipation of incentive devaluation implies cueing by contextual cues previously paired with incentive downshift, usually a day earlier. This is not true for consummatory situations, in which rats drink the downshifted sucrose solution for a few seconds before rejecting it during postshift trials. For example, rats show no changes in the latency to the first licking response after incentive downshift (Flaherty, Hrabinsky, & Grigson, 1990). Furthermore, a contextual shift from preshift to postshift does not disrupt cSNC (Grigson, Spector, & Norgren, 1993). These results suggest that cSNC does not depend on the violation of expectancies associatively reactivated via cued-recall, but rather on the animal's ability to recognize the change in incentive magnitude, probably triggered by similar stimulus elements between the pre- and postshift sucrose solutions. Papini and Pellegrini (2006) suggested that whereas iSNC is based on *cued-recall memory*, cSNC is based on *recognition memory*. The distinction between cued-recall and recognition memory is supported by substantial psychological and neurobiological evidence (Cabeza et al., 1997; Hasselmo & Wyble, 1997; West & Krompinger, 2005), and could provide a guide to understand the dissociation between iSNC and cSNC described above.

The hypothesis that cSNC depends on recognition memory does not imply necessarily that consummatory behavior cannot be modulated by expectancies associatively reactivated by cues paired with incentive downshift. The failure of changes in contextual cues to affect cSNC may be a consequence of training procedures, rather than of some intrinsic limitation of consummatory behavior. For example, in the contextual shift experiments reported by Flaherty et al. (1990), rats were placed in the conditioning box with the solution already available. Thus, immediate exposure to the sucrose solution may have overshadowed processing of contextual stimuli. A similar deficit has been reported in contextual fear conditioning when the delivery of electric shocks occurs as soon as the

rat is exposed to the context—the so-called immediate-shock deficit (Fanselow, 1986). Higher levels of contextual fear are obtained when a longer interval is interpolated between the moment in which the rat is placed in the context and the moment in which the first electric shock is administered. Thus, the opportunity to process contextual cues before contact with the reinforcing event may be critical to facilitate the modulation of cSNC by anticipatory processes. In addition, training conditions that emphasize the importance of contextual cues for predicting the upcoming reward may be necessary for contextual cues to control behavior. Flaherty et al. (1990) introduced a contextual shift only in the postshift phase—after more proximal cues may have gained greater associative strength. Exposure to both contexts during preshift trials, each paired with a different solution, may train the rat to discriminate between contexts as predictors of the upcoming reward.

The goal of the present experiments was to evaluate the possibility that contextual stimuli can modulate the cSNC effect. Experiment 1 introduced two procedural features designed to promote contextual control that differed from the conventional procedure: (1) Extending the time in the context before presenting the sucrose solution (thus favoring the processing of contextual stimuli) and (2) providing extensive exposure to both contexts prior to the downshift event (thus encouraging discriminative control by contextual stimuli). The remaining two experiments assessed the possible contribution of sequential effects arising from the use of a within-subject design, including the possibility of simultaneous contrast effects (Experiment 2) and a shift in the sequence of sucrose concentrations during postshift trials (Experiment 3).

Experiment 1

In the present experiment, two groups of rats received training in two distinct contexts, one paired with 16% sucrose solution and the other with 2% sucrose solution, in a pseudorandom order across days. In one group, rats were exposed to the context for an average of 90 s before the sipper tube was inserted automatically into the conditioning box, whereas in the other group, the tube was available immediately upon entry into the conditioning box. After 15 trials of exposure to each context, the 16% sucrose context was downshifted to 2% sucrose in both groups, whereas the 2% sucrose context continued to be paired with 2% sucrose. The questions of interest were, first, whether consummatory behavior in the downshifted context would undershoot the level obtained in the unshifted context and, second, whether the contrast effect would be stronger in the group exposed to the context for 90 s before each trial than in the group given immediate exposure to the solution.

Method

Subjects

Eighteen experimentally naïve male Long–Evans rats served as subjects. Animals were bred in the TCU vivarium under a 12:12 h light:dark cycle (lights on at 07:00 h) and free access to water at all times. Rats were housed in wire-bottom cages and food-deprived until they reached an 81–85% of their ad lib body weight (mean ad lib weight: 268 g). Training started when rats were approximately 3 months old and was administered during the light phase of the daily cycle.

Apparatus

Training was conducted in four conditioning boxes (MED Associates, Vermont). Two contexts, called X and Y, were created by arranging differences in visual, spatial, tactile, and olfactory cues in the same conditioning boxes. Fig. 1 shows the visual and spatial differences of these two contexts. *Context X* was the regular conditioning box. It was constructed of aluminum and Plexiglas and measured 29.3 cm in length, 21.3 cm in height, and 26.8 cm in width. The floor was made of steel rods, 0.4 cm in diameter and 1.6 cm apart, running parallel to the feeder wall. A tray located underneath the floor and filled with newspaper bedding provided olfactory cues. *Context Y* was created by inserting a metal box inside the regular conditioning box. This insert was 28.2 cm in length, 19.5 cm in height, and 23.6 cm in width. The metal insert had a smooth floor, and the wall opposite to that of the sipper tube was round (i.e., U shaped). All around the inside perimeter of this insert, the walls were painted with black and white vertical stripes (2.5 cm wide). The bedding tray was removed.

These contexts also had a series of common features. Against the feeder wall was an elliptical hole, 1 cm wide, 2 cm high, and 4 cm from the floor, through which a sipper tube, 1 cm in diameter, could be inserted. When fully inserted, the sipper tube protruded 1 cm into the box. In context Y, the insert had a circular hole of 3 cm in diameter that coincided with the sipper tube. A house light (GE 1820) located in the center on the ceiling, provided diffuse light for both contexts. Each conditioning box was placed in a sound-attenuating chamber that contained a speaker to deliver white noise and a fan for ventilation. Together, the speaker and fan produced noise with an intensity of 80.1 dB (SPL, scale C). A computer located in an adjacent room controlled the presentation and retraction of the sipper tube. The computer also detected contact with the sipper tube by way of a circuit involving the steel rods in the floor.

