Scaling relative incentive value in anticipatory behavior

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Abstract

Papini and Pellegrini (Papini, M. R., & Pellegrini, S. Scaling relative incentive value in consummatory behavior. *Learning and Motivation*, in press) observed that, within limits, the level of consummatory responding of rats exposed to incentive downshifts in the concentration of sucrose solutions was similar when the ratio of test/training solutions was the same. For example, $32 \rightarrow 4\%$ and $16 \rightarrow 2\%$ downshifts (1:8 test/training ratios) lead to similar levels of consummatory behavior, despite differences in the absolute concentrations of the solutions involved in the downshift. This suggests the applicability of Weber's law to spaced-trial, incentive-downshift situations. Experiment 1 extended these results to runway performance using food pellets as reward, and Experiment 2 to lever pressing performance, using an autoshaping procedure and sucrose solutions as rewards. The results conform well to the test/training ratio suggesting that Weber's law is applicable to anticipatory behavior. A simple mathematical rule that can be easily incorporated into models based on linear operators describes the results of consummatory and anticipatory behavior experiments.
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Experiments on the effects of incentive downshifts on consummatory behavior show that despite striking differences in the absolute concentrations of various sucrose solutions,

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consummatory responding to 8%, 4%, and 2% sucrose solutions during downshifted trials (called test solutions) is similar for groups of rats previously exposed to 64%, 32%, and 16% sucrose, respectively (called training solutions; Papini & Pellegrini, in press). Thus, consummatory responding following incentive downshift appears to obey Weber's law. As applied to sensory-perceptual judgments, Weber's law refers to the fact that the discrimination of a change in stimulation is a function of the ratio between the amount of change, ΔI (assumed here to be equivalent to the test solution) and the intensity of the stimulus, I (assumed here to be equivalent to the training solution; Fechner, 1966; Luce & Krumhansl, 1988). The results also indicated that, for example, consummatory responding to a 4% test solution was significantly less in a group that had received 32% training solution than in one that had received 16% training solution. The latter result is interpreted as a special case of consummatory successive negative contrast (cSNC) in which the comparison is across groups with different training solutions, but the same test solution. The conventional comparison involves a downshifted group vs. an unshifted control also differing in terms of the training solution, but exposed to the same test solution (Flaherty, 1996). Within limits, then, the level of consummatory responding during the downshift trial was a direct function of the test/training ratio of solution concentrations.

In previous experiments, rats were used as subjects, consummatory responding was the dependent variable, and a relatively long interreinforcement interval was introduced between the last presentation of the training solution and the first presentation of the test solution (40 min and 24 h in different experiments; Papini & Pellegrini, in press). These results have at least three implications that merit further experimental work. First, they suggest that the hedonic value of current incentives was compared to the reactivated memory of incentives experienced 24 h earlier. Traditional psychophysical studies use intervals in the order of seconds to a few minutes (e.g., Stevens, 1969; but see Hubbard, 1994). Under such conditions, the critical comparison may be between the current incentive and the sensory trace of an incentive presented shortly before. Papini and Pellegrini (in press) have referred to this process as sensory relativity, to distinguish it from instances in which the comparison involves the current incentive and the reactivated memory of a previously presented incentive. Studies on the applicability of Weber's law to animal behavior, including choice (e.g., Kacelnik & Brito e Abreu, 1998) and simultaneous contrast (Flaherty & Sepanak, 1978), used massed trial procedures in which the alternative reward values were experienced within a given training session. Thus, these results do not necessarily speak to the applicability of Weber's law to situations in which the alternative reward values are administered in different sessions separated by considerably long intervals. An exception is provided by studies on interval timing. As Gibbon and Church (1984) suggested, the critical comparison in interval timing experiments is between a time interval estimated at the end of the current trial and the average length of similar intervals computed over many previous trials and stored in long-term memory. In fact, the application of Weber's law to timing (e.g., Gibbon, 1977; Malapani & Fairhurst, 2002) served as a guide for the present studies. An assessment of the applicability of Weber's law to comparisons involving a current incentive and the reactivated memory of a past incentive requires the use of training parameters that encourage long-term encoding of incentive properties and discourage the use of short-term, decaying sensory traces.

Second, the evidence of cSNC in the results reported by Papini and Pellegrini (in press) suggests the presence of a negative emotional reaction induced by the incentive downshift. This emotional component is well documented in situations involving surprising reward

omissions (Papini & Dudley, 1997). For example, cSNC is accompanied by corticosterone release (Flaherty, Becker, & Pohorecky, 1985), it is enhanced by posttrial administration of corticosterone (Bentosela, Ruetti, Muzio, Mustaca, & Papini, 2006), and it is reduced by pretrial administration of anxiolytics and opioids (Flaherty, Grigson, & Rowan, 1986, 1996; Mustaca, Bentosela, & Papini, 2000; Rowan & Flaherty, 1987; Wood, Daniel, & Papini, 2005). Thus, the finding that the level of consummatory suppression after incentive downshift obeys Weber's law may indicate that it is the strength of the emotional reaction per se that varies in accordance to Weber's law.

Third, consummatory behavior has traditionally been considered stereotyped and relatively fixed, as opposed to the more malleable appetitive behavior (Craig, 1918). Craig's distinction reflected the position of a given response relative to the direct interaction between organism and incentive. Thus, appetitive behavior preceded contact with the incentive (e.g., search, orientation, and approach to a source of food), whereas consummatory behavior involved direct interaction with the incentive (e.g., handling, chewing, and swallowing food). Thus, it is possible that the dependency of consummatory behavior on the test/training ratio reflects the operation of unique underlying mechanisms that may not apply to appetitive behavior. It is unclear, for example, whether Weber's law as assessed during incentive downshift operations similar to those implemented by Papini and Pellegrini (in press) would also hold for the type of anticipatory conditioned responses most commonly used in conditioning experiments.

The present experiments are concerned with these three implications of the findings reported by Papini and Pellegrini (in press). They asked two fundamental questions. First, does constant proportionality apply to anticipatory appetitive behavior, just as it does to consummatory behavior? As in previous experiments, an interval of about 24 h was interpolated between the last exposure to the training incentive and the first exposure to the test incentive to minimize the effects of decaying traces of previous rewards on current performance. Second, does constant proportionality depend on the presence of an SNC effect? The occurrence of SNC implies an emotional reaction induced by incentive downshift that may not be necessary to obtain evidence for constant proportionality. For this reason, Experiment 1 used parameters that were shown in previous research to yield evidence of SNC (i.e., runway performance; Crespi, 1942), whereas Experiment 2 used parameters that were shown in previous research to yield no evidence of SNC (i.e., anticipatory conditioning with sucrose solutions as the reward in rats; Sastre, Lin, & Reilly, 2005). The rest of this introduction discusses the rationale behind the selection of these two procedures.

Papini and Pellegrini (in press, see their Fig. 1) distinguished three forms of incentive relativity, that is, the dependence of responding to one incentive on the value of incentives experienced previously under similar conditions (see Flaherty, 1996). They were labelled sensory relativity, recognition relativity, and cued-recall relativity, and were distinguished on the basis of some key procedural features. *Sensory relativity* involves short training-test intervals (from seconds to a few minutes), that allow for the comparison to be between the current test incentive and the sensory trace of the training incentive. It is the procedure used in typical psychophysical experiments (e.g., Stevens, 1969) and in simultaneous consummatory contrast experiments with animals (Flaherty & Sepanak, 1978). *Recognition relativity* involves the reactivation of a long-term memory of the training stimulus triggered by exposure to the test stimulus. It is assumed that this type of process involves recognition memory and is responsible for cSNC. In a typical experiment involving a downshift from 32% to 4% sucrose solution, the long-term memory of the 32% training

solution is reactivated by exposure to the 4% test solution during the first postshift trial; a matching failure triggered by recognition memory suppresses consummatory behavior. Recognition memory can only apply after the animal has interacted directly with the downshifted incentive. This interpretation is consistent with several properties of the cSNC effect, including its relative invulnerability to contextual shifts (Flaherty, Hrabinski, & Grigson, 1990), the lack of changes in latency to the first lick response across preshift and postshift trials (Grigson, Spector, & Norgren, 1993), and the relatively unimportant role played by the hippocampus (Flaherty, Rowan, Emerich, & Walsh, 1989), a property that characterizes recognition memory in humans (e.g., Hasselmo & Wyble, 1997).

