Available online at www.sciencedirect.com
ScienceDirect
Learning and Motivation 37 (2006) 357–378
Learning and Motivation
www.elsevier.com/locate/l&m

Scaling relative incentive value in consummatory behavior ☆

Mauricio R. Papini [a,*], Santiago Pellegrini [b]

[a] *Department of Psychology, Texas Christian University, Box 298920, Fort Worth, TX 76129, USA*
[b] *Instituto de Biología y Medicina Experimental (CONICET) and Universidad de Buenos Aires, Vuelta de Obligado 2490, 1428-Buenos Aires, Argentina*

Received 3 November 2005; received in revised form 16 January 2006
Available online 17 April 2006

Abstract

Surprising downshifts from more preferred (training incentive) to less preferred incentives (test incentive) are usually accompanied by emotional activation and suppression of conditioned behavior in rats. Two experiments were designed to determine whether consummatory behavior is similarly affected by downshifts of equal proportions. Within limits, the degree of consummatory responding during incentive downshift was similar with equal ratios of test concentration to training concentration. Thus, 32–4% and 16–2% downshifts (1:8 test/training ratios) caused similar levels of consummatory behavior, despite differences in the absolute concentrations of the solutions involved in the downshift. An interpretation based on sensory contrast was discarded because of the long intervals between training and test solutions (40 min and 24 h in Experiments 1 and 2, respectively). It is suggested that Weber's law regulates behavioral suppression after reward downshifts. A theoretical framework for the interpretation of these data is presented.

Keywords: Incentive contrast; Weber's law; Recognition relativity; Cued-recall relativity; Rats

☆ The research reported in this article was partially supported by Grant P602, UBACYT, and Grant N1022/03, CONICET, to S.P., and by Grant 60213, TCU/RCAF, to M.R.P. The authors thank Charles Bond for helping with the multilevel statistical analyses, to Pablo Gomez for contributing to the implementation of Experiment 2, and to Alba Mustaca, Ruben Muzio, and Mariana Bentosela for thoughtful discussions about these experiments.
* Corresponding author. Fax: +817 257 7681.
E-mail addresses: m.papini@tcu.edu (M.R. Papini), santiago.pellegrini@gmail.com (S. Pellegrini).

0023-9690/$ - see front matter
doi:10.1016/j.lmot.2006.01.001

Introduction

"The evidence shows that reinforcing agents behave like psychophysical stimuli being scalable on continua having neutral or indifferent regions and in being subject to both series and anchor effects," argued Helson (1964, pp. 448–449). If this is correct, psychophysical laws derived from the study of sensory processes should be applicable to incentive learning phenomena, and vice versa. One such psychophysical law is the notion that judgments of stimulus change are constant at a constant at proportion of the ratio of stimulus change (ΔI) to stimulus intensity (I), known as Weber's law (Fechner, 1965; Luce & Krumhansl, 1988). Considering the potential relevance of this issue for an understanding of incentive processes, it seems surprising that Helson's suggestion had little impact in the study of conditioning. More than four decades after, available evidence about the relationship between Weber's law and conditioning phenomena is scarce in the animal literature (e.g., interval timing; Staddon & Cerutti, 2003), although less so in the human cognitive literature (Hubbard, 1994). The present studies focused on the applicability of Weber's law to situations involving surprising reward downshifts with relatively long time intervals between the large-preshift and the small-postshift rewards. The central question was whether responding after the downshift is determined by the ratio of the postshift incentive magnitude (here called the *test incentive*, assumed to be equivalent to ΔI) to the preshift incentive magnitude (the *training incentive*, assumed to be equivalent to I). Positive evidence would indicate that relative incentive value obeys Weber's law. The rest of this introduction describes this rationale in detail.

Incentive relativity: A classification

Although some reinforcers are more effective than others in maintaining conditioned responding, this does not imply that reinforcers have an absolute value determined by their sensory and physiological properties. Rather, research involving incentive downshifts shows that the capacity of a given reward to maintain conditioned responding is inversely related to the magnitude of the reward experienced previously in the same situation (Amsel, 1992; Flaherty, 1996). Therefore, incentive value is better conceptualized as a property determined, at least in part, by an evaluative process in which memory and expectation play a major role. Following Flaherty (1996), this will be referred to as *incentive relativity*.

Incentive relativity effects have been known since the late 1920s (Elliot, 1928; Tinklepaugh, 1928) and have mostly been studied in the context of the successive negative contrast (SNC) effect. In the SNC situation, the consummatory or instrumental performance of an experimental group exposed to a downshift from a large to a small reward is compared to the performance of an unshifted control group always exposed to the small reward. In a typical consummatory SNC situation (cSNC), rats given free access to a 32% sucrose solution (training incentive) during several trials exhibit greater consummatory suppression when shifted to a 4% solution (test incentive) than animals given always the 4% solution (Vogel, Mikulka, & Spear, 1968). Similarly, rats running in a runway for a large amount of food (training incentive) later show suppression of running speed when shifted to a small amount of food (test incentive), relative to unshifted controls (instrumental SNC or iSNC; Crespi, 1942). In SNC, the degree of behavioral deterioration following incentive downshift is inversely related to the magnitude of the training incentive. For example, rats trained to run for either 1, 2, 4, 8, or 16 food pellets for 20 daily trials and subsequently downshifted to 1 pellet for 14 additional trials, showed greater performance deterioration as the magnitude of the training incentive increased from 2 to 16 pellets (DiLollo & Beez, 1966; see also Flaherty, Becker, & Osborne, 1983).

If the cSNC effect is taken as a point of reference, incentive relativity effects can be produced by at least three different processes. One possibility, here called *sensory relativity*, is that the test incentive is presented at a time when the sensory trace of the training incentive is still active (Fig. 1A). This requires a short temporal interval between the two incentives. For example, in the cSNC situation, sensory adaptation from exposure to the training

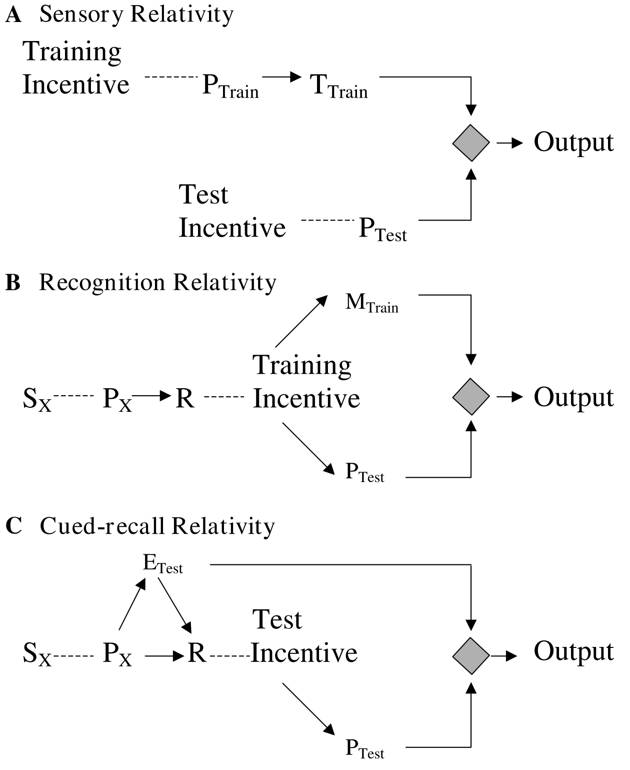

Fig. 1. A representation of the critical components of the comparison process assumed to operate in sensory (A), recognition (B), and cued-recall relativity (C). E_{Train}, expectancy of the training incentive. M_{Train}, memory of the training incentive. P_{Train}, the sensory-perceptual encoding of the training incentive. P_{Test}, the sensory-perceptual encoding of the test incentive. P_X, the sensory-perceptual encoding of the effective exteroceptive stimulus controlling behavior. *R*, response. *S*, effective exteroceptive stimulus. T_{Train}, the decaying sensory trace left by exposure to the training incentive. (It is assumed that all the rewards have a sensory trace, but only T_{Train} is represented because it is the only one assumed to participate in the comparison process during sensory relativity.) Training and Test Incentives denote contact and consumption of the large and small rewards, respectively. Arrows represent causal connections between psychological events. Dashed lines represent organism–environment interactions. Diamond boxes represent the comparison process. The Output is not elaborated, but it refers to a series of processes affecting consummatory behavior. A parallel-process associative structure inspired in two-process learning theory is assumed for the case of cued-recall relativity (Mowrer, 1947), with S–R and S–E–R links in parallel.

solution could cause the lower solution to be perceived as less sweet (Bitterman, 1976; Flaherty & Sepanak, 1978).