Procedure

All animals were exposed to contexts X and Y according to a sequence derived from Gellermann (1933) series. A single trial per day was administered. Rats were randomly assigned to one of two groups. Within each group, the pairing of each context to each of the two sucrose solutions was counterbalanced (half of the rats in each group were

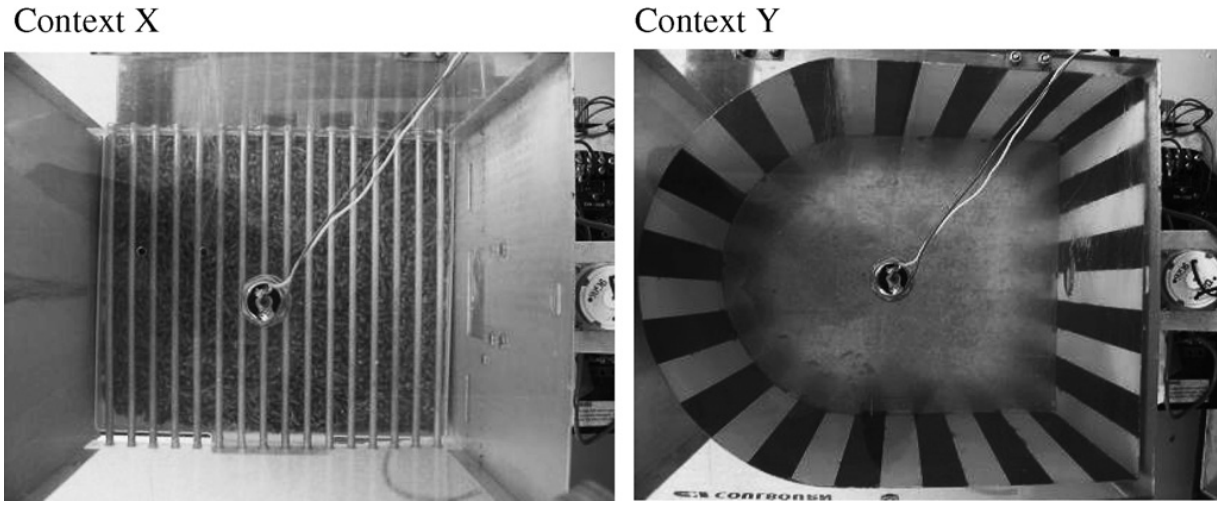

Fig. 1. Contexts X and Y used in the present experiments. See text for details.

exposed to X-16%, Y-2%, and the rest to X-2%, Y-16%). Sucrose solutions were prepared by mixing w/w commercial sugar with distilled water (e.g., the 16% solution was prepared by mixing 16 g of sucrose for every 84 g of distilled water). These particular concentrations were used, rather than the more common 32% and 4% sucrose solutions, because the 16-2 and 32-4 downshifts tend to produce the same degree of consummatory suppression, but greater differentiation of behavior during the preshift trials (Papini & Pellegrini, 2006). Rats were moved from the housing room to a holding room in a transport rack that fit up to 16 cages. For training, the transport rack was moved to the training room, where rats were placed inside the conditioning boxes. Rats were run in squads of 4, with the order of squads varying across days. Each rat was always trained in the same conditioning box. For Group 90 ($n = 10$), each trial started with an average pretrial interval of 90 s (range: 70–110 s). At the end of this interval, the bottle dispensing the sucrose solution was automatically inserted into the conditioning box and the rat was free to start drinking. For Group 0 ($n = 8$), the bottle dispensing the sucrose solution was already inserted when the rats were placed in the conditioning box. For all animals, the bottle was available for 5 min starting from the first contact with the sipper tube. At the end of the trial, the sipper tube was automatically withdrawn and the house light was turned off after a 10-s period, ending the trial. The rat was placed in its cage and returned to the holding room. When all the rats in the transport rack were run, the entire group was moved back to the housing room. Before the start of each trial and after all rats completed their daily training, conditioning boxes were cleaned with a damp paper towel and feces were removed when present.

There were a total of 30 preshift trials, 15 in each context and with access to each of the two sucrose solutions. The actual preshift sequence of 16% (shifted context, S) and 2% (unshifted context, U) trials for the initial 28 trials was: S U S S U U S U S U U S U S S U S U S U S S U U S U S U. Pilot research suggested that not all trial sequences during the downshift period resulted in similar levels of consummatory suppression. Thus, only three sequences were implemented in the present experiment (the vertical bar denotes the downshift): S U|S U (4 rats in each group), S U|U S (three rats in Group 90 and two in Group 0), and U S|U S (three rats in Group 90 and two in Group 0). Thus, the sequence U S|S U, which failed to produce evidence of cSNC in pilot studies, was not included in this experiment (this issue is addressed in Experiment 3 and General discussion). The remaining three variations were balanced across groups to avoid the possibility that the findings would be attributable to a particular downshift sequence. After the second postshift trial, the remaining trials were the same for all rats until they completed five postshift trials in each context: S U S S U U S U. During these postshift trials, all rats received access to the 2% solution in both contexts.