The original experiments on the effects of incentive downshifts involved instrumental conditioning situations (Crespi, 1942; Elliot, 1928). For this reason, the effect is known as instrumental SNC (or iSNC). In Crespi's (1942, Experiment 3) classic demonstration of the iSNC effect, rats received a single trial per day and were reinforced for running to the goal box of a straight runway apparatus with about 5.12 g of Purina dog biscuit (about 68% of the 7.5 g received as a daily maintenance diet). After 20 such trials, rats were shifted to 0.32 g per trial (chosen to correspond to a 16:1 preshift:postshift ratio of reward magnitudes) for an additional 8 trials. These animals exhibited a sharp decline in running speed during the postshift trials, undershooting the performance of rats that had received 0.32 g per trial all along. The feature of interest for the present argument is the use of a single trial per day, also common in similar demonstrations of iSNC (e.g., Elliot, 1928). A single trial per day was used to keep a constant motivational state at the start of each trial and to allow for the delivery of a large reward magnitude. An additional consequence of this procedure is that running a single trial per day prevents the effective use in any trial of sensory traces left over by exposure to food in the previous trial. Although this assumption was not tested directly, it is widely posited, in theoretical and empirical contexts, that sensory traces decay spontaneously in time and are completely inactive seconds to a few minutes after stimulus presentation (Atkinson & Shiffrin, 1968; Hull, 1943; Roberts & Grant, 1976; Weinstock, 1954). It is highly unlikely that information about the magnitude of an incentive will remain active, without decay, across a 24-h period during which the animal eats, drinks, and sleeps.

Since running speed was measured before the rat contacted the food located in the goal box, any effect of incentive downshift on running speed had to be first learned at the goal box and then reactivated in the following trial, in an anticipatory form, by exposure to the situational cues paired with incentive downshift. iSNC is, therefore, truly anticipatory in nature and cannot be explained in terms of recognition memory since the critical memory is reactivated before the animal arrives in the goal box. Such anticipatory internal responses have traditionally been called expectancies (e.g., Tolman, 1932; Trapold & Overmier, 1972), that is, anticipations of the impending occurrence of some event triggered by a signal previously paired with that event. In this sense, the degree of performance deterioration after incentive downshift may be thought of as reflecting the value of the small incentive relative to the memory-reactivated value of an expected large incentive. Papini and Pellegrini (in press) suggested that iSNC is an example of *cued-recall relativity* to be distinguished from cSNC, which is taken as an instance of recognition relativity.

Evidence consistent with the distinction between cued-recall relativity and recognition relativity comes from experiments in which consummatory and anticipatory responses were measured in the same animals. In one experiment (Flaherty & Caprio, 1976), rats received 20 trials of training in a runway (2 trials/day separated by a 45-s interval), and

were reinforced with 1-min access to either 32% or 4% sucrose solution. The speed of running (instrumental) and the licking responses to the sipper tube (consummatory) were the dependent measures. Whereas there was no evidence of iSNC in running speed, there was a significant cSNC in licking rate. These results replicated the extensive series of experiments showing that iSNC does not emerge when sucrose solutions are used as incentives (see below for references), and also showed that rats experience incentive contrast when measured in terms of consummatory behavior. One implication consistent with human memory data is that recognition memory, as assessed in the consummatory situation, provides a more sensitive measure of contrast than cued-recall memory, as measured by anticipatory running. Furthermore, the results of experiments involving brain lesions support this dissociation of iSNC and cSNC. For example, damage to 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 (Flaherty et al., 1989; Leszczuk & Flaherty, 2000). As mentioned above, the fact that the hippocampus plays a larger role in iSNC than in cSNC is consistent with research on recognition and cued-recall memory in humans (e.g., Hasselmo & Wyble, 1997).

The present experiments were designed so that they would provide more than just a demonstration of Weber's law in conditions involving anticipatory responding. Given the relatively orderly relationship observed between iSNC and the size of the discrepancy between the magnitudes of the training and test incentives (DiLollo & Beez, 1966), it can be expected that conditions that promote iSNC would also provide evidence for constant proportionality. An especially important issue is whether Weber's law requires the presence of a significant SNC effect, or whether it is part of the cognitive assessment of incentive downshifts that would regulate behavior even in the absence of SNC. This issue was approached in Experiment 2 by choosing a reinforcer downshift manipulation (shifts in the concentration of sucrose solutions) known to yield no evidence of iSNC in experiments with rats.

Experiment 1

The present experiment was designed to test the applicability of Weber's law to the behavioral changes induced by incentive downshifts in an instrumental conditioning situation known to produce iSNC (e.g., Crespi, 1942). Running speed in a straight runway apparatus was measured in five groups of rats receiving a single conditioning trial per day. The groups differed in terms of the amount of food pellets they received in each of the two conditioning phases. The amount of food pellets were chosen so as to generate two test/training ratios: 0.125 and 0.25. These ratios produced the clearest evidence for Weber's law in the consummatory situation (Papini & Pellegrini, in press). This was achieved by scheduling the following incentive downshifts (group labels refer to the number of food pellets delivered in the goal box): 16–2 and 32–4, to generate a ratio of 0.125; and $16 \rightarrow 4$ and $32 \rightarrow 8$ to generate a ratio of 0.25. In addition, one unshifted control received training with 4 pellets throughout the experiment.

Method

Subjects

The subjects were 40 adult, male, experimentally naïve, 90-day old Wistar rats. Animals were kept at 80–85% of their ad libitum weight by restricted posttrial feeding, at least

20 min after the end of the daily training trial. The mean free-food weight for the entire sample was 415 g (range: 321–484 g). The colony was under a 12-h light, 12-h dark cycle (lights on at 07:00 hours).

Apparatus

The apparatus consisted of a start box (30 cm long, 21 cm wide), a runway (202 cm long, 21 cm wide), and a goal box (30 cm long, 21 cm wide) made of stainless steel and painted black. The walls were 20 cm high. The entire apparatus had a transparent Plexiglas cover. The end wall of the goal box had a feeder cup (4 cm high, 6 cm in diameter), made of aluminum. Three pairs of photocells were placed at 20 cm, 190 cm, and 225 cm from the door separating the start box from the runway section. These photocells allowed recording of running times in 0.2-s units by means of appropriate circuitry connected to a computer. The sliding door at the start box was manually operated, but the sliding door at the goal box was automatically operated by the computer. Noyes precision pellets (standard formula, 45 mg) were used as reinforcers by placing the appropriate amount into the food cup before each session.

Procedure

Rats were matched in terms of their ad libitum weight and randomly assigned to preshift conditions. The experiment included groups labelled according to the amount of pellets administered during preshift (training incentives) and postshift trials (test incentives): 4–4, 16–2, 16–4, 32–4, and 32–8. These amounts were chosen to generate test/training ratios of 0.25 for two groups (16–4, 32–8), and 0.125 for the other two groups (16–2, 32–4) while simultaneously testing two groups trained differentially during preshift trials, but given the same postshift amount (16–4, 32–4). Group 4–4, was included as the standard unshifted control group.

Rats were familiarized with the runway in two initial daily trials with no presentation of food pellets in the goal box. During each of these two preexposure trials, rats were allowed to explore the runway for 3 min. Rats remained in their home cages during the next two days, where they received 18 Noyes precision pellets (45 mg, rat formula) per day at approximately the same time when training would be conducted throughout the experiment. Beginning the day after food preexposure in the home cage, each rat received a single runway training trial per day. There were 24 preshift trials followed by 20 postshift trials. In each trial, the rat was placed in the start box with the guillotine door closed. After 10 s, the door was opened and the rat was allowed to traverse the runway. The goal box door was closed upon activation of the goal box photocell. The rat remained in the goal box until it consumed all the food pellets and was then returned to its home cage.

If an animal took more than 3 min and 20 s to move out of the start box after the door was opened and activate the first photocell, or between the activation of two adjacent photocells, it was gently placed in the goal box, where it had access to the incentive scheduled for that particular trial. Rats taken to the goal box in more than 4 consecutive trials were discarded from the experiment.

At the end of the preshift phase, rats trained with 16 or 32 pellets were matched in terms of their running performance and then randomly assigned to their postshift condition to conform the four downshifted groups (32–8, 32–4, 16–4, 16–2). This type of performance matching ensures similar preshift performance for animals assigned to a given training incentive. The running order of 4-rat squads was randomized across groups and days.

At the end of each session the runway was swept with a damp paper towel. There were three dependent measures: (1) start latency (from start door opening to activating the first photocell), (2) run latency (from activation of the first photocell to activation of the second photocell), and (3) goal latency (from activation of the second photocell to activation of the third photocell). Latency values were transformed into $\log_{10}$ units to improve normality for low values expected to characterize behavior at the time of incentive downshift. These scores were subjected to conventional analysis of variance (ANOVA) with an α value set at the 0.05 level for all analyses. Specific p values were not stated in the text for brevity, except when reporting the result of LSD pairwise tests.

Results and discussion

Absolute response measures

Five animals were discarded due to the established criterion (see *Procedure* section). Because the goal of this experiment was to assess response decrements after incentive downshifts, only animals that developed some minimum amount of responding could potentially provide useful data. The final group sizes were: $n = 6$ for Group 4–4, $n = 7$ for Groups 32–4, 32–8, and 16–2, and $n = 8$ for Group 16–4. Fig. 1 shows the results for all the groups in terms of mean running times in the three sections of the runway (start, run, and goal latencies). In each measurement, but especially in terms of start latencies, there was a tendency for latencies to be shorter for the groups receiving 32 pellets as reinforcement during the preshift trials. The groups trained with 4 and 16 pellets tended to overlap more extensively. A Training Incentive (4, 16, 32 pellets) × Trial (1–25) analysis for each dependent measure indicated the following results. For all three latency measures (start, run, goal), only the change across trials was significant, $Fs(24, 768) > 5.50$. The main effect of training incentive and the interaction between training incentive and trials failed to reach significance, $Fs < 1.16$.