A second possibility is that cSNC arises from a comparison between the value of the test incentive and the remembered value of the training incentive experienced previously under similar conditions. This possibility, here called *recognition relativity*, is based on a recognition memory mechanism with at least three different components (Fig. 1B): (1) perception of the test solution reactivates the memory of the training solution; (2) current (test) and remembered (training) solutions are compared with each other; and (3) mismatch detection leads to consummatory suppression. The last two components merit one further comment. Evidence from spaced-trial situations indicates that when current and remembered values are compared, and a difference is detected, an emotional reaction is engaged. For example, a downshift from 32 to 4% sucrose is accompanied by pituitary–adrenal activation (Flaherty, Becker, & Pohorecky, 1985), whereas corticosterone administration after the first downshift experience enhances the cSNC effect (Bentosela, Ruetti, Muzio, Mustaca, & Papini, 2006). It is conceivable that smaller downshifts are detected, but do not result in measurable emotional reactions. Research concerned with the emotional response that follows incentive downshift has produced results consistent with Amsel's (1992) frustration theory (Papini, 2003; Papini & Dudley, 1997; Papini, Wood, Daniel, & Norris, 2006), according to which the behavioral suppression that follows incentive downshift is driven by unconditioned and conditioned frustrative reactions. Thus, recognition relativity involves an emotional component.

Incentive relativity may also arise from a comparison between an anticipatory reward expectancy and current reward perception—*cued-recall relativity* (Fig. 1C). According to this mechanism, stimuli preceding reward administration activate expectancies that orient the animal to the goal. This reward expectancy is then compared to the current reinforcer value. Cued-recall relativity is clearly implicated in iSNC because the critical behavioral measure is taken before the animal contacts the reward (Crespi, 1942). However, its role in cSNC is called into question by the apparent failure of contextual cues to control consummatory suppression (Flaherty, Hrabinski, & Grigson, 1990). The role of conditioned frustration in iSNC is suggested by the effects of anxiolytics, which reduce or eliminate the effect (Rosen & Tessel, 1970).

Implications of the proposed classification

The distinction between these three forms of incentive relativity—sensory, recognition, and cued recall—is based on the temporal properties of the training protocol, a fact suggesting that these mechanisms differ in their temporal resolution. Sensory relativity has a temporal resolution in the order of seconds to minutes because stimulus traces are generally assumed to spontaneously decay in time at a relatively rapid rate (Atkinson & Shiffrin, 1968; Hull, 1943; Roberts & Grant, 1976). These effects are particularly strong when stimuli are presented over short time intervals, so that the sensory-perceptual trace of one stimulus is compared with the direct perception of the other (e.g., Lawless, Horne, & Spiers, 2000; Moskowitz, 1970; Stevens, 1969). Recognition and cued-recall relativity are less restricted temporally, because they depend on a stable long-term memory of the training incentive. Experiments introducing a retention interval between the last exposure to the training incentive and the first exposure to the test incentive show that both cSNC [see summary of several studies in (Flaherty, 1996, pp. 40–42)], and iSNC (Gleitman & Steinman, 1964) survive for several days, but are eventually eliminated.

This analysis of incentive relativity in terms of three distinct processes provides insights into two issues. First, the distinction between recognition and cued-recall relativity may shed light on the heretofore unexplained dissociation between iSNC and cSNC when sucrose solutions are delivered as rewards. No evidence of iSNC has been found when rats are reinforced with sucrose solutions of different concentrations for running in a runway (e.g., Barnes & Tombaugh, 1973; Rosen, 1966; Rosen & Ison, 1965; Sastre, Lin, & Reilly, 2005; Shanab, France, & Young, 1976; Spear, 1965). Furthermore, whereas rats fail to show iSNC in instrumental behavior, the same rats exhibit cSNC in the goal box (Flaherty & Caprio, 1976). This dissociation suggests that cSNC provides a more sensitive measure of incentive relativity than iSNC, implying that cSNC may be based on a more efficient memory-retrieval process than iSNC. The failure of contextual cues to influence cSNC (Flaherty et al., 1990) further suggests that the triggering factor in the consummatory situation is the initial perception of the downshifted solution. These findings suggested the conceptualization of cSNC as a recognition-memory task (see Fig. 1B). A comparison of recognition and cued-recall memory in humans suggests that the underlying neural networks may be distinguishable (Cabeza et al., 1997; Hasselmo & Wyble, 1997; West & Krompinger, 2005). Interestingly, systemic administration of scopolamine, a cholinergic antagonist, affects cued-recall but not recognition recall (Ghoneim & Mewaldt, 1977). This is consistent with the lack of effects of scopolamine on cSNC (Bentosela et al., 2005; Flaherty & Meinrath, 1979). Similarly, lesions of the hippocampus, an area rich in cholinergic receptors, eliminate iSNC (Franchina & Brown, 1971), but do not affect cSNC (Flaherty, Rowan, Emerich, & Walsh, 1989).

The second insight derived from the distinction between different types of incentive relativity suggests the question explored in these experiments: Is Weber's law applicable to incentive relativity? If judgments about a change in the sweetness of a sucrose solution are a function of the $\Delta I/I$ ratio, at least within limits (Lawless et al., 2000), then would a similar invariance apply when one of the terms, I, is a reactivated memory, rather than a sensory trace?

Rationale of the present studies

The present studies ask whether the level of consummatory responding following incentive downshift is a function of a test/training ratio, rather than of the absolute intensity of the postshift solution, or of the difference between the postshift and preshift solutions. It is proposed here that the test/training ratio is equivalent to Weber's law (Fechner, 1965; Luce & Krumhansl, 1988). Weber's law is a well-documented regularity for sensory relativity effects that also applies to the detection of differences in sucrose solutions of various concentrations (Lawless et al., 2000; Moskowitz, 1970; Stevens, 1969), but it has not been explored in the conventional SNC situation in which incentive downshift occurs after considerably longer time intervals. To test this hypothesis in a cSNC procedure, the consummatory behavior induced by different test incentives must be assessed as a function of various training incentives, but under conditions that make it implausible that sensory traces of the training solution are still active when the test solution is presented. This can be achieved by lengthening the interval between the training and test solutions. If it can be assumed that sensory traces of the training solution were minimized or eliminated, relativity effects can be attributed to a comparison between the current test solution and the reactivated memory of the training solution. In Experiment 1, the training incentive was treated as a between-subject factor whereas the test incentive was treated as a within-subject factor. In Experiment 2, both test and training incentives were treated as between-subject factors. The training-test interval was 40 min in Experiment 1 and about 24 h in Experiment 2, both sufficiently long to assume the complete decay of sensory traces of the training solution.

cSNC was not assessed in relation to unshifted control groups, but consumption of the same test incentive in animals that experienced different training incentives was compared. In addition to minimizing the number of animals, this procedure was adopted for the following reasons. First, the hypothesis tested in this experiment does not require the occurrence of cSNC as defined in terms of a difference between downshifted and unshifted controls. Rather, it requires a comparison of the effects of different magnitudes of incentive downshift on consummatory behavior. Second, the extensive literature on downshifts of sucrose concentrations (Flaherty, 1996) suggests that the conventional cSNC effect would occur under the present training parameters. Furthermore, cSNC has been observed in previous experiments from the authors' laboratories in which animals received training under the same conditions employed in Experiment 2 (e.g., Pellegrini & Mustaca, 2000, Experiment 1; Wood, Daniel, & Papini, 2005). Third, and most importantly, whereas an assessment of SNC in terms of a comparison between downshifted and unshifted controls may be seen as the paradigmatic case, the essential comparison requires different training conditions but the same testing conditions. The paradigmatic comparison between $32 \rightarrow 4$ and $4 \rightarrow 4$ meets this requirement, but so do other special cases in which both training solutions are different from the test solutions, such as, for example, a comparison between $32 \rightarrow 4$ and $8 \rightarrow 4$. Greater behavioral suppression in the former than in the latter provides prima facie evidence for incentive relativity because the design meets the conditions of the essential comparison criterion outlined above (for evidence, see Crespi, 1942; DiLollo & Beez, 1966; Flaherty et al., 1983). Finally, experiments employing the autoshaping procedure in rats, with sucrose solutions as rewards, showed that incentive relativity effects arise even in the absence of SNC, as assessed in the paradigmatic comparison between downshifted and unshifted groups (Pellegrini & Papini, in press).

Two experiments are reported in this paper, both providing evidence that the degree of consummatory suppression after incentive downshift is a constant function of the proportion between the incentive magnitudes of the preshift and postshift sucrose solutions. In both experiments, the downshift operation was administered after time intervals long enough to minimize or eliminate traces of the training solution: 40 min in Experiment 1 and 24 h in Experiment 2. All together these data show that SNC obeys Weber's law, at least within limits.