The dependent variable was goal-tracking time, defined as the total amount of time in contact with the sipper tube, measured in 0.05-s units and with a maximum of 5 min. Under the conditions used in the present experiments, the more typical licking rate measure tends to yield variable scores both across subjects and across trials for a given subject. Goal-tracking time has also been shown to correlate positively and significantly with the amount of fluid ingested during 5-min long trials (Mustaca, Freidin, & Papini, 2002) and to produce essentially the same results with either fluid consumption (Papini, Mustaca, & Bitterman, 1988) or licking rate (Riley & Dunlap, 1979). Goal-tracking time has also shown some of the same problems exhibited by licking rate, including yielding higher scores for the lower sucrose concentration than the higher, or nondifferential scores during

preshift trials (e.g., Flaherty, 1996, p. 56, for licking, and Wood, Daniel, & Papini, 2005, for goal-tracking time). Scores were subjected to nonparametric statistical tests. Mann–Whitney tests were used for pairwise between-subject comparisons and Wilcoxon signed-rank tests for pairwise within-subject comparisons. All tests were two-tailed and the alpha value was set at the 0.05 level.

Results and discussion

The preshift performance of both groups in each of the two contexts is shown in Fig. 2. Goal-tracking times increased steadily in the 16% contexts in both groups, more so than in the 2% context. The effect of incentive magnitude was analyzed by comparing the overall means for all the preshift trials in each context. There was a significantly higher average preshift performance in the 16% than in the 2% context for both groups (Zs > 2.49; ps < 0.02).

Postshift performance was analyzed by matching subjects in terms of the position of each trial relative to the incentive downshift. Fig. 3 shows the results for each group separately. In Group 90, performance in the shifted context during the first trial after the downshift dropped below the level of the unshifted context in the equivalent trial ($Z = 2.29$; $p < 0.03$), and subsequently recovered to match the level of the unshifted context (Zs < 0.87; ps > 0.38). In Group 0, consummatory performance in the shifted context dropped to the level of the unshifted context in all postshift trials, including the second trial (Zs < 0.29; ps > 0.77).

A small but reliable cSNC effect was observed when rats had the opportunity to process contextual stimuli for an average of 90 s before having access to the sucrose solution, compared to a condition in which access to the sucrose solution was immediate upon entry into the conditioning box. This cSNC effect was significant, but small in strength. It is unclear whether the small size of this effect could be attributed to the use of 16% and 2% sucrose. In within-subject downshifts (but without context manipu-

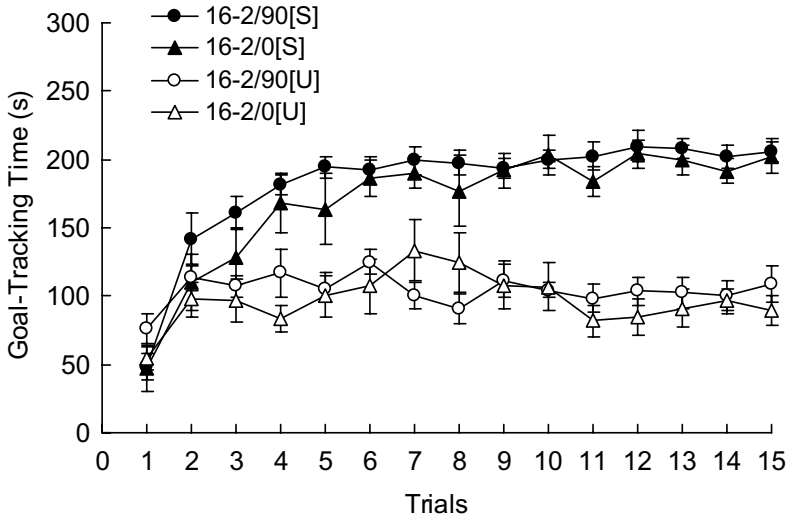

Fig. 2. Goal-tracking time (±*SEM*) during the 15 preshift daily training trials in each context. 16-2 refers to the concentration (16% and 2%) of the sucrose solution received in each of the two contexts. 0: immediate availability of sucrose upon entering the conditioning box. 90: an average pretrial interval of 90 s before the sucrose became available. S: shifted context. U: unshifted context.