The results obtained during the postshift trials generally show longer latencies for all the groups exposed to incentive downshifts, relative to the unshifted control. Notice, however, that this design allows for two main comparisons. First, Group 4–4 is the appropriate group to evaluate iSNC in Groups 32–4 and 16–4. As expected, the general tendency was for greater performance deterioration in Group 32–4 than in Group 16–4. This is evident in terms of start and goal latencies, although not for run latencies (see Fig. 1). A Training Incentive (4, 16, 32 pellets) × Trial (26–44) analysis calculated for each of the latency measures in the relevant groups (4–4, 16–4, and 32–4) indicated the following results. In the start latency, there were significant effects across training incentives, $F(2, 18) = 4.64$, and across trials, $F(18, 324) = 2.21$. The interaction between these factors was not significant, $F(36, 324) = 1.31$. LSD pairwise tests with training incentive as the independent factor indicated significant differences between Groups 32–4 and 4–4, $p < 0.007$. Other comparisons were not significant, $ps > 0.11$. In the run latency measure, there was only a significant change across trials, $F(18, 324) = 1.79$. The other effects were not significant, $Fs < 1.18$. In the goal latency measure, as was the case for start latencies, there were significant effects for the training incentive, $F(2, 18) = 4.19$, and across trials, $F(18, 324) = 2.43$, but not for their interaction, $F < 1$. LSD tests with training incentive as the independent factor indicated significant differences between Groups 32–4 and 4–4, $p < 0.01$. Other comparisons were not significant, $ps > 0.10$. These results provide evidence of iSNC in the runway situation used in this experiment, thus confirming many previous
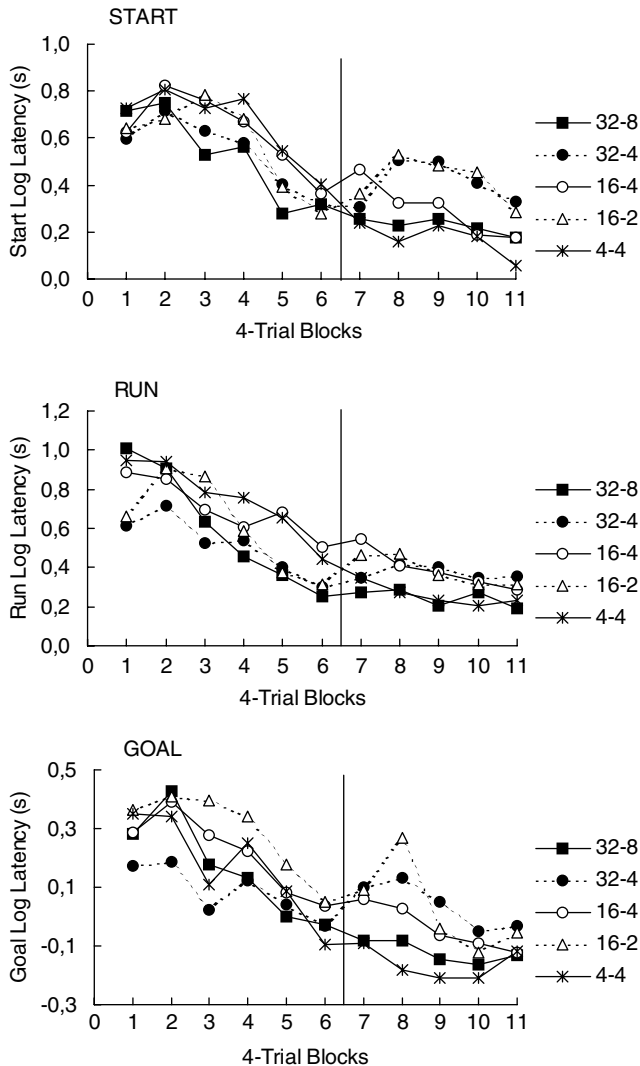
Fig. 1. Mean time to traverse the start (upper panel), run (middle panel), and goal (bottom panel) sections of a straight alley (in $\log_{10}$ of seconds) for the five experimental groups reinforced with different amounts of food pellets during the preshift and postshift phase, as a function of sessions.

results obtained under similar conditions (e.g., Crespi, 1942). The postshift latencies of Group 32–4 were significantly higher than those of Group 4–4 in the start and goal sections of the runway. Although average performance was ordered in the right direction, there was no statistical evidence of iSNC in the comparison between Groups 16–4 and 4–4, or in the special case involving Groups 32–4 and 16–4.

Second, the main comparison in this study is that between groups exposed to the same test/training ratios, namely Groups 32–4 and 16–2 (ratio = 0.125) and Groups 32–8 and 16–4 (ratio = 0.25). The best alignment along the test/training ratios occur in terms of

the start latency measure (see Fig. 1). A Ratio (0.125, 0.25) × Training Incentive (16, 32 pellets) × Trial (26–44) analysis was calculated for each latency measure with the following results. In the start latency measure, there were significant main effects of ratio, $F(1, 25) = 8.33$, and trials, $F(18, 450) = 2.29$, and of the ratio by trial interaction, $F(18, 450) = 1.88$. No other effects were significant, $Fs < 1$. In the run latency measure, there was only a significant change across trials, $F(18, 450) = 2.61$; all other effects were not significant, $Fs < 1.41$. In the goal latency measure, there were significant main effects of ratio, $F(1, 25) = 4.58$, and trials, $F(18, 450) = 4.95$. No other effect achieved significance, $Fs < 1.23$. These results suggest that the test/training ratio described the postshift performance of these groups better than the incentive magnitude received during preshift trials.

Relative response measures

Whatever the source of behavioral change during the postshift trials, any transformation that reduces the influence of individual differences in performance would enhance the visibility of the effect. Therefore, the data were transformed according to a difference score computed for each rat separately. A baseline score was computed by obtaining the average response speed for sessions 21–25 in each animal. These asymptotic scores are plotted in Fig. 2 for each section of the runway. Good linear fits were obtained for the start and run latencies, where the average values were inversely related to training incentive magnitude. This was clearly not the case for goal latencies. Then, the mean response speed for each session was subtracted from baseline. The group averages for each runway section are plotted in Fig. 3. Considerable agreement according to the ratio is observed in terms of the start latency. The run latency data show overlapping performance for Groups 32–4 and 16–2, both with a test/training ratio of 0.125, but less agreement for Groups 32–8 and 16–2, both with a ratio of 0.25. As for the goal latency, there was good agreement with the ratios only during the initial two 4-trial blocks.

The statistical analyses confirmed these conclusions. As with absolute data, these groups can be organized into two main sets. First, Groups 32–4, 16–4, and 4–4 provide evidence of iSNC. A Training Incentive (4, 16, 32 pellets) × Trial (25–44) analysis was computed for each dependent measure. In the start latency measure, there were significant differences across training incentive groups, $F(2, 18) = 10.31$, and across trials, $F(18, 324) = 2.21$; the interaction between these factors was not significant, $F(36, 324) = 1.31$. LSD pairwise tests with training incentive as the independent factor indicated a significant difference between Groups 32–4 and 4–4, $p < 0.001$, and between Groups 32–4 and 16–4, $p < 0.009$. In the run and goal latency measures, only a significant change across trials was detected, $Fs(18, 324) > 1.79$; the other effects were not significant, $Fs < 1.70$. These results agree with the results of absolute latencies in providing evidence of iSNC. Furthermore, the performance of Group 32–4 deteriorated to a larger extent than the performance of Group 16–4, thus providing additional evidence of iSNC.

Second, a comparison of Groups 32–8, 32–4, 16–4, and 16–2 highlights the relative contribution of the test/training ratio vs. the training incentive to iSNC. A Ratio (0.125, 0.25) × Training Incentive (16, 32 pellets) × Trial (25–44) analysis was computed for each dependent measure. In the start latency measure, there were significant main effects of ratio, $F(1, 25) = 5.02$, and trials, $F(18, 450) = 2.29$, as well as of their interaction, $F(18, 450) = 1.88$. No other effects were significant, $Fs < 1$. In the run and goal latency measures,
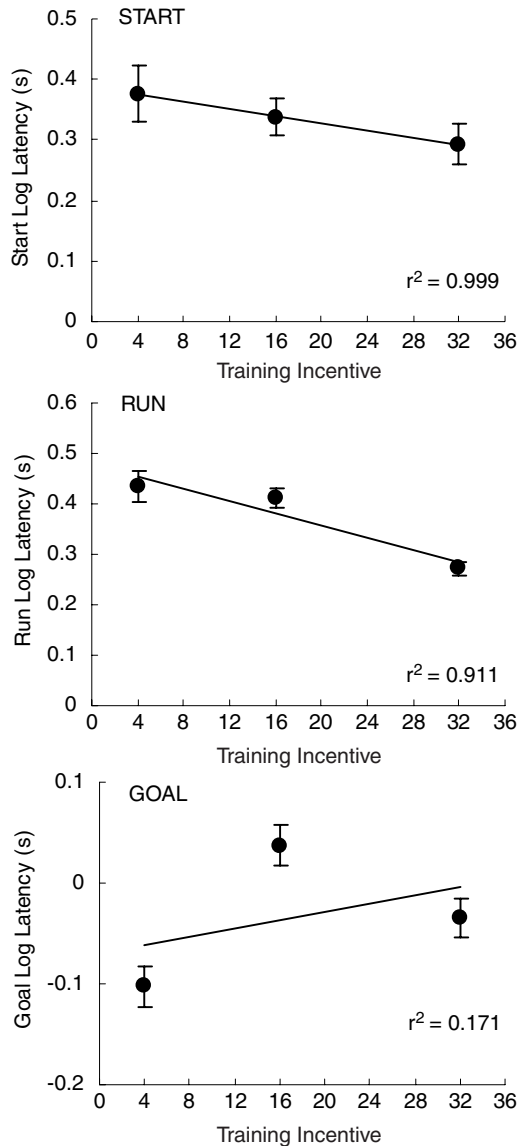
Fig. 2. Mean time (trials 21–25) to traverse the start (upper panel), run (middle panel), and goal (bottom panel) sections of a straight alley (in $\log_{10}$ of seconds) for groups reinforced with different amounts of food pellets during the preshift phase (training incentive).