Experiment 1

Experiment 1 was designed to collect data on the effects of incentive downshifts of various magnitudes on consummatory performance. Three groups of rats received access to 16, 24, or 32% sucrose solutions in four daily trials (training solutions). After consummatory performance was established, the solution was shifted to one of a variety of values ranging between 1 and 32% (test solutions), chosen to represent six different test/training ratios, from 0.0625 to 1.00. Because the goal of this experiment was to assess recognition relativity, rather than sensory relativity, a major concern was to drastically reduce the possibility for sensory interactions. As previously mentioned, sensory relativity may explain the consummatory behavior of rats when the sucrose solutions of different magnitudes are administered sufficiently close in time for the sensory effects of the first solution to affect the processing of the second (e.g., Flaherty & Sepanak, 1978). Thus, the interval between successive trials, each of which involved access to a single magnitude, was lengthened to 40 min. Available evidence indicates that preference for a sucrose solution over water decreases as the time between tests is lengthened. For example, rats exposed to a 6% sucrose solution and water decreased preference for the solution as the time between tests was lengthened from 15 to 60-s, with no detectable preference for the 6% solution at 60-s intervals (Beck, Nash, Viernstein, & Gordon, 1972). It was expected that the 40-min long intertrial interval used in the present experiment, substantially longer than the 60-s used in the Beck et al. study, would minimize sensory relativity. Additionally, extensive exposure to the training concentration (16, 24, or 32% in independent groups) was expected to facilitate the establishment of a memory of the training solution against which the test solution could be compared in occasional downshift trials. The parameters used in Experiment 1 were, therefore, assumed to promote recognition relativity, rather than sensory relativity.

Method

Subjects

The subjects were 24 adult, male, experimentally naïve, 110-day old Wistar rats. The average free-food weight was 380.6 g (range: 357–419 g). Rats were kept at an 80–85% of their ad libitum weight by posttrial feeding, about 20 min after the last trial of the day. The colony was under a 12:12 h light:dark cycle (light on at 07:00 h). Temperature was maintained at 22 °C and humidity between 40 and 45%. Trials were administered between 12:30 and 18:30 h.

Apparatus

Rats received training in 4 conditioning chambers, each enclosed in a sound-attenuating cubicle. Each chamber was $40 \times 59 \times 38$ cm (W×L×H), with a floor made of stainless steel bars, 0.5 cm in diameter and spaced 1.7 cm apart, center to center. Located in the center of the front wall was a hole, 1 cm in diameter and 4 cm above the floor. A stainless steel drinking spout (0.6 cm in diameter) was inserted through this hole automatically and protruded 1.5 cm into the chamber. A speaker and fan provided background noise and ventilation, respectively (80 dB, scale C). The chambers remained dark during trials. 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. A computer located in an adjacent room controlled the presentation of the solutions and recorded goal tracking time (0.05-ms units).

Procedure

Triplets of rats matched by weight were randomly assigned to Groups 16, 24, or 32 (these numbers refer to the concentrations administered on training trials). The following procedural description uses the word “session” in reference to the total practice administered in a given day and the word “trial” in reference to a single placement in the conditioning chamber. Thus, "session" is used whenever more than one trial per day was administered to the rats. Rats were familiarized with the chambers in two initial daily trials (5 min each) without the sucrose solution. One session per day was administered thereafter. Sessions 1–3 involved 5 trials each; starting on session 4 and for the rest of the experiment, there were 4 trials per session. Each trial started and ended with a 30-s interval (range: 15-45 s). The drinking tube was automatically presented and remained available during 2.5 min from the time the rat met a starting criterion of making contact with the tube for a cumulative total of 5 s within an interval of 30 s. At the end of the 2.5-min, the drinking tube was automatically withdrawn. During the intertrial interval (about 40 min), each rat was returned to its cage located outside the conditioning room. The training phase lasted a total of 27 trials.

The test phase followed. Rats continued to receive 4 trials/session of access to their respective training solution (16, 24, and 32%), except that every other day a test solution was presented on the second or third trial (counterbalanced across subjects), instead of the usual training solution (all else remained constant). The 6 test solutions (%) were the following: For Group 32: 2, 4, 8, 16, 24, and 32%; for Group 24: 1.5, 3, 6, 12, 18, and 24%; for Group 16: 1, 2, 4, 8, 12, and 16%. These solutions were chosen to generate 6 test/training ratios common to all groups: 0.0625, 0.125, 0.25, 0.50, 0.75, and 1. The order of test solution presentations across days was counterbalanced for each group. The running order of each 4-rat squad was randomized across groups and days. Chambers were swept with a damp paper towel after each trial.

The dependent variable was the cumulative time in contact with the sipper tube, recorded in 0.05-s units. Under the conditions of training described here, this measure yields more orderly results than the more typical lick rate measure. As a consequence, it has been employed in previous research from this lab (Pellegrini, Muzio, Mustaca, & Papini, 2004; Wood et al., 2005). In addition, Mustaca, Freidin and Papini (2002) found significant positive correlations between goal tracking time and sucrose solution intake under conditions similar to those used in the present experiment. Scores were subject to conventional analysis of variance (ANOVA). The alpha value was set to 0.05 in all the statistical tests reported in this paper.

Results and discussion

The procedure used in Experiment 1 yielded somewhat higher goal tracking times for Group 16 during training trials, than for Groups 24 and 32. Nevertheless, scores were very close to the maximum possible of 2.5 min. The mean goal tracking times during the training phase were 140.6 s for Group 16, 136.9 s for Group 24, and 127.1 s for Group 32. A Group × Trial analysis of variance computed on goal tracking times over the 27 daily trials of the training phase yielded significant effects of group, $F(2, 21) = 3.64$, and trials, $F(26, 546) = 6.23$, but not of their interaction, $F(52, 546) = 1.17$. Pairwise Scheffé comparisons using the mean goal tracking time of each subject during the training phase yielded no significant differences between groups, $p\text{s} > 0.05$. A Group × Trial analysis computed on the data from the last training day (involving 4 trials) yielded nonsignificant effects of groups, trials, and their interaction, $F\text{s} < 1.70$.

Fig. 2 (top) shows goal tracking times as a function of the concentration of the test solution. These average scores tend to be similar at both ends of the scale, but divergent in the middle section of the scale. Groups differed in their consumption of a test solution

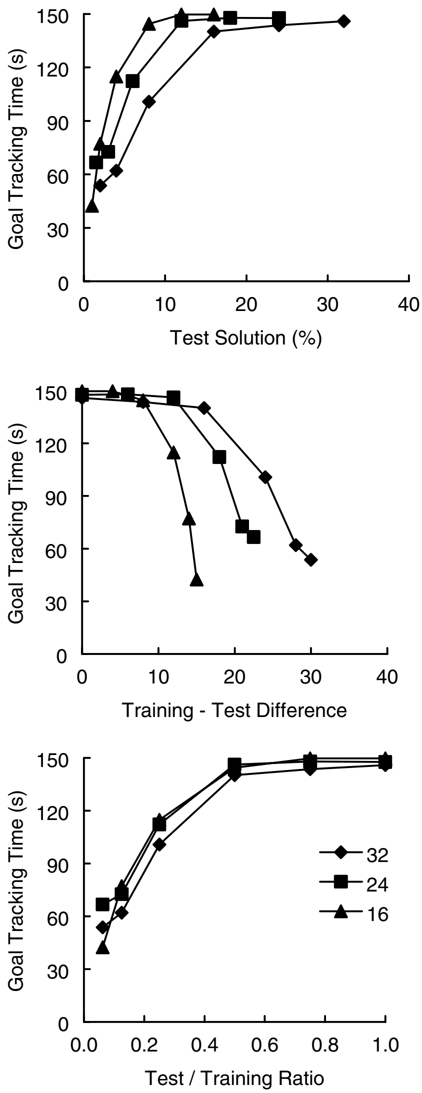

Fig. 2. Results of Experiment 1 presented as a function of the absolute magnitude of the test solution (top), of the difference between training and test solutions (middle), and of the test/training ratio (bottom).

depending on the training value. For example, consumption of the 4, 8, and 16% test solutions was significantly higher after training with 16 than 32% solutions, $Fs(1, 14) \geqslant 4.91$. These results provide evidence of incentive relativity. Goal tracking time for the 2% test solution was not statistically different between the groups, $F(1, 14) = 1.46$.