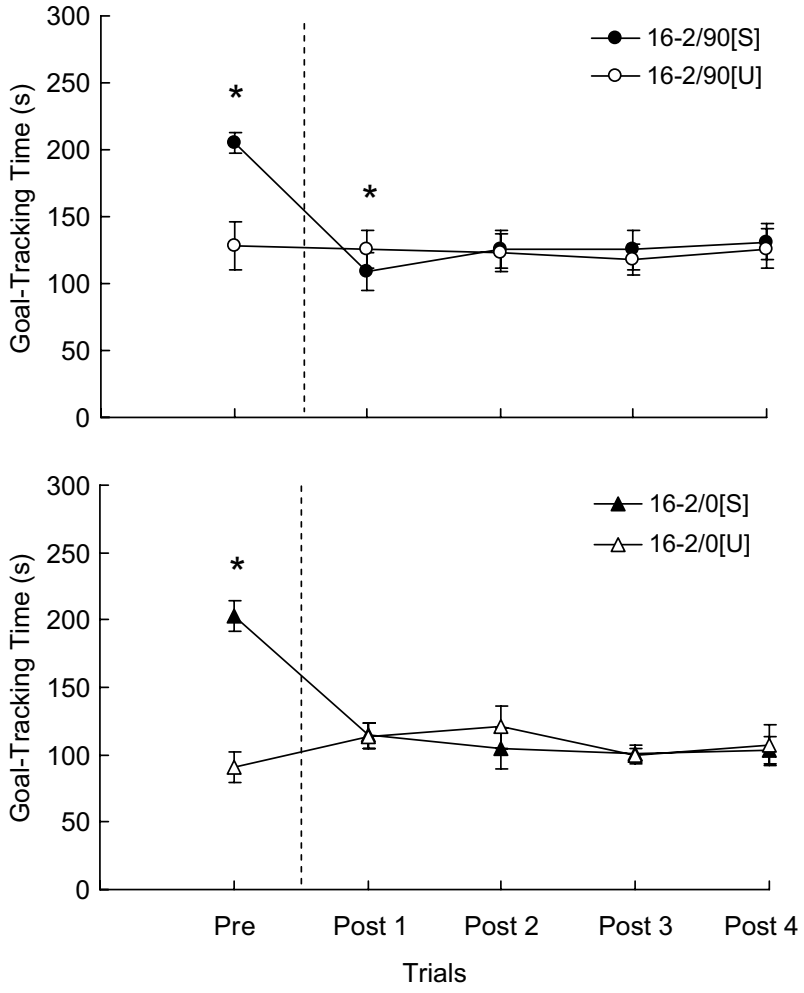

Fig. 3. Goal-tracking time (±*SEM*) during the postshift trials plotted separated for the group receiving access to sucrose after 90 s (Group 16-2/90, top panel) or immediately upon entrance in the conditioning box (Group 16-2/0, bottom panel). S: shifted context. U: unshifted context. Trials were equated across subjects to correspond to the last preshift trial (Pre) and to each of four postshift trials. Stars denote statistically significant effects.

lations), 16-2 and 32-4 downshifts produced similar levels of consummatory suppression, prompting the hypothesis that cSNC depends on the ratio of the pre- and postshift sucrose concentrations, rather than on their absolute difference (Papini & Pellegrini, 2006). The small size of the effect may be related to the context discrimination procedure. In this procedure, the early exposures to the 16% and 2% solutions may have effectively been analogous to a partial reinforcement procedure (to be precise, they may be analogous to a variable magnitude training procedure; see Amsel, 1992). Strict partial reinforcement in which rats receive a pseudorandom sequence of trials with access to 32% sucrose and water is known to attenuate cSNC after a downshift to 4% sucrose (Pellegrini, Muzio, Mustaca, & Papini, 2004). If the small size of the present cSNC effect is related to a failure to discriminate the two contexts early in training, then treatments that facilitate discrimination should increase the within-subject cSNC effect. One such treatment is nonreinforced preexposure to the contexts, a procedure known to facilitate subsequent discrimination learning—the so-called perceptual learning effect (e.g., Prados, Artigas, & Sansa, 2007).

Nonetheless, this result provides support for the hypothesis that cSNC can be shifted from a recognition to a cued-recall task by adjusting training parameters. Notice, however, that in this particular situation exposure to the context modulates the consummatory response, rather than the anticipatory response measured in iSNC situations. In the language of Pavlovian conditioning, one may describe the present effect in terms of contextual modulation of the unconditioned response to the unconditioned stimulus (Domjan, 2005). Still, to the extent that such modulation is detectable, the implication is that contextual cues elicit an expectancy of 16% sucrose whose violation leads to a transient, but detectable, level of rejection of the 2% solution specific to the downshifted context.

Experiment 2

Two aspects of the results of Experiment 1 merit further examination. First, although statistically reliable, the absolute size of the cSNC effect was notably small and transient. In view of this, it was deemed important to verify whether the effect was replicable. Second, an intriguing aspect of Fig. 3 is that the postshift performance of rats given immediate access to the solution in the unshifted context increased slightly, peaked on the second postshift trial, and then decreased to preshift levels. The postshift performance of the 90-s group did not show such a trend. This may indicate a potential interaction across contexts, such that changes in the incentive conditions in one context may affect performance in the other context. One possibility is that context performance is affected by a simultaneous contrast effect. In simultaneous contrast situations, rats receive experience with both large and small incentives in trials signaled by different discriminative stimuli and usually separated by short intervals. Under such conditions, rats run faster (i.e., anticipatory behavior) in the presence of a stimulus paired with the large incentive than controls exposed only to the large incentive, and slower in the presence of the stimulus paired with the small incentive than small-only controls (Bower, 1961). In Experiment 1, experience with both rewards during preshift trials may enhance performance in the 16% context (positive simultaneous contrast) and suppress responding in the 2% context (negative simultaneous contrast). The downshift in the 16% context could then alleviate this simultaneous contrast leading to a transient inflation of performance in the 2% context. Thus, cSNC may be facilitated by such a change in performance in the control context, rather than by a change in performance in the downshifted context. As previously stated, although there was a hint of this effect in the unshifted context in only the 0-s group, the role of simultaneous contrast in the current training situation needs to be assessed directly. Thus, Experiment 2 included three groups, all matched with respect to the sequence of context presentations. One group replicated the training conditions of Group 90 from Experiment 1, whereas the other two groups were exposed only to 16% or to 2% sucrose in both contexts.

Method

Subjects and apparatus

The subjects were 18 Long–Evans hooded rats, 8 females and 10 males, all experimentally naïve, and 90 days old at the start of the experiment. The housing conditions, maintenance of animals, training apparatus, and contexts were those described in Experiment 1, except that when fully inserted, the sipper tube protruded 0.5 cm into the box (rather than 1 cm).

Procedure

The training procedure was identical to that of Experiment 1, except as described below. Rats were randomly assigned to one of three groups. Rats in Group 16-2 ($n = 6$; two males, four females) received 16% sucrose in one context and 2% sucrose in the other. Context assignment was counterbalanced across subjects. Group 16 ($n = 6$; three males, three females) received 16% sucrose in both contexts, whereas Group 2 ($n = 6$; two males, four females) received 2% sucrose in both contexts. Groups were matched on the basis of ad libitum weight. All groups received 90-s pretrial intervals of exposure to the context before each trial. As in Experiment 1, the transition sequence U S|S U was not included in this experiment.