there were only significant effects across trials, Fs(18, 450) > 2.61; all other effects were nonsignificant, Fs < 1.41. The performance of these groups was most clearly determined by the test/training ratios of the incentive magnitudes employed during the experiment, rather than of the absolute magnitude experienced during the preshift trials. This conclusion applied well to the start latency measure, but control of performance by the test/training ratio was not observed in the run and goal latencies. This suggests a spatial gradient in
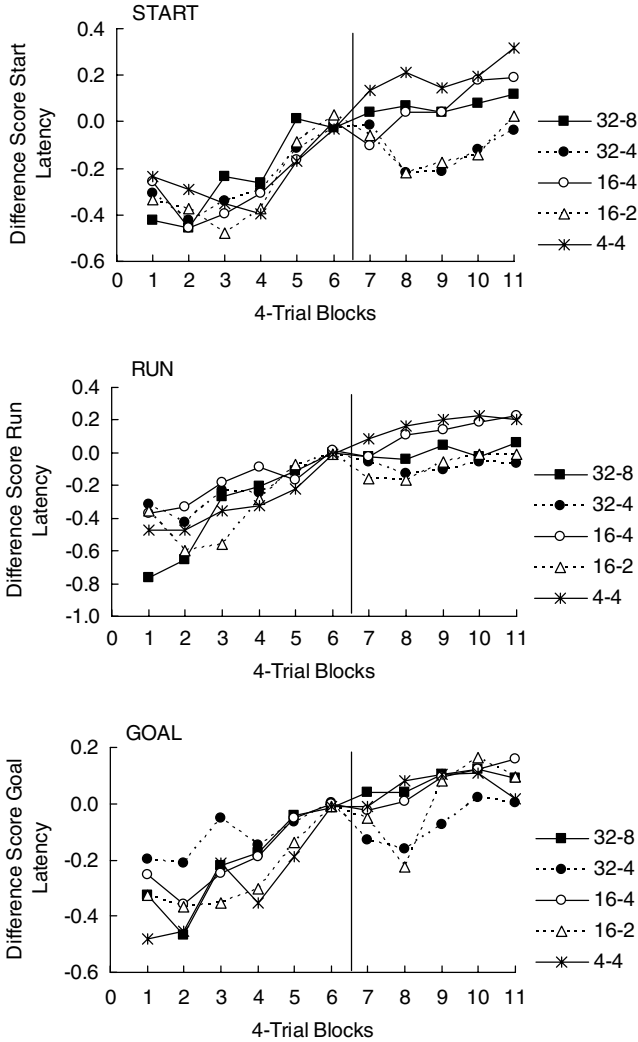
Fig. 3. Difference score ($\log_{10}$ of seconds on session "n" minus mean $\log_{10}$ of seconds on sessions 21–25) for the start (upper panel), run (middle panel), and goal (bottom panel) sections of a straight alley of five experimental groups reinforced with different amounts of food pellets during the preshift and postshift phase, as a function of sessions.

the ability of constant proportionality to control instrumental performance, which was greater farther rather than closer to the goal. Instrumental behavior was not influenced in any detectable manner by the incentive magnitude experienced during the preshift trials.

Experiment 2

Several studies published since the 1960s suggest that iSNC does not occur in the runway situation when rats are exposed to downshifts in the concentration of sucrose

solutions (e.g., Barnes & Tombaugh, 1973; Flaherty & Caprio, 1976; Flaherty, Riley, & Spear, 1973; Goodrich & Zaretsky, 1962; Rosen, 1966; Rosen & Ison, 1965; Sastre et al., 2005; Shanab, Domino, & Ralf, 1978; Spear & Hill, 1965). Instead, rats adjust their performance after the downshift without undershooting the unshifted control group. There is some indication that iSNC also fails to occur when sucrose pellets are downshifted in terms of the sucrose concentration or in terms of the number of pellets (Burns, McCrary, McRae, & Lorig, 1984; Shanab et al., 1978). A successful demonstration of iSNC involving downshift in the concentration of sucrose solutions was reported by Weinstein (1970), but these results are open to an alternative explanation. In Weinstein's experiment, rats deprived of food and water received free-operant training in which each lever press gave them access to either a 16% or a 4% sucrose solution for 2 s in independent groups. The lever and dipper were sufficiently close spatially for rats to operate the lever and drink the solution at the same time. After a downshift from 16% to 4% sucrose, rats exhibited a significant decrease in response rate below the level of the unshifted 4% controls. Although technically a case of iSNC, the close spatial proximity between the manipulandum and the goal, the use of a free-operant procedure, and the continuous reinforcement contingency suggests that this may be more properly framed as a case of cSNC, rather than iSNC. A consummatory rejection of the 4% solution would have resulted in rats moving away from the goal area (e.g., Pellegrini & Mustaca, 2000), thus incidentally reducing the rate of lever pressing. This possible artefact is prevented when the anticipatory response and the goal response are spatially segregated, as it is the case in the runway situation (Flaherty & Caprio, 1976). If this discrepant result is set aside, then the evidence points to a special status for downshifts in sucrose concentrations in the SNC situation.

As reinforcers, however, sucrose solutions and pellets exhibit other standard properties. For example, just as with food pellets, sucrose pellets promote single alternation patterning (Burns, 1984), suggesting that they leave a stimulus trace that can acquire control over instrumental behavior. Moreover, Burns and Wiley (1984) found evidence that rats can anticipate the occurrence of a 30% sucrose solution when reinforced (R) and nonreinforced (N) trials are administered in regular sequences. Groups trained in either an R–N–N or an R–N–R sequence showed differential responding on the second trial, with greater response strength in the R–N–R sequence than in the R–N–N sequence, suggesting anticipation of the 30% sucrose reward in the former. This suggests that a representation of the sucrose solution (or of some general appetitive event) can be accessed in a cued-recall situation. Of course, sequential procedures involving R and N trials differ in one important respect from the typical iSNC situation: In iSNC rats must compare two different sucrose concentrations, rather than R and N. Would rats show behavioral patterning if exposed to two different concentrations of sucrose solutions? These failures of iSNC when sucrose is used as the incentive suggest they should not show such patterning.

Experiment 2 had two goals. The first was to extend the study of SNC with sucrose solutions as the incentive to a new situation: autoshaping in rats. In the autoshaping situation used in this experiment, the presentation of a retractable lever (the conditioned stimulus, CS) was paired with the response-independent delivery of sucrose solutions of various concentrations (the unconditioned stimulus, US). Anticipatory behavior was assessed in terms of responses directed at the CS, which could be recorded automatically. Sucrose solutions were used on the hypothesis that autoshaping, like running behavior, should exhibit behavioral change without contrast after a downshift in sucrose concentration. Previous experiments indicated both that autoshaping with sucrose solution as the

US is a viable training procedure and that shifts in US magnitude with solid food pellets as the US yields two types of successive contrast effects, the regular SNC effect and faster extinction after training with large number of food pellets than with a small number of pellets (Papini, Ludvigson, Huneycut, & Boughner, 2001). The autoshaping procedure has the additional property of combining instrumental learning (as shown by the sensitivity of autoshaped lever pressing to omission contingencies; Antip, 1977; Davey, Oakley, & Cleland, 1981; Stiers & Silberberg, 1974), with the precision of Pavlovian procedures, in which the parameters of training are under the experimenter's control. (Thus, this is still referred to below as iSNC despite the use of Pavlovian contingencies.)