When plotted as a function of the difference between the training and testing concentrations (i.e., training minus testing concentration; Fig. 2, middle), the degree of consummatory suppression increases as the difference between the solutions increases in all the groups. However, although the groups overlapped on the lower end of the scale, they diverged markedly on the higher end of the scale. Consistent with this, independent analyses of the two training-test difference scores for which there were overlapping groups, 8% (Group 16 tested with 8% and Group 32 tested with 24%) and 12% (Group 16 tested with 4% and Group 24 tested with 12%), indicated the following results. For an 8% difference between training and test solutions, Group 16 did not differ significantly from Group 32, $F < 1$, whereas for a 12% difference between training and test solutions, Group 16 performed significantly below Group 24, $F(1, 14) = 11.14$.

When the same test performance was plotted in terms of the test/training ratio, the groups overlapped extensively across all values of the scale and the differences between groups with equal ratio values dissipated (Fig. 2, bottom). A Group × Ratio analysis performed on the data of all three groups indicated a significant effect of ratio, $F(5, 105) = 72.78$, but the effect of group and the group x ratio interaction were not significant, Fs < 1.

The results plotted in Fig. 2 were also fit with multilevel models (Baumler, Harrist, & Carvajal, 2003). Three such models were constructed, each predicting goal tracking time from the linear and quadratic components of a within-group independent variable and from between-group differences in these components. The within-group independent variable for each model corresponded to the three panels in Fig. 2, namely, the absolute test concentration, the training-test difference, and the test/training ratio. Results showed that groups differed in both the linear and quadratic effects on goal tracking time of absolute test concentrations (Fig. 2, top), χ^2 s(2) > 14.75, and both the linear and quadratic effect of the training-test difference (Fig. 2, middle), χ^2 s(2) > 62.82. However, the groups did not differ in either the linear or quadratic effects of the test/training ratio (Fig. 2, bottom), χ^2s(2) < 2.68.

These data are consistent with the conclusion that the degree of consummatory suppression was best described by a ratio of the test solution to the training solution, rather than the absolute concentration values of test and training solutions, or their difference. A similar degree of consummatory suppression was observed when, for example, the concentration of the test solution was one-fourth that of the training solution, independently of whether the training value was 16, 24, or 32%, or the testing value was 4, 6, or 8%.

Experiment 2

Experiment 2 had two goals. The first was to test the application of Weber's law to incentive downshift under conditions that are more typical of experiments that study recognition relativity, that is, using a single trial per day (Flaherty, 1996). The second was to evaluate the applicability of Weber's law to the rate of recovery from incentive downshift. In Experiment 1, rats were occasionally downshifted to a lower solution and then returned to the training value, thus evaluating only the initial reaction to incentive downshift. It is well documented that the mechanisms underlying the initial reaction to incentive downshift are dissociable from those determining consummatory performance after some experience with the downshifted incentive (see Flaherty, 1996; Papini, 2003; Wood et al., 2005). Therefore, a scaling rule that applies to the initial reaction may or not apply to the recovery that follows.

Evidence for a dissociation between the initial reaction and the recovery of behavior comes mainly from physiological manipulations. In a typical procedure, rats are exposed to 32% sucrose for 10 trials and subsequently shifted to 4% sucrose for 5 or 6 additional trials. The effects of any given factor on the initial reaction to incentive downshift or on the subsequent recovery of consummatory behavior can be evaluated by comparing performance on trial 11 vs. trial 12—first vs. second postshift trials. Thus, corticosterone release is increased after trial 12, but not after trial 11 (Flaherty et al., 1985), and benzodiazepine anxiolytics attenuate cSNC on trial 12, but not on trial 11 (Flaherty, Grigson, & Rowan, 1986). Additional information suggests that these effects depend on experience with the postshift solution. Corticosterone is elevated on trial 11 (Flaherty et al., 1985), and anxiolytic treatment is more effective on trial 11 (Mustaca, Bentosela, & Papini, 2000), provided the trial is longer than the typical 5-min duration. Similarly, chlordiazepoxide effectiveness on trial 11 increases after repeated incentive downshifts (Flaherty, Clark, & Coppotelli, 1996). Conversely, there is at least one factor, the delta opioid receptor agonist DPDPE, that attenuates consummatory suppression when administered before trial 11, but not when administered before trial 12 (Wood et al., 2005). A delta opioid receptor antagonist, naltrindole, also shows selective enhancement of cSNC on trial 11 (Pellegrini, Wood, Daniel, & Papini, 2005). As a result of this dissociation between the initial reaction to incentive downshift and the recovery that follows, it is not necessarily the case that Weber's law, which applies to the results of occasional downshifts from Experiment 1, would also apply to the rate of recovery from incentive downshift.

In this experiment, 10 groups of rats received access to sucrose solutions of various concentrations during 10 preshift trials, followed by 6 postshift trials in which the concentration was downshifted. Concentrations were chosen so as to collect data from two test/training ratios that showed a good fit to Weber's law in Experiment 1: 0.125 and 0.25.

Method

Subjects

The subjects were 56 adult, male, experimentally naïve, 110-day-old Wistar rats. The average free-food weight was 313.6 g (range: 210–482 g). Deprivation, daily feeding, light:dark cycle, temperature, housing, and solution mixing were as described in Experiment 1. Humidity was not controlled in Experiment 2.

Apparatus

Four conditioning boxes enclosed in sound-attenuating cubicles were used. Each box measured $29.2 \times 24.1 \times 21$ cm (W × L × H). The floor of each box was made of aluminum bars, 0.4 cm in diameter, and separated by gaps measuring 1.1 cm. In the center of the front wall was a square, 5-cm hole, 3.5 cm deep, and 1 cm above the floor level. A sipper tube was introduced into this hole from the outside and protruded 2 cm when fully inserted. Goal tracking was measured by a photocell positioned so as to detect the position of the head within 0.5 cm of the tip of the sipper tube. As already mentioned, this measure correlates positively and significantly with fluid intake (Mustaca et al., 2002). A diffuse light was located directly above the sipper tube and 18 cm from the floor.

Procedure

Context familiarization was as described for Experiment 1. There were 16 trials, one trial/day, 10 preshift trials followed by 6 postshift trials. In each trial, the rat was placed in a chamber and given access to a solution dispensed through a drinking tube. The running order of 4-rat squads was randomized across groups and days. Each trial started immediately after the animal inserted its head into the hole where the sipper tube was fixed before the animal was introduced into the box. At the end of the 5-min trial, the animals were immediately withdrawn from the boxes and the chambers were swept with a damp paper towel.

Experiment 2 included 10 groups, labelled according to the concentration (%) of the sucrose solution administered during preshift–postshift trials: 0–0, 2–0.5, 4–1, 8–2, 16–2, 16–4, 32–4, 32–8, 64–8, and 64–16. These solutions were chosen to generate test/training ratios of 0.25 for 6 groups (2–0.5, 4–1, 8–2, 16–4, 32–8, and 64–16), and 0.125 for three groups (16–2, 32–4, and 64–8). Group 0– 0 (water in all trials) served as a baseline control.

Results and discussion

The parametric design of Experiment 2 allows for an inspection of the asymptotic relationship between sucrose solution magnitude and goal-tracking time. Fig. 3 shows goal-tracking time averaged over the last 5 preshift trials as a function of the concentration of the sucrose solution. As others have shown for fluid intake and licks, the function is non-monotonic, with a decrease at higher values of sucrose concentration (Sclafani & Ackroff, 2003). For our purposes, however, goal-tracking time increases monotonically for the segment of the function encompassing the postshift concentrations used in these experiments (0–16%).

Fig. 4 shows the main results by separating groups according to their test/training ratio; Group 0–0 was included in both graphs as a point of reference. There are two main results to be drawn from these data. First, the initial impact of the downshift (trial 11) was similar for groups trained under the same test/training ratio, with two exceptions: Groups 4–1 and 2–0.5 (Fig. 4, top). In these two groups, the low value of the postshift sucrose concentration was apparently not enough to sustain consummatory performance. In the rest of the groups, it is evident that the initial postshift performance was a direct function of the size of the test/training ratio. This is more clearly seen in Fig. 5, which follows the same transformations used in Fig. 2 and shows goal tracking time in trial 11 as a function of the absolute value of the test solution (top), of the difference between training and testing concentrations (middle), and of the test/training ratio (bottom). The ratio transformation results in a greater degree of

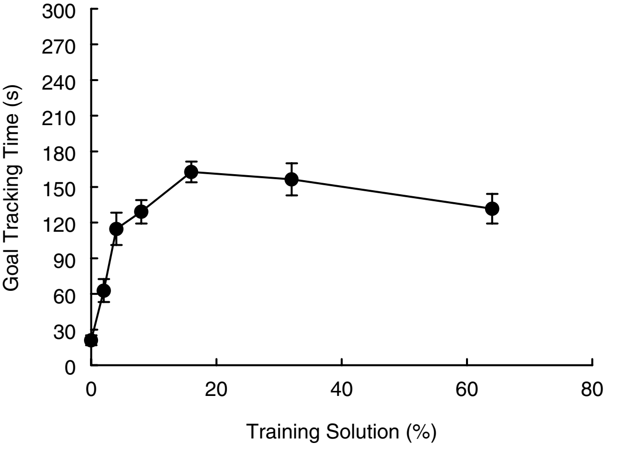

Fig. 3. Mean terminal preshift performance of rats trained with seven incentive magnitudes in Experiment 2.