Results and discussion

Fig. 4, top panel, shows the preshift performance of the three groups. Group 16-2 exhibited the same differential performance across contexts as the 90-s group of Experiment 1. Mean preshift performance indicated significantly higher goal-tracking times in the 16% context than in the 2% context for Group 16-2 ($Z = 2.20$; $p < 0.03$). More importantly, the performance of Group 16-2 in each of the two contexts was virtually identical to that of the respective controls, offering no indication of simultaneous contrast. If anything, the tendency was in the opposite direction during early acquisition trials, when the 2% performance of Group 16-2 was actually higher than that of Group 2. An analysis of the overall means for all preshift trials indicated that the performance in the 16% and 2% contexts in Group 16-2 was not different from the 16% and 2% contexts of Groups 16 and 2, respectively (Zs < 1.30; ps > 0.21).

The bottom panel of Fig. 4 presents the results of the incentive downshift manipulation. As in Experiment 1, there was evidence of cSNC in the comparison between the shifted and unshifted contexts in Group 16-2. In this case, however, the effect reached significance only on the second postshift trial ($Z = 2.20$; $p < 0.03$). No differences were observed in other postshift trials (Zs > 0.94; ps > 0.08). Unlike in Experiment 1, the performance of rats in the unshifted context was not flat, peaking also on the second postshift trial. Although these changes do not seem to be caused by a simultaneous contrast effect, they are related to the downshift manipulation and therefore introduce some uncertainty about the interpretation of the significant difference observed in the second postshift trial. To be sure, a comparison of the performance on Trial 3, shifted context, vs. performance on Trial 1, unshifted context, was not significant ($Z = 0.94$; $p > 0.34$). Thus, the level of consummatory behavior recorded in the downshifted context during the second postshift trial was not below the preshift level in the unshifted context. This suggests that the statistical significance obtained in the second postshift trial is due mostly to an increase in performance in the unshifted context, rather than a decrease in the downshifted context. Again, this problem was not evident in Group 90 of Experiment 1, which received the same training as the current Group 16-2.

Experiment 3

It was mentioned in Experiment 1 that the U S|S U sequence proximal to the downshift failed to produce evidence of cSNC in a pilot study. Obviously, any within-subject demonstration of cSNC would require that exposure to the different incentive magnitudes

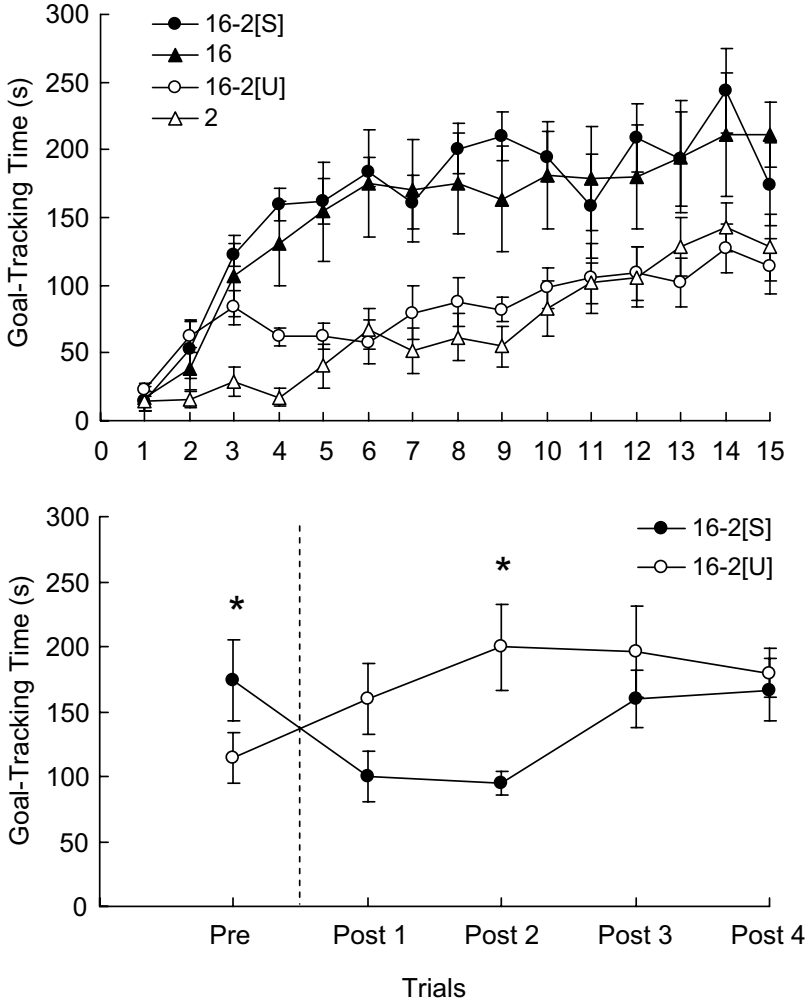

Fig. 4. Goal-tracking time (±*SEM*) during the 15 preshift training trials in each context (top panel), for groups given access to 16% and 2% sucrose in different contexts (Group 16-2; S: shifted context. U: unshifted context), to 16% sucrose in both contexts (Group 16), or to 2% sucrose in both contexts (Group 2). The bottom panel shows the postshift performance of the group that received an incentive downshift (Group 16-2) in the shifted [S] context, while maintaining access to 2% in the unshifted [U] context. Trials were equated across subjects to correspond to the last preshift trial (Pre) and to each of four postshift trials. Stars in the bottom panel denote statistically significant effects.