The second, main goal of this experiment was to determine whether downshifts in the concentration of sucrose solutions used as the US lead to changes in performance that can be described in terms of the test/training ratio, as it was done with consummatory behavior (Papini & Pellegrini, in press) and with running performance (Experiment 1). This outcome would be particularly interesting if it were to occur in the absence of iSNC, since it would indicate that constant proportionality is not necessarily tied to the emotional consequences of incentive downshift. Four groups of rats received autoshaping training with sucrose solutions of different concentrations chosen so as to generate the same test/training ratios studied in Experiment 1: 0.125 and 0.25. This was achieved by scheduling the following incentive downshifts (all numbers refer to the percentage of sucrose in the solution delivered as the US): $16 \rightarrow 2$ and $32 \rightarrow 4$, to generate a ratio of 0.125; and $16 \rightarrow 4$ and $32 \rightarrow 8$ to generate a ratio of 0.25. In addition, three unshifted controls received training with sucrose concentrations of 2%, 4%, and 8% throughout the experiment, to assess iSNC in the conventional comparison of downshifted vs. unshifted groups.

Method

Subjects

The subjects were 66 adult, male, 120-day old ($n = 35$) and 180-day old ($n = 31$) Wistar rats. Animals were kept at 80–85% of their ad libitum weight by posttraining feeding, at least 20 min after the daily training session. The mean free-food weight for the entire sample was 331 g (range: 203–437 g). General maintenance conditions were the same described as those in Experiment 1. Twenty seven rats were experimentally naïve, whereas 39 had previously participated in a cSNC experiment (Papini & Pellegrini, in press, Experiment 2).

Apparatus

Rats received training in 4 conditioning chambers (MED Associates, Vermont) enclosed in sound-attenuating cubicles. Each cubicle was equipped with a fan that helped circulate the air and provided background masking noise. Each box measured $29.2 \times 24.1 \times 21$ cm ($W \times L \times H$). The floor was made of aluminum bars, 0.4 cm in diameter, and separated by gaps measuring 1.1 cm. On the front wall, near the door, was a square hole, 5-cm on each side, 3.5 cm deep, and 1 cm above the floor level. A liquid dipper, 0.6 cm in diameter (containing 1 ml of liquid solution), could be introduced into this hole from the outside. A diffuse light was located in the center of the front wall and 18 cm from the floor. A retractable lever was located 6.8 cm above the floor and at 5 cm from the reward site. The lever was 4.8 cm wide and 1.9 cm deep when fully inserted. A sign-tracking response was recorded whenever the rat moved the lever sufficiently to

close a circuit. Minimum force on the lever was required to record a lever press. A computer controlled the presentations of the CS and US, and recorded sign tracking. The sucrose solutions were prepared by mixing commercial grade cane sugar with distilled water, w/w (e.g., the 32% solution was prepared by mixing 32 g of sugar for every 68 g of distilled water). Solutions were prepared the day before and presented at room temperature.

Procedure

Rats were matched in terms of previous experience and randomly assigned to the new conditions. Naïve rats were randomly assigned to the conditions. The experiment included seven groups labeled according to the sucrose concentration (%) administered during preshift (training incentives) and postshift trials (test incentives): 2–2, 4–4, 8–8, 16–2, 16–4, 32–4, and 32–8. These solutions were chosen to generate test/training ratios of 0.25 for 2 groups (16–4, 32–8), and 0.125 for the other two groups (16–2, 32–4), while simultaneously testing two groups trained differentially during preshift trials, but given the same postshift solution: Groups 16–4 and 32–4. Groups 2–2, 4–4, and 8–8 where included as unshifted controls.

One session per day was administered throughout the experiment. Rats received two daily sessions of habituation to the training context, each lasting 20 min—the approximate duration of subsequent training sessions. Neither the lever nor the sucrose solution was presented during these two habituation sessions. There were 15 preshift sessions followed by 15 postshift sessions. In each session, the rat was placed in a chamber and given 10 trials consisting of a 10-s lever presentation followed by a 10-s presentation of the liquid dipper. A 1-s long beep was presented each time the lever was inserted into the box. At the start and end of each session, and between successive trials, there was an average interval of 100 s (range: 64–140 s). The running order of 4-rat squads was randomized across groups and days. At the end of each session, animals were immediately withdrawn from the boxes and the chambers swept with a damp paper towel. The downshifts occurred across sessions, with about 23.5 h between the last presentation of the training incentive and the first presentation of the test incentive.

Sign tracking was recorded in terms of the number of times a rat pressed the lever during the 10-s period of lever presentation. These scores were subjected to conventional analysis of variance as described for Experiment 1.

Results and discussion

Absolute response measures

Animals that had performed on average fewer than 5 lever-pressing responses during the last 5 preshift sessions (sessions 11–15) were discarded from all data analyses. This criterion was established to correct for animals that performed at a very low level or did not respond at all, a relatively common outcome in autoshaping experiments (Tomie, Aguado, Pohorecky, & Benjamin, 2000). Because the goal of this experiment was to assess response decrements after incentive downshifts, only animals that developed some minimum amount of responding could potentially provide useful data. A total of 12 animals (out of 66 rats) failed to reach this criterion. As a result, the final group sizes were: $n = 7$ for Group 2–2, $n = 6$ for Group 4–4, $n = 6$ for Group 8–8, $n = 10$ for Group 16–2, $n = 10$ for Group 16–4, $n = 7$ for Group 32–4, and $n = 8$ for Group 32–8.

Fig. 4 shows the results for Groups 2–2 and 16–2 (upper panel), Groups 4–4, 16–4, and 32–4 (middle panel), and Groups 8–8 and 32–8 (lower panel), in terms of the mean lever-pressing responses during preshift (1–15) and postshift sessions (16–30). Groups receiving the same test incentive were plotted separately to better visualize the effects of incentive downshifts. There were substantial US-magnitude effects on autoshaping performance
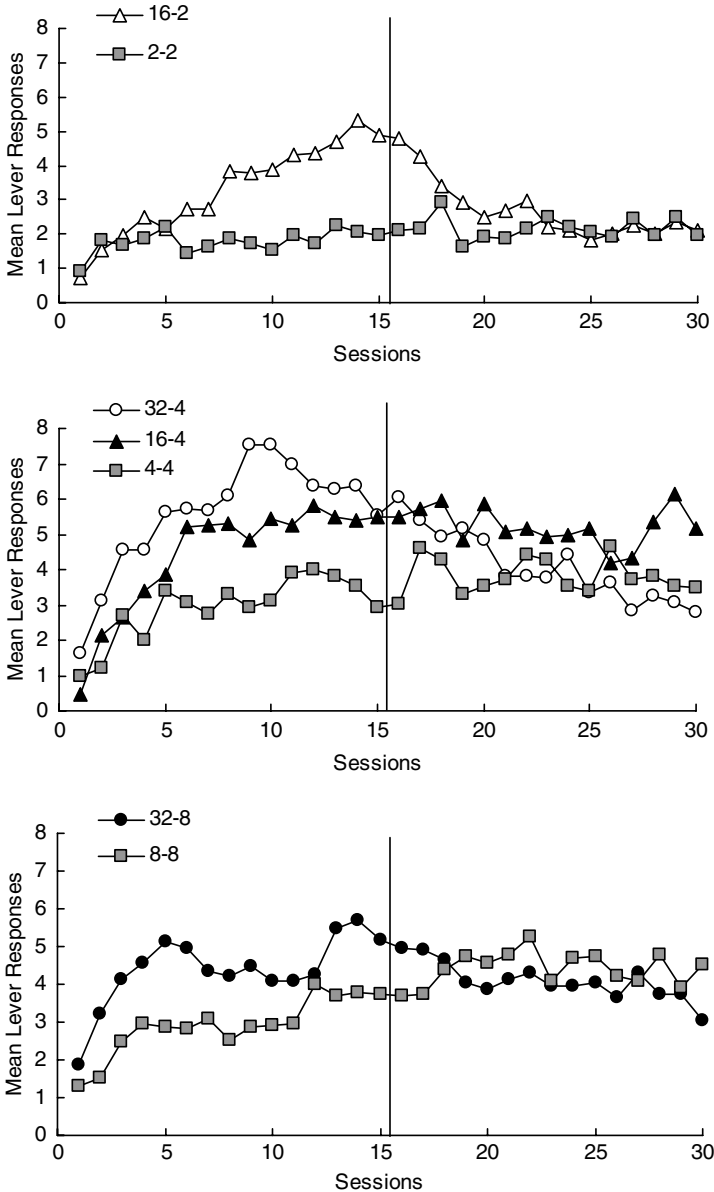

Fig. 4. Sign tracking measured in terms of the rate of lever-pressing responses for groups with postshift sucrose solutions of 2% (upper panel), 4% (middle panel), and 8% (bottom panel), as a function of sessions.

during the preshift sessions. In all cases, the order of group performance was directly related to the magnitude of the sucrose concentration. Separate Training Incentive x Session analyses were computed to evaluate the difference between each downshifted group and its respective unshifted control during the preshift and postshift phases. Preshift performance was analyzed with four Training Incentive (2 vs. 16, 4 vs. 16, 4 vs. 32, 8 vs. 32) × Session (1–15) analyses. The results indicated significant acquisition effects in all four comparisons, $Fs > 3.61$. The interaction between training incentive and session was significant only for the comparison between Groups 2–2 and 16–2, $F(14, 210) = 3.57$. None of the other main effects or interactions was significant in any of these analyses, $Fs < 2.99$. Sign tracking increased in all groups, irrespective of the concentration of the sucrose solution used as the US, with the smallest changes occurring in the 2% sucrose group and the highest in the 32% sucrose groups.