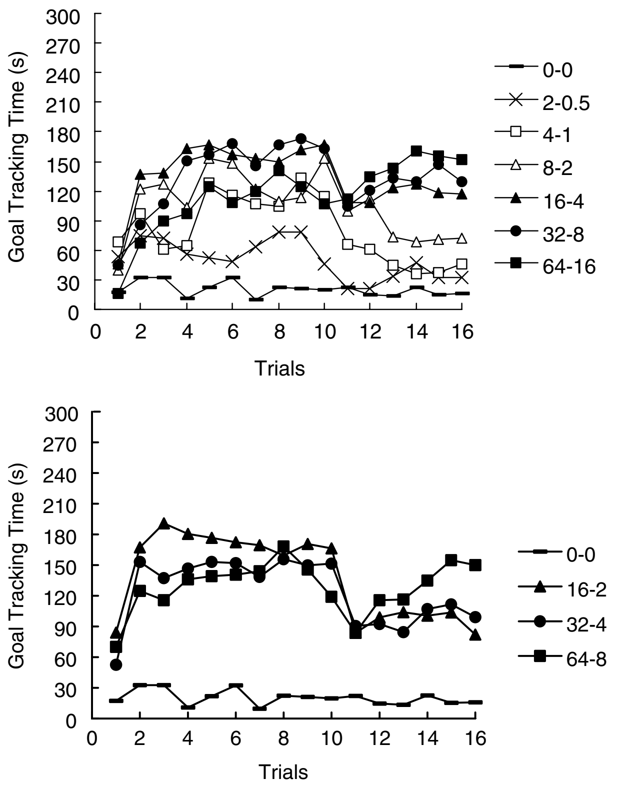

Fig. 4. Results of Experiment 2. Incentive downshift occurred on trial 11. Graphs represent groups with test/training ratios of either 0.25 (top) or 0.125 (bottom).

overlap among the groups than plotting the data in terms of either the absolute test concentration or the training-test difference. Obviously, these data cannot be subject to the same multilevel analyses used in Experiment 1 because there are only two data points for each of the training concentrations. The ratio data, however, were analyzed according to a Preshift Solution (16, 32, 64) × Ratio (0.125, 0.25) design. In agreement with Weber's law and the present hypothesis, trial 11 data showed a significant effect of ratio, $F(1, 30) = 7.87$, but nonsignificant effects for either the preshift solution or their interaction, $F\text{s} < 1$.

Second, the rate of recovery was relatively similar for Groups 16–4 and 32–8 (with a 0.25 ratio), and for Groups 16–2 and 32–4 (with a 0.125 ratio); the broader picture, however, suggests that the terminal level was a function of the postshift concentration, rather than of the test/training ratio. In groups with a test/training ratio of 0.25 (Fig. 4, top), postshift performance recovered at a rate roughly correlated with the postshift concentration: $16 > 8 > 4 > 2 > 1 \simeq 0.5$. A similar trend appears in groups with a ratio of 0.125: $8 > 4 \simeq 2$ (Fig. 4, bottom). Group × Trial analyses were computed on each of these two sets of groups (Group 0–0 was excluded). In the groups with a test/training ratio of 0.25, the group effect was significant, $F(5, 27) = 22.53$; but the effects of trial and the group × trial interaction were not significant, $F\text{s} < 1.33$. A second analysis computed on trial 16 data for the same groups yielded a significant group effect, $F(5, 27) = 11.54$. Scheffé pairwise tests indicated that Group 2–0.5 consumed significantly less than Groups 16–4, 32–8, and 64–16;

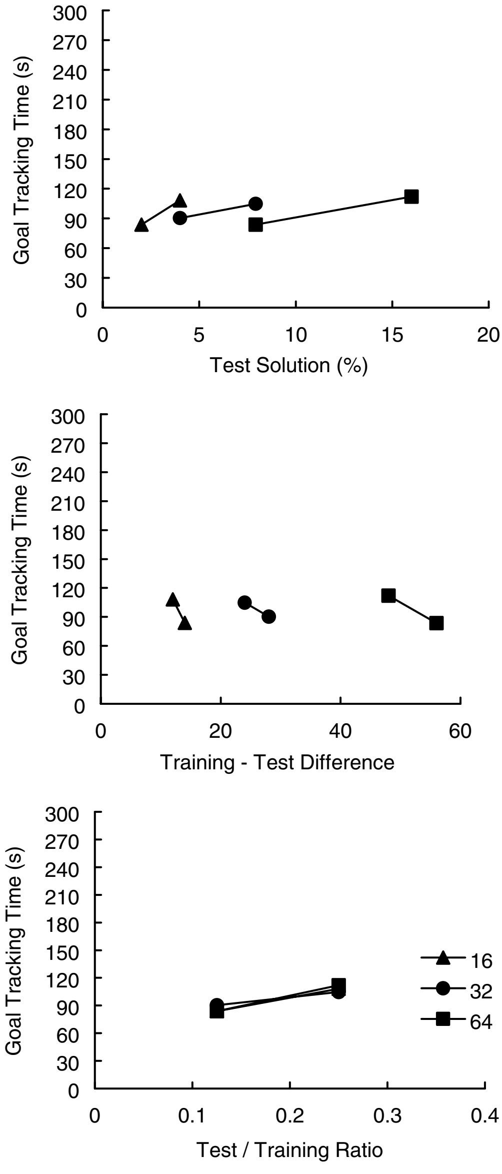

Fig. 5. Results of Experiment 2 presented as a function of the absolute magnitude of the test solution (top), of the difference between training and test solutions (middle), and of the test/training ratio (bottom).

Group 4–1 consumed less than Groups 32–8 and 64–16; and Group 8–2 consumed less than Group 64–16. Other comparisons were not significant. In the groups with a test/training ratio of 0.125, there were significant effects of trial, $F(5, 75) = 7.59$, and of group × trial interaction, $F(10, 75) = 3.16$, but not of groups, $F(2, 15) = 2.59$. The analysis of trial-16 data indicated a significant difference across groups, $F(2, 15) = 5.03$. Scheffé comparisons showed that Group 16–2 consumed significantly less than Group 64–8.

The initial impact of the downshift and subsequent recovery are shown in Fig. 6 for groups with a test/training ratio of 0.25 for the first and last postshift trial. On trial 11, the first postshift trial, the function is quite flat except for the two lowest values. The flat portion reveals proportional scaling. As for the diverging values at the lower end of the scale, such deviations are common in psychophysical experiments in which stimuli are presented in close temporal contiguity (Luce & Krumhansl, 1988), and they emerge also in the present experiment in which the downshifted test solution is compared to the memory of the training solution. The two lowest postshift solutions (0.5 and 1%) are so diluted that they either cannot sustain consummatory behavior or are close to the absolute lower threshold (Richter & Campbell, 1940; Sclafani & Nissenbaum, 1987). Recovery from reward downshift appears to involve further distortion of the function at both ends, depressing values in the lower end and increasing them at the higher end of the scale. Separate one-way, repeated-measure ANOVAs were computed on each of the groups assigned to the six preshift solutions (2, 4, 8, 16, 32, and 64%), comparing the first and last postshift trials (trials 11 and 16). Trials were significantly different for preshift solution 4%, $F(1, 4) = 7.90$; 8%, $F(1, 4) = 9.12$; and 32%, $F(1, 5) = 9.84$. Nonsignificant differences were found for the 2, 16, and 64% preshift solutions, $F\text{s} < 2.83$.

These results confirmed and extended the results of Experiment 1. First, the initial impact of incentive downshift followed the same proportionality in Experiment 2 that was also observed in Experiment 1. Second, for postshift concentrations in the middle of the range (4–8% solutions), proportionality also applied to the rate of recovery from incentive downshift. However, recovery rates deviate from Weber's law when the concentration of the postshift solution is either too low (2% or lower) or too high (16%). In these cases, consummatory performance recovers at lower (deterioration) and higher rates, respectively, than is the case for groups tested with postshift concentrations in the middle of the range. The use of long intertrial intervals in Experiments 1 and 2 makes it implausible that the behavior of rats during the postshift trials was under the control of sensory interactions, thus lending credibility to the hypothesis that these results reflect the scaling properties of the process underlying recognition relativity.