occurs in a sequence, in addition to each being paired with a specific context. This raises the question of the relative importance of the sequence of solutions vs. context-solution pairings in the control of consummatory behavior under the present conditions. It is plausible, for example, that rats learn to track the daily sequence of solutions, rather than relying on contextual cues, to predict the sucrose concentration that they are more likely to receive in any given trial. In the case of the Gellermann (1933) series used in these experiments, if the rat received 16% sucrose on a given trial, then it was more likely to receive 2% on the following trial than 16% again. Consider the sequence used in the present experiments and listed in Experiment 1. This sequence includes a total of 27 preshift transitions from one day to the next. Of these, 21 (78%) were either S→U or U→S, whereas 6 (22%) were either S→S or U→U. If rats are using sequential information, preshift sequences ending in U S| should lead to a stronger expectation of 2% sucrose than of 16% sucrose on the first downshifted trial because the previous trial (S) involved access to 16% sucrose. This is

true even if the context predicts 16% sucrose. Among the four possible sequences (S U|S U, S U|U S, U S|U S, and U S|S U), the one that failed to yield evidence of cSNC in pilot observation inserts the shift in between two successive trials with the shifted context (i.e., U S|S U). Thus, if rats are using sequential information based on the previous trial, they should be predicting a 2% solution after receiving a 16% sucrose trial (the last preshift trial, S|). As a result, the first downshifted trial (|S) would fit that prediction and thus attenuate the impact of the contextual discrepancy, if any, for that trial. As a comparison, consider the U S|U S arrangement, also ending with an S| trial before the downshift. A prediction of 2% sucrose coincides with the first "postshift" trial (in quotes because the shift has not yet really occurred), but the first real downshift trial (the second trial after the shift (i.e., |U S) is not predicted by either the sequence or the context, both of which predict the occurrence of a 16% trial. In the other two possible sequences (S U|S U, S U|U S), the first downshift trial occurs after an unshifted trial which, based on sequential information, should have led to a stronger expectation of 16% sucrose, rather than the actual 2% sucrose. Thus, U S|S U is the only sequence in which sequential control would tend to minimize the effect of the contextual discrepancy, thus reducing the size of the cSNC effect. As will be shown below, Experiment 3 was designed to determine whether sequential effects such as this one are significant determinants of performance under the present conditions.

Another interesting observation from the two previous experiments is the transient increase in responding to the 2% sucrose solution in the unshifted context during postshift trials. Such an increase suggested the possibility that the downshift in one context would affect performance in the unshifted context, thus creating the conditions for a simultaneous contrast effect. This possibility was tested and discarded in Experiment 2. The possibility still remains that the incentive downshift occurring in one context affects performance in the unshifted context. A feature characterizing the postshift phase of training is that, unlike in preshift trials, postshift trials involve a string of 2% sucrose trials (i.e., there is no longer a mixture of 16% and 2% sucrose trials). Thus, suppression of performance in the downshifted context may reflect, at least in part, a change in the sequence of sucrose concentrations.

The goal of Experiment 3 was to examine the possibility that the sequence of trials with the two concentrations of sucrose solution (16% and 2% sucrose) is controlling expectations more strongly than contextual cues. This may help explain, first, the apparent ineffectiveness of the U S|S U sequence to produce significant consummatory suppression and, second, the apparent postshift changes in consummatory behavior in the unshifted context. Two groups of rats were exposed to the Gellermann sequence of training trials for a total of 20 trials (10 in each context). During the final 10 trials, one group (Group 16/2→16/2) continued to receive exposure to both contexts, each paired with one of the solutions (16% or 2% sucrose), whereas the other group (Group 16/2→2) received only exposure to the context paired with 2% sucrose during the 10 trials. Thus, Group 16/2→2 received a sequence shift, but not an incentive downshift paired with a specific context (i.e., the 2% context was presented in all 10 postshift trials). If the sequence of incentives is responsible for the ineffectiveness of the U S|S U transition as speculated above, then a stream of 2% sucrose trials should lead to a substantial suppression of performance as rats would start a trial with a strong expectation of 16% sucrose. In such a case, the consummatory performance of Group 16/2→2 should be lower than the performance of Group 16/2→16/2 on 2% sucrose trials. On the other hand, if the elevation of consumma-

tory performance observed in the unshifted context during postshift trials in Experiments 1 and 2 were related to sequential changes during postshift trials (rather than to the incentive downshift per se), then the performance of Group 16/2→2 should be elevated relative to the performance of Group 16/2→16/2 on 2% sucrose trials.

Method

Subjects and apparatus

The subjects were 11 experimentally naïve Long–Evans rats (five males, six females) approximately 115 days old at the start of the experiment. Rats were purchased from Harlan when they were approximately 50 days of age. On arrival, they were housed in the TCU vivarium under a 12:12 h light:dark cycle (lights on at 07:00 h). Housing, maintenance, contexts, and apparatus were the same as described in Experiment 1, except that the fully-inserted sipper tube protruded 0.5 cm into the box, as in Experiment 2.

Procedure

Training lasted for a total of 30 daily trials. Rats were randomly assigned to one of two groups balanced by sex. Group 16/2→16/2 ($n = 5$) received the same training as that of Group 16-2/90 in Experiment 1, except that only the 30 preshift trials, 15 in each context, were run. For simplicity, "S" and "U" labels can be used to describe the sequence of trials, although there was no downshift in this experiment. The sequence of 30 trials for Group 16/2→16/2 was: S U S S U U S U S U U S U S S U S U U S|U S S U S U S U S U (the vertical line marks the 20th trial).

Group 16/2→2 ($n = 6$) was also exposed to the 16% and 2% solution in different contexts during the initial 20 trials (10 in each context) and following the same sequence administered to Group 16/2→16/2. However, training conditions differed across groups during the last 10 trials. Rats in Group 16/2→2 received only trials with the context paired with 2% sucrose during the last 10 trials. No exposure to the context paired with 16% sucrose was provided during these final 10 trials. The actual sequence was: S U S S U U S U S U U S U S S U S U U S|U U U U U U U U U U. Thus, these rats experienced a disruption in the sequence of sucrose concentrations, just as rats in a regular downshifted condition, without experiencing the contextual downshift. As usual, the context assignment was counterbalanced across subjects for each group. Other conditions of training were the same as those described in Experiment 1.