Postshift performance is also depicted in Fig. 4. There was no clear evidence of iSNC in any of the groups, in agreement with what was expected based on the results of analogous runway experiments. Four new Training Incentive (2 vs. 16, 4 vs. 16, 4 vs. 32, 8 vs. 32) × Session (16–30) analyses were computed on the postshift data. The results indicated a significant change in behavior across sessions for the comparisons involving Groups 2–2 and 16–2, $F(14, 210) = 3.87$, and Groups 4–4 and 32–4, $F(14, 154) = 2.10$. The interaction between training incentive and session was also significant for the comparisons between Groups 2–2 and 16–2, $F(14, 210) = 3.32$, and between Groups 4–4 and 32–4, $F(14, 154) = 4.25$. None of the other main effects or interactions were significant, $Fs < 1.41$. Although these results provided no evidence of iSNC in terms of the comparison between downshifted and unshifted groups, the incentive downshift operation was followed by clear performance changes in three of the four groups, exhibiting little or no change only in Group 16–4 (Fig. 4, middle panel). Groups 8–8 and 32–8 (Fig. 4, bottom panel) came closest to exhibiting a conventional iSNC effect, with a clear crossing over of the average group scores. However, as shown above, this effect was nonsignificant.

As noted in Experiment 1, SNC can be demonstrated in a comparison between two downshifted groups receiving the same test incentive, as is the case for Groups 32–4 and 16–4. Fig. 4 indicates that Group 32–4 exhibited a greater change than Group 16–4 during postshift sessions. However, a Training Incentive × Session analysis of the postshift performance of these two groups provided no evidence of SNC. The effects of training incentive, $F < 1$, and of the interaction between training incentive and sessions, $F(14, 210) = 1.48$, were both nonsignificant. There was only evidence of a significant change across sessions, $F(14,210) = 6.95$. Thus, there was no evidence of iSNC in the autoshaping situation with sucrose solutions as the incentives even with the special case of contrast provided by a comparison between Groups 16–4 and 32–4.

Relative response measures

Fig. 5 shows the relationship between US magnitude and the terminal performance level during the preshift phase. Each point represents the average response rate for each group during the last five preshift sessions (11–15). Asymptotic sign tracking was a monotonic exponential function of training incentive. However, there was considerable individual variability in responding, as shown by the standard error bars. Independent one-way ANOVAs conducted on the two group pairs exposed to 16% or 32% sucrose solutions indicated nonsignificant differences, $Fs < 1$. An additional one-way ANOVA was then conducted on the five concentration groups (2%, 4%, 8%, 16%, 32% sucrose), pooling
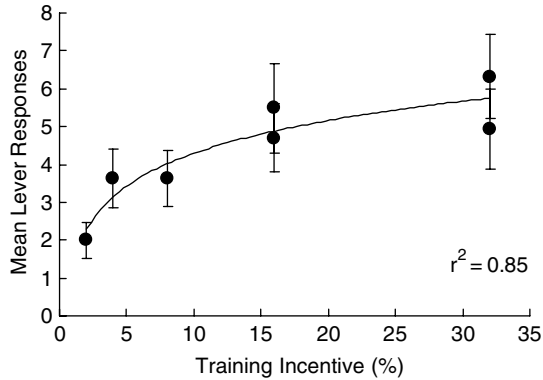
Fig. 5. Mean (± SEM) sign tracking in sessions 11–15 for all the groups as a function of preshift sucrose concentration.

animals from the two groups exposed to 16% and 32% sucrose. This analysis showed a small but statistically significant effect, $F(4, 54) = 2.60$. Pairwise LSD comparisons confirmed that the sources of this effect were the significant differences between 2% and both 16% and 32%, ps < 0.02. None of the other comparisons yielded a significant difference, ps > 0.08.

Based on these asymptotic values, the data were transformed according to the same difference score used in the previous experiment. The mean number of responses for each session, in each rat, was subtracted from the mean obtained for sessions 11–15 in that rat. The resulting group averages are plotted in Fig. 6. There are two main features in these results. First, the performance of the unshifted control groups remained relatively stable throughout postshift sessions. Second, the degree of change in postshift performance was a direct function of the size of the preshift-to-postshift discrepancy in sucrose concentration. Notice that although these functions give the appearance of SNC effects, the dependent variable (a measure of relative change) only reflects rates of change, not the undershooting in absolute scores that defines SNC. Larger behavioral changes were observed in Group 16–2 and 32–4, than in Groups 16–4 and 32–8.

Analyses of the preshift performance were based on independent Training Incentive (2 vs. 16, 4 vs. 16, 4 vs. 32, 8 vs. 32) × Session (1–10) ANOVAs. Only sessions 1–10 were incorporated into these analyses because sessions 11–15 were the source of the asymptotic response rates used to compute the difference scores. The results indicated significant acquisition effects for all four pairwise analyses, Fs > 2.95. The main effect of training incentive and of the interaction between training incentive and sessions were significant only for the comparison between Groups 2–2 and 16–2, $F(1, 15) = 18.3$ and $F(9, 135) = 2.51$, respectively. None of the other main effects or interactions was significant, Fs < 1.75. These preshift results are in general agreement with those shown in Fig. 5 for absolute response averages.

Similar analyses were conducted on the postshift data with the following results. Significant changes across sessions were obtained for the comparisons between Groups 2–2 and 16–2, $F(14, 210) = 3.86$, and Groups 4–4 and 32–4, $F(14, 154) = 2.10$. The interaction between training incentive and sessions was significant for the comparisons between
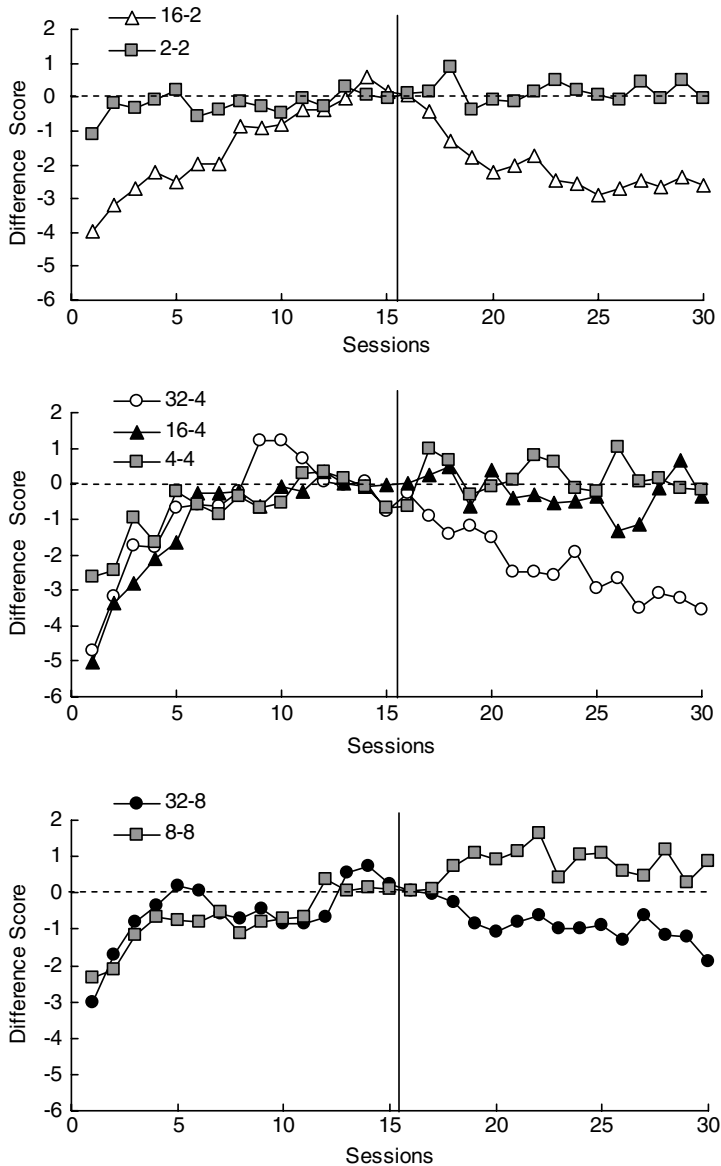
Fig. 6. Difference score (sign tracking on session "n" minus mean sign tracking on sessions 11–15) for groups trained with a postshift solution of 2% (upper panel), 4% (middle panel), and 8% (bottom panel), as a function of sessions.

Groups 2–2 and 16–2, $F(14, 210) = 3.23$, and Groups 4–4 and 32–4, $F(14, 154) = 4.25$. There was also a significant main effect of training incentive for Groups 2–2 and 16–2, $F(1, 15) = 10.98$. These analyses yielded no additional significant effects, $Fs < 4.45$.