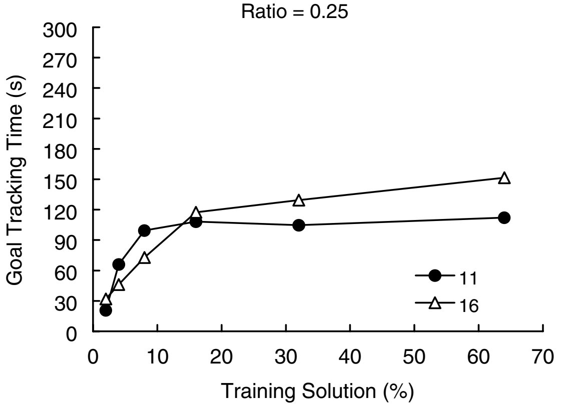

Fig. 6. Postshift performance of groups trained under a test/training ratio of 0.25 in Experiment 2. Goal tracking time is plotted as a function of training solution magnitude and postshift trial (only trials 11 and 16 are shown).

General discussion

Incentive relativity effects have been known since the late 1920s (Elliot, 1928) and have played an important role in the development of learning theory (Flaherty, 1996). Memory-based incentive relativity implies that the value of a current reward is assessed against the value of an incentive that was expected on the basis of prior experience in a similar situation. The present results extend this notion and suggest that the specific rule behind recognition relativity is one involving ratios of present and past rewards, such that very different magnitudes may actually have similar behavioral consequences if they are introduced under conditions of constant proportionality between the postshift and preshift magnitudes. This fits the popular belief that situations that are objectively very different may, in fact, lead to very similar reactions. Imagine, for example, two casino gamblers drinking alcohol at a table where they both lose a sum equivalent to 75% of their annual income. Let's assume for the purpose of this example that the amount of alcohol intake reflects the incentive value of the gamblers' present situation. Although both are likely to have a gambling problem (Welte, Barnes, Wieczorek, & Tidwell, 2004), the present research suggests that they would both drink approximately the same amount of alcohol even if one of them has lost several times more money than the other.

Sensory relativity, memory-based relativity, and frustration

There is extensive evidence that the surprising loss of food induces an aversive emotional reaction with behavioral and physiological consequences (Amsel, 1992; Flaherty, 1996; Papini & Dudley, 1997). Traditionally, manipulations involving surprising reward omissions have been linked to the induction of a frustrative reaction, whether because the rewards are removed, or because a barrier is interposed between the response and the reward (Amsel, 1992; Williams & Williams, 1943). The results reported in this article were obtained with procedures that involved surprising downshifts in reward magnitude, and it is therefore appropriate to ask whether the observed relativity effect is a property not only of changes in consummatory behavior, but also of the emotional activation that is presumably determining behavioral suppression.

SNC may be considered as a paradigmatic example of a situation involving surprising reward loss associated with a variety of emotional correlates (Flaherty, 1996). Recent results from consummatory response situations indicate that incentive downshift suppresses agonistic behavior (Mustaca, Martínez, & Papini, 2000) and disrupts male sexual behavior (Freidin & Mustaca, 2004). The initial reaction to incentive downshift is modulated by opioid peptides (Rowan & Flaherty, 1987; Pellegrini et al., 2005; Wood et al., 2005), by posttrial treatment with corticosterone (Bentosela et al., 2005), and by preshift exposure to a regimen of partial reinforcement training that acts as "stress inoculation" against the suppressive effects of incentive downshift (Pellegrini et al., 2004). When iSNC is not observed, as in runway experiments with a downshift in sucrose concentrations, evidence indicates that the same animals exhibit cSNC in the goal box of the runway (Flaherty & Caprio, 1976). Thus, it is possible that animals undergo emotional activation even in situations in which incentive downshift does not lead to a measurable SNC effect (see Pellegrini & Papini, in press).

Interestingly, if it is assumed that the degree of behavioral suppression after incentive downshift in the consummatory situation is an index of the intensity of an emotional reaction of frustration, then the present experiments suggest that such emotional reaction obeys Weber's law, at least within limits. There are two relatively more parsimonious explanations of these results than the emotional account offered in the preceding paragraph. The first one is an explanation based on sensory relativity, which would simply assert that the scaling property described by these data reflects the functioning of the taste system, rather than the properties of an emotional system. The technique used in Experiments 1 to control for the sensory carry-over of taste stimuli from the training to the testing trials was to lengthen the intertrial interval. In Experiment 2, there was an interval of 24 h between the last preshift session and the first postshift session. It has been traditionally assumed that stimulus traces decay in time and are susceptible to retroactive interference by incoming stimuli (see, e.g., Atkinson & Shiffrin, 1968; Hull, 1943; Roberts & Grant, 1976). On this basis, the longer the time interval between successive presentations of a sucrose solution, the less likely it is that the trace of the first solution would remain sufficiently active to cause sensory relativity effects. Furthermore, since rats spent the intertrial interval in their individual cages, it is assumed that incoming stimulation from the activity displayed in the cage (Experiment 1) and from episodes of eating, drinking, and sleeping (Experiments 2) effectively interfered with traces of the training stimulus. Thus, any performance decrement observed in postshift trials should be the result of a comparison between the current incentive and the memory of the training solution received previously in the conditioning box. As schematized in Fig. 1, such a memory is assumed to be either associatively reactivated by the test solution (recognition relativity), or by antecedent stimuli present both at the time of training and also at the time of testing (cued-recall relativity). (For a distinction between sensory carry-over and associative reactivation, see Couvillon, Brandon, Woodard, & Bitterman, 1980.)

The second parsimonious explanation of the present results would accept that incentive downshift suppresses consummatory behavior because of a memory-based comparison between current sensory input (from the test solution) and the associatively reactivated memory of the training solution, but without assuming any additional emotional process. Indeed, if all that were known about the effects of incentive downshifts were the results of the present experiments, one would have to opt for this explanation over one stressing a frustrative reaction merely on the basis of parsimony. However, and as mentioned above, there is substantial evidence that incentive downshift is accompanied by an emotional reaction of aversive hedonic value (Papini, 2003; Papini & Dudley, 1997). Any nonemotional hypothesis would have to be able to explain, for example, why the pituitary–adrenal axis plays a role in incentive downshift, whether as studied in the contrast situation or in extinction of appetitively motivated behavior (Carbonaro, Friend, Dellmeier, & Nuti, 1992; Dantzer, Arnone, & Mormede, 1980; Flaherty et al., 1985; Lyons, Fong, Schrieken, & Levine, 2000; Thomas & Papini, 2001). Thus, the hypothesis that recognition relativity is a property of the frustrative reaction induced by incentive downshift has the advantage of relating more clearly to the results of other experiments.

Extending the domain of Weber's law

It is unclear whether Weber's law would apply to other reward downshift situations. Disparity between incentive levels administered successively may be required to induce the type of comparison between an actual event and the memory of a past event (whether in terms of recognition or cued recall) that may result in behavioral changes reflecting Weber's law. Experiments involving fear (e.g., induced by the administration of electric shocks), disgust (e.g., induced by toxins), or sexual arousal (e.g., induced by presenting sexually receptive partners) rarely contemplate successive shifts in incentive magnitude. When they do, however, incentive shifts are typically studied in the context of contrast effects, in which the behavior of shifted animals is compared to that of unshifted controls, rather than with that of other shifted conditions involving variations in preshift and postshift incentive values. For example, using an escape conditioning task with rats, Nation, Wrather and Mellgren (1974) reported both successive negative and successive positive contrast effects. In one experiment, rats escaped from electric shocks with an intensity of 0.2, 0.4, or 0.8 mA; after 20 trials, all groups received 0.4 mA shocks. The group shifted from 0.2 to 0.4 mA escaped at a higher speed than the 0.4-mA unshifted control (positive contrast), whereas the group shifted from 0.8 to 0.4 mA escaped at a lower speed than the unshifted control (negative contrast). Another potentially suitable procedure is that used by Woods, Davidson and Peters (1964). In this preparation, rats swim on a submerged runway to a shallower goal box where they can stand on their hind feet. The incentive is provided by a change in ambient temperature from the alley to the goal box of the runway (it is reported that temperature could be controlled within 0.1 °C). Larger differences in temperature between alley and goal (e.g., 15–40 °C), led to higher speeds than lower differences (35–40 °C): 0.85 vs. 0.26 feet/s (Woods et al., 1964, Table 1). In one experiment based on this procedure, a shift from a low to a high temperature failed to produce evidence of a positive contrast effect, but a shift from a high to a low temperature was accompanied by a negative contrast effect in runway speed (Woods, 1967). Such procedures could be easily adjusted to study the scaling properties of escape conditioning under parametric variations in incentive magnitude, although provisions should be made to avoid potential carry-over effects across trials (i.e., sensory relativity). For example, in Nation et al.'s (1974) experiments, rats received 4 trials per session separated by an intertrial interval of 2–3 min. Although there was evidence that incentive shifts affected behavior in the first trial of the shifted phase (a fact that implicates cued recall), a cleaner demonstration of memory-based relativity, rather than sensory relativity, would require intertrial intervals of the size used in the present experiments.