Results and discussion

Fig. 5, top panel, shows the results of the initial 10 trials in each context, before the change in sequence was implemented. As expected, there was a clear difference in the amount of goal-tracking time recorded in the 16% sucrose vs. the 2% sucrose contexts. Analyses of the overall preshift performance indicated that responding to the 16% context was significantly higher than responding to the 2% in both groups (Zs > 2.02, ps < 0.05). Additionally, responding to the 16% context was not different across groups ($Z = 0.00$, $p = 1.00$), as was the case for responding in the 2% context ($Z = 1.10$, $p > 0.27$).

Fig. 5, bottom panel, shows the daily performance of the two groups. As indicated by the number in brackets, in the figure, rats in Group 16/2→16/2 received training in either the 16% or the 2% context in any given day, whereas rats in Group 16/2→2 received train-

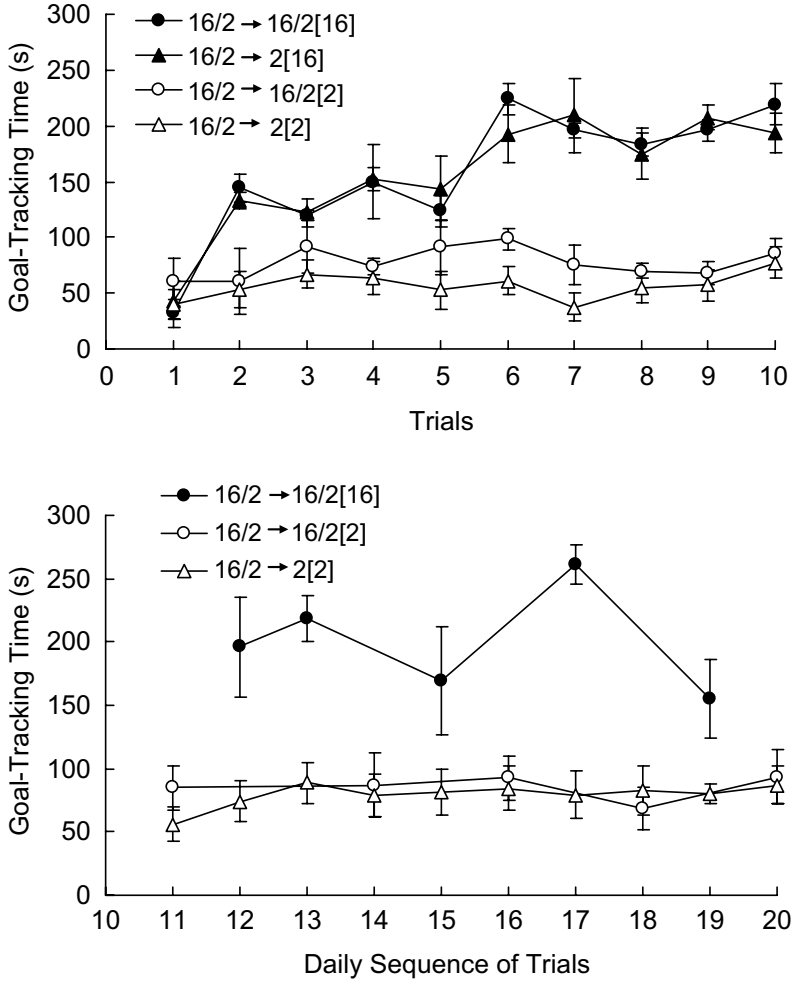

Fig. 5. Goal-tracking time (±*SEM*) during 10 training trials in each context for groups given access to 16% and 2% sucrose in different contexts (top panel). The groups differed during the second phase (bottom panel). Group 16/2→16/2 continued to receive 16% and 2% sucrose in the same manner as during the initial 10 trials in each context. Group 16/2→2 received a stream of 10 trials in the 2% context, with access to 2% sucrose (i.e., without additional exposure to the 16% context and sucrose).

ing in the 2% context in all 10 trials. The comparisons of interest are those involving the performance of both groups in the 2% trials. There were five trials in which both groups received training in the 2% context in the same day (trials 11, 14, 16, 18, and 20). In none of these trials was the performance of Group 16/2→2 different from that of Group 16/2→16/2 (Zs < 1.28, ps > 0.20). Thus, switching to a 2%-only sequence of trials did not cause any deviation in performance relative to a control that continued to receive a mixture of 16% and 2% trials across days. As for Group 16/2→16/2, the average performance in 16% sucrose trials continued to be significantly above the average performance on 2% trials during this portion of the experiment ($Z = 2.02$, $p < 0.05$).

This experiment demonstrated that shifts in the sequence, but not the context, are not sufficient to induce a significant reduction in consummatory behavior below the level of an unshifted control. Evidence of cSNC was obtained only when there was an actual incentive downshift in the context previously paired with the large reward. Furthermore, the transient increase in responding to the solution in the unshifted context during postshift trials observed in Group 0, Experiment 1, and in Group 16-2, Experiment 2, seems to be unrelated to the change in incentive sequence, and reflects true control of cSNC by contextual cues.

General discussion

A small but reliable within-subject cSNC was obtained when consummatory behavior in a downshifted context was compared to consummatory behavior in an unshifted context. Unlike in a typical iSNC experiment and in experiments studying the immediate-shock deficit, in which the dependent measure involves anticipatory behavior (runway latencies before entering the goal box and contextual freezing before delivery of the first shock, respectively), the present experiments suggest the possibility that contextual stimuli can modulate consummatory behavior. According to the distinction drawn previously between recognition and cued-recall (Papini & Pellegrini, 2006), these experiments suggest that the training conditions leading to cSNC can be adjusted so that the cued-recall of an incentive expectancy can modulate the unconditioned response to the incentive.