The critical groups are those shifted conditions that shared a common test/training ratio. Given that the difference scores cancelled out individual differences, any control
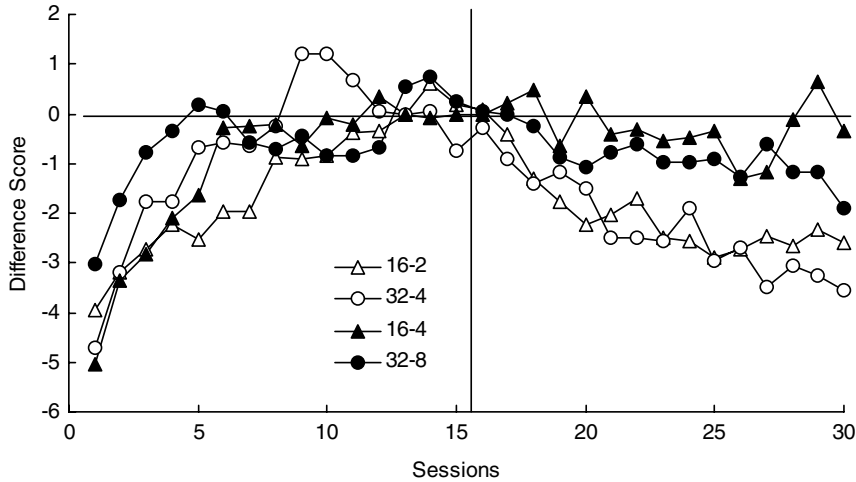
Fig. 7. Sign tracking difference score for groups with preshift/postshift ratios of 0.125 (Groups 16–2 and 32–4) and 0.25 (Groups 16–4 and 32–8) as a function of sessions.

of postshift performance by the ratio should be clearly visible. As shown in Fig. 7, the four critical groups were ordered according to the test/training ratio. The two groups exposed to a ratio of 0.125 (Groups 16–2 and 32–4) changed at about the same rate, and both changed faster than the two groups exposed to a ratio of 0.25 (Groups 16–4 and 32–8). A Ratio (0.125, 0.25) × Training Incentive (16, 32) × Session (16–30) analysis confirmed these conclusions. Postshift performance was significantly affected by the test/training ratio, $F(1, 31) = 5.78$, but not by the training incentive, $F < 1$. There was also a significant interaction between ratio and sessions, $F(14, 434) = 1.93$. The change across sessions was significant, $F(14, 434) = 7.03$. All the other effects were negligible, $Fs < 1$. Notice that all the effects involving training incentive were nonsignificant. Autoshaping performance after incentive downshift was determined by the ratio of the solutions involved, rather than of their absolute values.

Fig. 7 also shows the preshift performance. In this case, a Ratio (0.125, 0.25) × Training Incentive (16, 32) × Session (1–10) analysis indicated a significant effect across sessions, $F(9, 279) = 19.25$, and a significant triple interaction, $F(9, 279) = 2.34$. None of the other effects was significant, $Fs < 1.42$. The triple interaction captured the extensive crossing over between functions. However, there was no clear trend among the groups during preshift sessions.

General discussion

The present experiments studied the effects of downshifts in incentive magnitude using anticipatory behaviors as response measure in the straight runway and autoshaping situations with rats. The distinctive aspect of the present experiments was the parametric manipulation of the training and test magnitudes that allowed a determination of the extent to which behavioral change following the downshift was a function of the absolute vs. the relative magnitudes of the incentives. Previous research using a consummatory response preparation had shown that, within limits, the level of consummatory responding

observed after the downshift was a function of the ratio between the magnitude of the test (postshift) incentive to that of the training (preshift) incentive (Papini & Pellegrini, in press). It was suggested that these results represent a special case of Weber's law, widely applied to sensory data, but less well understood in relation to comparisons in which one of the terms is an associatively reactivated memory (see Gibbon & Church, 1984; Hubbard, 1994). As noted in the introduction, the typical consummatory training situation, where a rat's direct contact with the incentive is the dependent measure, leads to a type of incentive relativity dependent on recognition memory. The present experiments had two main goals: (1) To investigate whether a similar type of constant proportionality applies to anticipatory behavior, that is, to behavior that occurs before the animal makes direct contact with the incentive, and (2) To determine whether constant proportionality occurs in the absence of a SNC effect and, therefore, in the absence of behavioral evidence for emotional activation. The results indicated that the downshifted anticipatory performance of rats was significantly related to the test/training ratio, even in the absence of a conventional SNC effect.

Consider the results of these experiments and the potential problems of interpretation they pose for the conclusions drawn in the previous paragraph. First, it is usually assumed that despite being based on a Pavlovian procedure, autoshaping in rats carries a significant instrumental component. This assumption is based on the sensitivity of rat autoshaping to omission contingencies (Antip, 1977; Davey et al., 1981; Stiers & Silberberg, 1974). Another claim relevant to this issue is that running behavior in a runway can be best understood as arising from Pavlovian contingencies that control goal-approach behavior (Dickinson & Balleine, 1994). In fact, rats find it difficult to adjust to a variation of omission contingency in the runway that requires them to spend a minimum amount of time before arriving at the goal. However, as shown by Logan (1960) in a variety of experiments, they do eventually adjust to these conditions. Thus, there are no reasons to seriously object to the assumption that autoshaping responding in rats, like running in the runway, involves both Pavlovian and instrumental components.

Second, based on analogous runway experiments, it was expected that downshifts in the concentration of sucrose solutions should not lead to a conventional iSNC in the autoshaping situation implemented in Experiment 2. This was required to answer the question of whether anticipatory behavior would obey Weber's law in the absence of any behavioral evidence of emotional activation. The phrase "conventional iSNC effect" implies a comparison between a downshifted and an unshifted control, and, as far as this comparison is concerned, the results replicated the lack of iSNC reported in a variety of runway experiments (see references in the introduction to Experiment 2). However, the essence of SNC is that groups given different preshift treatment are compared under the same postshift conditions of incentive magnitude. This requirement is met by the conventional downshifted-unshifted comparison, but also by groups downshifted to the same test magnitude from different training magnitudes. Using this special case, iSNC was demonstrated in the runway situation (Experiment 1), but still failed to emerge in the autoshaping situation (Experiment 2).

The basic result reported in the present experiments and in Papini and Pellegrini (in press) is that the scaling of relative incentive value obeys Weber's law. One may assume that, in general, discriminable differences between incentives of different magnitudes conform to Weber's law. In agreement with this assumption, progressive ratio performance shows a linear relationship between the breaking point (the largest ratio completed before

responding stops) and the concentration of the sucrose solution reinforcer, when varied according to a geometric progression (i.e., 2, 4, 8, 16, 32, and 64; Sclafani & Ackroff, 2003). This observation is consistent with the hypothesis that incentive value is a negatively accelerated function of incentive magnitude (e.g., number of pellets or sucrose concentration). This assumption however, does not solve the problem posed by incentive contrast effects: A $32 \rightarrow 4$ downshift produces a transient reduction in performance compared to $16 \rightarrow 4$ and $4 \rightarrow 4$ conditions. An effective theoretical resolution requires a hypothesis that predicts SNC, as well as the negatively accelerated relationship between asymptotic responding and incentive magnitude.

To explain the results of learning experiments, mathematical models have been frequently developed on the assumption of a linear relationship between conditioned responding and incentive value. Furthermore, a deep-rooted tradition in the theoretical modeling of learning phenomena is based on the assumption that changes in associative strength that occur during conditioning can be explained using linear operators that preserve linear combinations (e.g., Bush & Mosteller, 1951; Rescorla & Wagner, 1972). Can the application of Weber's law to incentive relativity be derived from the linear relationship between conditioned responding and incentive value?

Although Bush and Mosteller (1951) pointed out in passing that their linear operator hypothesis was in general agreement with Crespi's (1942) iSNC data, the results under consideration allow for a more extensive evaluation and point to a potential theoretical solution for the problem generated by incentive relativity phenomena for several current conditioning theories. The data to be explained are summarized in Table 1. For each experiment, the column labeled "Post" reflects the performance in downshifted trials (Papini & Pellegrini, in press, Experiment 1/c; were "c" stands for "consummatory"), during the first postshift trial (Papini & Pellegrini, in press, Experiment 2/c), or during the entire postshift phase (present Experiments 1/r and 2/a; were "r"stands for "runway" and "a" for "autoshaping"). The column labeled $\Delta I/I$ shows a computation of the proportion of behavioral change due to reward downshift. Accordingly, ΔI was assessed in terms of the test performance, whereas I was assessed in terms of training performance. The fraction $\Delta I/I$ is used to estimate Weber's fraction, given that if Weber's law is at all applicable

Table 1
Summary of empirical results and predictions derived from the Rescorla–Wagner and ratio models

| Group | Ratio | Data | | | | | | | | Simulations | | | |
| | | Exp. 1/C | | Exp. 2/C | | Exp. 1/R | | Exp. 2/A | | RW Model | | Ratio Model | |
		Post	$\Delta I/I$	Post	$\Delta I/I$	Post	$\Delta I/I$	Post	$\Delta I/I$	Post	$\Delta I/I$	Post	$\Delta I/I$
32–8	0.25	101	0.69	105	0.68	0.72	1.35	4.08	0.95	8	0.25	0.25	0.25
16–4	0.25	115	0.77	108	0.67	0.63	1.26	5.22	0.97	4	0.25	0.25	0.25
32–4	0.125	62	0.42	90	0.61	0.46	0.79	4.07	0.65	4	0.13	0.13	0.13
16–2	0.125	77	0.52	84	0.50	0.49	0.96	2.69	0.59	2	0.13	0.13	0.13