In aversive situations involving pain or coldness, the reinforcing event is the transition to a state of less pain or warmer temperature. In traditional learning theory language (cf. Mowrer, 1960), the emotional state with such reinforcing properties has been termed relief (Denny, 1991). Evidence consistent with the hypothesis that relief is the incentive in aversive contrast situations is provided by experiments demonstrating that a downshift in the amount of time spent in the safe compartment of a one-way avoidance chamber leads to the deterioration of avoidance performance beyond the level of an unshifted control (Candido, Maldonado, Megias, & Catena, 1992). To the extent that relief and frustration may be thought of as internal states aroused by conditions involving downshifts in incentives (appetitive in the case of frustration and aversive in the case of relief; Amsel, 1992; Denny, 1991), then similar scaling properties to those described here may be predicted for situations involving aversive events.

Concluding comments

The foregoing discussion has implicitly assumed that any downshift in incentive magnitude leads to emotional activation. Although rats may detect incentive downshifts involving a high test/training ratio, this may cause insufficient emotional activation to disrupt consummatory behavior. For example, in Experiment 1, a test/training ratio equal to 0.5 yielded no indication of consummatory suppression, relative to a ratio of 1.0. However, it seems plausible that rats could detect the transition, although clearly a different procedure would be needed to measure such detection. Most likely, frustration is induced when the incentive downshift falls below a certain ratio. In theoretical terms, such a ratio would be equivalent to a threshold. This idea has potential implications for the use of the consummatory procedure as an animal model of anxiety (Flaherty, 1991). It would be of considerable interest to determine, for example, whether such well-studied effects as the activation of the pituitary–adrenal axis or attenuating effects of anxiolytics and some opioid agonists exhibit similar scaling properties. In such a case, these effects could help establishing the test/training ratio that leads to measurable levels of emotional activation.

Research on animal learning has moved from stressing absolute quantities to stressing the relationship among critical parameters of the training situation. A case in point is provided by the interval between the conditioned and unconditioned stimuli in Pavlovian conditioning, once thought to be optimal at a value of 0.5 s. For example, Kimble (1961, p. 156) concluded that evidence "indicates that the optimal interval is much shorter than 5 s, probably being something more like a tenth of that value" (see also his Table 13, pp. 156–157). This statement, which was very influential, was called into question 20 years later after the extensive reanalysis of conditioning data provided by Gibbon and Balsam (1981). That analysis demonstrated that there is no single optimal absolute value for this particular interval. The speed of acquisition is better described by the ratio of the interreinforcer interval and the duration of the conditioned stimulus (see also Gallistel & Gibbon, 2000). The discovery of incentive contrast already suggested that reward value must be understood in relative terms. The present results extend this relativistic view by suggesting that Weber's law applies to recognition relativity processes and yields the same incentive value (and perhaps the same level of emotional activation) for rewards of different absolute magnitude, provided that such rewards are experienced within the constraints of the same test/training ratio.

References

Amsel, A. (1992). *Frustration theory*. Cambridge, UK: Cambridge University Press.

Atkinson, R. C., & Shiffrin, R. M. (1968). Human memory: A proposed system and its control processes. In K. W. Spence & J. T. Spence (Eds.), *The psychology of learning and motivation* (Vol. 2, pp. 89–195). New York: Academic Press.

Barnes, W., & Tombaugh, T. N. (1973). Another failure to obtain negative incentive contrast following reductions in sucrose reward. *Psychological Reports, 33*, 801–802.

Baumler, E. R., Harrist, R. B., & Carvajal, S. (2003). Analysis of repeated measures data. In S. P. Reise & N. Duan (Eds.), *Multilevel modeling: Methodological advances, issues, and applications* (pp. 138–156). Mahwah, NJ: Erlbaum.

Beck, R. C., Nash, R., Viernstein, L., & Gordon, L. (1972). Sucrose preferences of hungry and thirsty rats as a function of duration of stimulus presentation. *Journal of Comparative and Physiological Psychology, 78*, 40–50.

Bentosela, M., D'Ambros, M. A., Altamirano, A., Muzio, R. N., Baratti, C., & Mustaca, A. E. (2005). Posttrial administration of cholinergic drugs doew not affect consummatory successive negative contrast in rats. *International Journal of Comparative Psychology, 18*, 91–99.

Bentosela, M., Ruetti, E., Muzio, R. N., Mustaca, A. E., & Papini, M. R. (2006). Administration of corticosterone after the first downshift trial enhances consummatory successive negative contrast. *Behavioral Neuroscience, 120*, 371–376.

Bitterman, M. E. (1976). Incentive contrast in honey bees. *Science, 192*, 380–382.

Cabeza, R., Kapur, S., Craik, F. I. M., McIntosh, A. R., Houle, S., & Tulving, E. (1997). Functional neuroanatomy of recall and recognition: A PET study of episodic memory. *Journal of Cognitive Neuroscience, 9*, 254–265.

Candido, A., Maldonado, A., Megias, J. L., & Catena, A. (1992). Successive negative contrast in one-way avoidance learning in rats. *Quarterly Journal of Experimental Psychology, 45B*, 15–32.

Carbonaro, D. A., Friend, T. H., Dellmeier, G. R., & Nuti, L. C. (1992). Behavioral and physiological responses of dairy goats to food thwarting. *Physiology and Behavior, 51*, 303–308.

Couvillon, P. A., Brandon, S. E., Woodard, W. T., & Bitterman, M. E. (1980). Performance of pigeons in patterned sequences of rewarded and nonrewarded trials. *Journal of Experimental Psychology: Animal Behavior Processes, 6*, 137–154.

Crespi, L. P. (1942). Quantitative variation in incentive contrast studies involving discrete-trial procedures. *American Journal of Psychology, 55*, 467–517.

Dantzer, R., Arnone, M., & Mormede, P. (1980). Effects of frustration on behaviour and plasma corticosteroid levels in pigs. *Physiology and Behavior, 24*, 1–4.

Denny, M. R. (1991). Relaxation/relief: The effect of removing, postponing, or terminating aversive stimuli. In M. R. Denny (Ed.), *Fear, avoidance, and phobias* (pp. 199–229). Hillsdale, NJ: Erlbaum.

DiLollo, V., & Beez, V. (1966). Negative contrast effect as a function of magnitude of reward decrement. *Psychonomic Science, 5*, 99–100.

Elliot, M. H. (1928). The effect of change of reward on the maze performance of rats. *University of California Publications in Psychology, 4*, 19–30.

Fechner, G. T. (1965). Elemente der psychophysik. (Translated by H.S. Langfeld). In R. J. Herrnstein & E. G. Boring (Eds.), *A source book in the history of psychology* (pp. 66–75). Cambridge, MA: Cambridge University Press.

Flaherty, C. F. (1991). Incentive contrast and selected animal models of anxiety. In L. Dachowski & C. F. Flaherty (Eds.), *Current topics in animal learning: Brain, emotion, and cognition* (pp. 207–243). Hillsdale, NJ: Erlbaum.

Flaherty, C. F. (1996). *Incentive relativity*. Cambridge, UK: Cambridge University Press.

Flaherty, C. F., & Caprio, M. (1976). Dissociation between instrumental and consummatory measures of incentive contrast. *American Journal of Psychology, 89*, 485–498.

Flaherty, C. F., & Meinrath, A. (1979). Influence of scopolamine on sucrose intake under absolute and relative test conditions. *Physiological Psychology, 7*, 412–418.

Flaherty, C. F., & Sepanak, S. J. (1978). Bidirectional contrast, matching, and power functions obtained in sucrose consumption by rats. *Animal Learning and Behavior, 6*, 313–319.

Flaherty, C. F., Becker, H. C., & Pohorecky, L. (1985). Correlation of corticosterone elevation and negative contrast varies as a function of postshift day. *Animal Learning and Behavior, 13*, 309–314.

Flaherty, C. F., Becker, H., & Osborne, M. (1983). Negative contrast following regularly increasing concentrations of sucrose solutions: Rising expectations or incentive averaging? *Psychological Record, 33*, 415–420.

Flaherty, C. F., Clark, S., & Coppotelli, C. (1996). Lack of tolerance to contrast-reducing actions of chlordiazepoxide with repeated reward reductions. *Physiology and Behavior, 60*, 645–652.