The effects reported here are notably small in size compared to the usual between-subject cSNC effect and to iSNC effects. Whereas there might be factors inherent in the current training procedure that led to these small effects (see discussion of Experiment 1), the possibility must be considered that cSNC is intrinsically unlikely to fall under contextual control. One possible explanation of this difference is based on the notion that some perceptual properties are more easily retrievable than others, with taste memories being among the most difficult to reactivate associatively. Such associative reactivation allows for a type of expectation that contains details about the perceptual properties of the incentive being anticipated. In the absence of such detail, the organism would be able to use only recognition memory (Papini & Pellegrini, 2006). There seems to be no available information concerning the possibility, hypothesized here, that taste memories cannot be so easily reactivated as can, say, visual memories. This would certainly be consistent with the classic finding that iSNC does not occur in runways when sucrose solutions are the incentives (for a recent report, see Sastre et al., 2005). Contrary evidence is provided by brain imaging studies. There is now evidence from studies with human participants that both taste (Kikuchi, Kubota, Nisijima, Washiya, & Kato, 2005) and olfactory (Djordjevic, Zatorre, Petrides, Boyle, & Jones-Gotman, 2005) memories can be reactivated by verbal cues in the absence of the taste or odor. In both cases, brain activity patterns similar to those observed when a person is directly exposed to the odor were reported. Because the experience of taste and olfaction usually go hand in hand, it may be possible to increase the size of the within-subject cSNC effect (and even obtain evidence of iSNC) by adding conspicuous odors to the sucrose solutions, which naturally lack an olfactory correlate.

Three pieces of evidence suggest that the sequence of incentives alone cannot account for the within-subject cSNC reported in Experiments 1 and 2. First, the context must be controlling behavior in the postshift to some degree, since the same rat drinking the same 2% solution drank less of it in a context previously paired with a 16% solution. Second, if the rats were only tracking the solution, the 0-s pretrial group in Experiment 1 should have provided evidence of cSNC, since the length of pretrial exposure to the context does not alter the sequence of incentives received during training. Third, Group 16/2→2, Experiment 3, showed no evidence of consummatory suppression in the 2% context, relative to a group receiving both 16% and 2% trials, after a shift to a 2%-only series of trials.

Within-subject designs require sequential exposure to both the solutions and contexts, therefore introducing a potential confound. Sequential information could potentially provide enough support for expectancies that could then control consummatory behavior in addition to (or instead of) the support provided by contextual cues. Determining whether

consummatory behavior in one trial is more strongly controlled by the sequence of incentives or by the strength acquired by contextual cues is likely to depend upon training parameters. In a single alternation procedure (e.g., S U S U S...), where 16% sucrose always predicts 2% and 2% always predicts 16% on the following trial, control by the context may be overshadowed by sequential control. Still, one might expect stronger cSNC in a single alternation experiment when both context and sequence predict 16% for the downshifted trial in which the rat receives 2% sucrose, than when only the context or the sequence predicts 16% sucrose. Similarly, a double alternation procedure (e.g., S S U U S S...) leads to an equal number of transitions from 16% to 16%, 16% to 2%, 2% to 16%, and 2% to 2%. In this case, the context may be a more reliable predictor of the upcoming reward than the sequence, and could thus overshadow sequential information. The training sequence used in the present experiments lies between these two extremes.

To the extent that cSNC can fall under the control of contextual cues, some interesting possibilities are open for future research. Consider the following two. First, this procedure is suitable to study how the conditioning process modulates the unconditioned response to the incentive (Domjan, 2005). Despite Pavlov's use of feeding as his prototypical unconditioned response, relatively little is known about the way in which conditioned stimuli modulate feeding. Signals for food modulate digestive processes by preparing the system to process food (Woods, 1991). However, such responses are anticipatory, like conventional conditioned responses, and therefore tell us little about whether and how feeding is influenced by expectancies. Evidence that expectancies can influence feeding was provided by experiments in which access to food during a period of food deprivation was signaled by a conditioned stimulus in either a forward, a backward, or a random arrangement (Zamble, 1973). In one experiment, rats exposed to forward pairings of a metronome and food ate more food and lost less weight than rats exposed to backward pairings. Similarly, a conditioned stimulus paired with food during a training phase later induced feeding in satiated rats (Weingarten, 1983). Furthermore, available evidence suggests that the mechanisms underlying the effects of a conditioned stimulus on feeding are different from those involved in the CS's ability to influence anticipatory responses (Holland & Petrovich, 2005; Weingarten & Martin, 1989). The present results suggest the possibility that feeding can be regulated by the violation of appetitive expectancies. Unlike the studies cited above, in which a conditioned stimulus presented before access to a meal increased feeding behavior, the present experiments dealt with the suppression of consummatory behavior following access to an incentive of a lower-than-expected magnitude.

Second, hippocampal lesions disrupt the iSNC effect (Franchina & Brown, 1971) but seem to have no influence on the cSNC (Flaherty, Rowan, Emerich, & Walsh, 1989). A similar outcome has been obtained within a single experiment for other types of brain lesions. For example, damage to the nucleus accumbens disrupts iSNC without affecting cSNC in the same animals trained in a runway situation (Leszczuk & Flaherty, 2000). This type of evidence suggests that iSNC and cSNC engage different mechanisms. One hypothesis relies on the dichotomy between recognition and cued-recall memory (Papini & Pellegrini, 2006), a distinction known to have empirical support (Cabeza et al., 1997). Because iSNC is measured in terms of anticipatory behavior, it can only occur if a rat retrieves information about past experiences of surprising incentive reductions, thus fitting the cued-recall model. In cSNC, however, suppression follows the initial consumption of the downshifted solution, thus suggesting that contrast arises from the recognition that the current solution is of lesser value than that of preshift trials. If the hippocampus, nucleus

accumbens, and other structures play a role in iSNC because it involves cued-recall, then one would expect that the within-subject cSNC effect reported here would also be disrupted by lesions in these structures. The within-subject procedure used in present experiments offers a possible route to approach these problems.

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