Note: Post: performance on occasional downshift trials for Experiment 1C, for trial 11 in Experiments 2/C, for 19 postshift sessions in Experiment 1/R, and for 15 postshift sessions in Experiment 2/A. $\Delta I/I$: proportion of behavioral change due to reward downshift, calculated by the formula b/a, where a equals performance on training trials in Experiment 1/C, on trial 10 in Experiments 2/C, and on the last five preshift sessions in Experiment 2/A, whereas b equals to postshift performance as calculated for Post (see above). Simulation parameters: $\alpha = \beta = 1$, except for the computation of μ, for which $\beta = 0.5$; $c = 0.01$.

to the data, $\Delta I/I$ should be similar for animals that experienced an equal shift ratio under equal training conditions. This behavioral psychophysical approach may be seen as in general accordance with previous psychophysical studies that used a comparative perspective (e.g., Sarris, 2002). For Experiment 1/c, these terms were calculated from the goal tracking times of the test trials (see Papini & Pellegrini, in press, Fig. 2); for Experiment 2/c, these terms were calculated from the goal tracking times collected during trials 10 and 11; and for the present Experiments 1/r and 2/a, training performance was assessed in terms of baseline data (i.e., average response rate during the last 5 preshift sessions) and test performance was assessed in terms of the mean response rate of all postshift sessions. Start latencies were used for Experiment 1/r because this measure showed the greatest control by the test/training ratio.

A model that correctly explains these experimental results needs to predict two features of the data presented in Table 1. First, it must predict the special case of SNC represented by a higher postshift responding for Group 16–4 than for Group 32–4. Second, it must predict similar $\Delta I/I$ fractions for groups exposed to the same test/training ratio, but higher $\Delta I/I$ fractions for groups exposed to a 0.125 ratio than to a 0.25 ratio. The agreement between $\Delta I/I$ values within any given ratio was generally good and very good in some cases (e.g., 0.68 and 0.67 for a 0.25 ratio, in Experiment 2/c). In addition, $\Delta I/I$ fractions were always larger for groups trained under a 0.125 ratio, than for groups trained under a 0.25 ratio. Although less than perfect, these numbers are in agreement with the two features that need explanation—the special contrast case and the constancy of $\Delta I/I$ fractions.

For the sake of simplicity, consider the model proposed by Rescorla and Wagner (1972), explicitly based on a variation of the Bush–Mosteller linear operator and incapable of accounting for incentive relativity effects (Miller, Barnet, & Grahame, 1995). According to this model, the conditioned response, R, is a monotonic function of the associative strength of the CS. This is represented in the following equation:

$$R = f(V_{n-1} + \Delta V_n) \tag{1}$$

where V_{n-1} represents the associative strength of a signal on trial $n - 1$ and ΔV represents the change in associative strength on trial n. ΔV_n changes according to the equation:

$$\Delta V_n = \alpha\beta(\lambda - V_{n-1}) \tag{2}$$

where α and β are learning rate parameters determined by stimulus properties (e.g., salience), and λ represents the total amount of associative strength a given reinforcer can support (i.e., associative strength at asymptotic levels). When applied to situations involving a successive downshift in incentive magnitude, the Rescorla–Wagner model predicts Weber's law but fails to predict SNC, regardless of the parameters used in the simulations. Instead of contrast, the Rescorla–Wagner model predicts a gradual response adjustment to a performance level equal to the absolute value of the postshift incentive. As a result, this model cannot explain incentive relativity. The highest possible values for α and β were chosen in the present simulations, so as to maximize change in V immediately after the downshift. As shown graphically in Fig. 8, top panel, Groups 16–4 and 32–4, both receiving 4% solution during postshift trials, achieved the same performance in the Rescorla–Wagner simulation, a result unlike that obtained in any of the experiments, including the present Experiment 2, which did not yield evidence of iSNC in the autoshaping situation with sucrose solutions as the US. However, notice that, in agreement with the empirical data, the Rescorla–Wagner model does predict a constant $\Delta I/I$ fraction within each
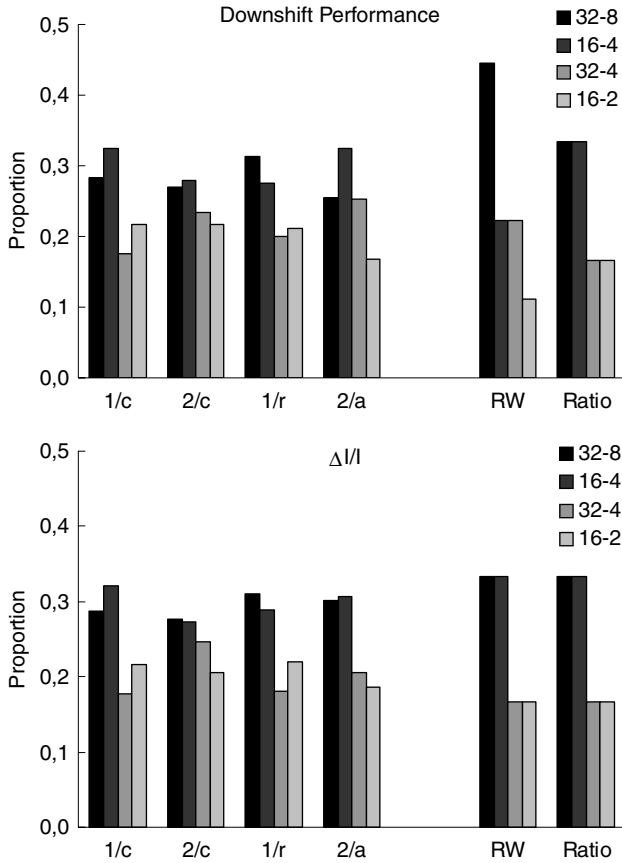
Fig. 8. Proportion of mean downshift performance (upper panel) and proportion of mean $\Delta I/I$ (bottom panel) calculated for each of four groups (32–8, 32–4, 16–4 and 16–2) trained in four different experiments (1/c, 2/c, 1/r and 2/a), and the respective proportions for simulated results obtained with the Rescorla and Wagner (1972) and ratio models. Each value represents the group's mean divided by the sum of all group means. The data used to calculate each proportion are shown in Table 1.

test/training ratio and a larger fraction for the 0.125 ratio than for the 0.25 ratio (Fig. 8, bottom panel).

The alternative view proposed here is referred to as the ratio rule. The ratio rule is based on an incentive averaging mechanism that maintains the general structure and predictions of the Rescorla–Wagner model, but that can account for incentive relativity effects. According to this rule,

$$\Delta V_n = \alpha\beta[\lambda/(\mu + c) - V_{n-1}] \tag{3}$$

where μ represents the memory of the average value of incentives experienced previously in the same situation and is calculated as a moving average that takes into account several past training trials. For simplicity, Eqs. (1) and (2) are proposed for calculating μ. In Eq. (3), c is a small constant. The ratio rule is based on the assumption that changes in associative strength, ΔV, are a function of the current incentive value, λ, weighted by the average value of recently experienced incentives, μ. As can be appreciated in Table 1

and Fig. 8, this model predicts both the special contrast case and the constancy of $\Delta I/I$ fractions in situations involving incentive downshifts. Additionally, Eq. (3) could predict the differences between the rapid changes observed in a consummatory situation and the slow changes observed in autoshaping situations, by assuming higher learning rate parameters (α and β) for the former than for the latter. Work beyond the scope of the present paper is needed to evaluate this and other predictions derived from the ratio rule.

Incentive value is one of the most relevant factors determining acquired behavior. The applicability of Weber's law to incentive relativity effects such as SNC strengthens the notion that the effective incentive value on any given conditioning trial is determined strongly and systematically by the value of previously experienced incentives. The cued-recall incentive-relativity effect observed in the start section of the runway, in Experiment 1, is especially interesting in this context. Because anticipatory behavior was recorded 24 h after the last experience with the incentive, alternative sensory or performance based explanations of this effect can be safely eliminated. The dissociation between SNC and Weber's law in Experiment 2 suggests that constant proportionality is more fundamental than the excessive behavioral changes afforded by incentive contrast effects. Because SNC is not a general phenomenon in vertebrate learning (Papini, 2002, 2003), the question remains at to whether species that do not normally show the effect would nonetheless exhibit constant proportionality in incentive downshift situations. Preliminary unpublished data suggest that pigeons, which do not exhibit iSNC in key-pecking experiments (Papini, 1997; Papini & Thomas, 1997), exhibit control by the absolute magnitude of the preshift reinforcer, rather than by the test/training ratio. Finally, the apparent failure of downshifts in sucrose concentrations to support cued-recall relativity remains an open issue. Visual, auditory, and even olfactory stimuli can be reactivated in memory (Stevenson & Case, 2005); thus, why would taste stimuli be an exception?

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