Flaherty, C. F., Grigson, P. S., & Rowan, G. A. (1986). Chlordiazepoxide and the determinants of negative contrast. *Animal Learning and Behavior, 14*, 315–321.

Flaherty, C. F., Hrabinski, K., & Grigson, P. S. (1990). Effect of taste context and ambient context changes on successive negative contrast. *Animal Learning and Behavior, 18*, 271–276.

Flaherty, C. F., Rowan, G. A., Emerich, D., & Walsh, T. (1989). Effects of intra-hippocampal administration of colchicine on incentive contrast and on radial maze performance. *Behavioral Neuroscience, 103*, 319–328.

Franchina, J. J., & Brown, T. S. (1971). Reward magnitude shift effects in rats with hippocampal lesions. *Journal of Comparative and Physiological Psychology, 76*, 365–370.

Freidin, E., & Mustaca, A. E. (2004). Frustration and sexual behavior in male rats. *Learning and Behavior, 32*, 311–320.

Gallistel, C. R., & Gibbon, J. (2000). Time, rate, and conditioning. *Psychological Review, 107*, 289–344.

Ghoneim, M. M., & Mewaldt, S. P. (1977). Studies on human memory: The interactions of diazepam, scopolamine, and physostigmine. *Psychopharmacologia, 52*, 1–6.

Hasselmo, M. E., & Wyble, B. P. (1997). Free recall and recognition in a network model of the hippocampus: Simulating effects of scopolamine on human memory function. *Behavioural Brain Research, 89*, 1–34.

Gibbon, J., & Balsam, P. D. (1981). Spreading association in time. In C. M. Locurto, H. S. Terrace, & J. Gibbon (Eds.), *Autoshaping and conditioning theory* (pp. 219–253). New York: Academic Press.

Gleitman, H., & Steinman, F. (1964). Depression effect as a function of retention interval before and after shift in reward magnitude. *Journal of Comparative and Physiological Psychology, 57*, 158–160.

Helson, H. (1964). *Adaptation-level theory*. Oxford, UK: Harper & Row.
Hubbard, T. L. (1994). Memory psychophysics. *Psychological Research, 56*, 237–250.
Hull, C. L. (1943). *Principles of behavior*. New York: Appleton-Century-Crofts.
Kimble, G. A. (1961). *Hilgard and Marquis' conditioning and learning*. New York: Appleton-Century-Crofts.
Lawless, H. R., Horne, J., & Spiers, W. (2000). Contrast and range effects for category, magnitude and labeled magnitude scales in judgements of sweetness intensity. *Chemical Senses, 25*, 85–92.
Luce, R. D., & Krumhansl, C. L. (1988). Measurement, scaling, and psychophysics. In R. C. Atkinson, R. J. Herrnstein, G. Llindzey, & R. D. Luce (Eds.), *Stevens' handbook of experimental psychology, 2nd Ed., Vol. 1, Perception and motivation* (pp. 3–74). New York: Wiley-Interscience.
Lyons, D. M., Fong, K. D., Schrieken, N., & Levine, S. (2000). Frustrative nonreward and pituitary-adrenal activity in squirrel monkeys. *Physiology and Behavior, 71*, 559–563.
Moskowitz, H. R. (1970). Ratio scales of sugar sweetness. *Perception and Psychophysics, 7*, 315–320.
Mowrer, O. H. (1960). *Learning theory and behavior*. New York: Wiley & Sons.
Mustaca, A. E., Bentosela, M., & Papini, M. R. (2000). Consummatory successive negative contrast in mice. *Learning and Motivation, 31*, 272–282.
Mustaca, A. E., Freidin, E., & Papini, M. R. (2002). Extinction of consummatory behavior in rats. *International Journal of Comparative Psychology, 15*, 1–10.
Mustaca, A. E., Martínez, C., & Papini, M. R. (2000). Surprising nonreward reduces aggressive behavior in rats. *International Journal of Comparative Psychology, 13*, 91–100.
Nation, J. R., Wrather, D. M., & Mellgren, R. L. (1974). Contrast effects in escape conditioning of rats. *Journal of Comparative and Physiological Psychology, 86*, 69–73.
Papini, M. R. (2003). Comparative psychology of surprising nonreward. *Brain, Behavior and Evolution, 62*, 83–95.
Papini, M. R., & Dudley, R. T. (1997). Consequences of surprising reward omissions. *Review of General Psychology, 1*, 175–197.
Pellegrini, S., & Mustaca, A. E. (2000). Consummatory successive negative contrast with solid food. *Learning and Motivation, 31*, 153–167.
Pellegrini, S., & Papini, M. R. (in press). Scaling relative incentive value in anticipatory behavior. *Learning and motivation*.
Pellegrini, S., Muzio, R. N., Mustaca, A. E., & Papini, M. R. (2004). Successive negative contrast after partial reinforcement in the consummatory behavior of rats. *Learning and Motivation, 35*, 303–321.
Pellegrini, S., Wood, M., Daniel, A. M., & Papini, M. R. (2005). Opioid receptors modulate recovery from consummatory successive negative contrast. *Behavioural Brain Research, 164*, 239–249.
Richter, C. P., & Campbell, K. H. (1940). Sucrose taste thresholds of rats and humans. *American Journal of Psychology, 128*, 291–297.
Roberts, W. A., & Grant, D. S. (1976). Studies of short-term memory in the pigeon using the delayed matching to sample procedure. In D. L. Medin, W. A. Roberts, & R. T. Davis (Eds.), *Processes of animal memory* (pp. 79–112). Hillsdale, NJ: Erlbaum.
Rosen, A. J. (1966). Incentive-shift performance as a function of magnitude and number of sucrose rewards. *Journal of Comparative and Physiological Psychology, 62*, 487–490.
Rosen, A. J., & Ison, J. R. (1965). Runway performance following changes in sucrose rewards. *Psychonomic Science, 2*, 335–336.
Rosen, A. J., & Tessel, R. E. (1970). Chlorpromazine, chlordiazepoxide and incentive shift performance in the rat. *Journal of Comparative and Physiological Psychology, 72*, 257–262.
Rowan, G. A., & Flaherty, C. F. (1987). The effects of morphine in the consummatory contrast paradigm. *Psychopharmacology, 93*, 51–58.
Sastre, A., Lin, J.-Y., & Reilly, S. (2005). Failure to obtain instrumental successive negative contrast in tasks that support consummatory successive negative contrast. *International Journal of Comparative Psychology, 18*, 229–241.
Sclafani, A., & Ackroff, K. (2003). Reinforcement value of sucrose measured by progressive ratio operant licking in the rat. *Physiology and Behavior, 79*, 663–670.
Sclafani, A., & Nissenbaum, J. W. (1987). Taste preference thresholds for polycose, maltose, and sucrose in rats. *Neurosciences and Biobehavioral Reviews, 11*, 181–185.
Shanab, M. E., France, J., & Young, T. (1976). Positive and negative contrast effects obtained following shifts in liquid sucrose reward in thirsty rats. *Animal Learning and Behavior, 4*, 9–12.
Spear, N. E. (1965). Replication report: Absence of a successive contrast effect on instrumental running behavior after a shift in sucrose concentration. *Psychological Reports, 16*, 393–394.

Staddon, J. E. R., & Cerutti, D. T. (2003). Operant conditioning. *Annual Review of Psychology, 54*, 115–144.

Stevens, S. S. (1969). Sensory scales of taste intensity. *Perception and Psychophysics, 6*, 302–308.

Thomas, B. L., & Papini, M. R. (2001). Adrenalectomy eliminates the extinction spike in autoshaping with rats. *Physiology and Behavior, 72*, 543–547.

Tinklepaugh, O. L. (1928). An experimental study of representative factors in monkeys. *Journal of Comparative Psychology, 8*, 197–236.

Vogel, J. R., Mikulka, P. J., & Spear, N. E. (1968). Effects of shifts in sucrose and saccharine concentrations on licking behavior in the rat. *Journal of Comparative and Physiological Psychology, 66*, 661–666.

Welte, J. W., Barnes, G. M., Wieczorek, W. F., & Tidwell, M.-C. (2004). Simultaneous drinking and gambling: A risk factor for pathological gambling. *Substance Use and Misuse, 39*, 1405–1422.

West, R., & Krompinger, J. (2005). Neural correlates of prospective and retrospective memory. *Neuropsychologia, 43*, 418–433.

Williams, S. B., & Williams, E. (1943). Barrier frustration and extinction in instrumental learning. *American Journal of Psychology, 56*, 247–261.

Wood, M., Daniel, A. M., & Papini, M. R. (2005). Selective effects of the δ opioid receptor agonist DPDPE on consummatory successive negative contrast. *Behavioral Neuroscience, 119*, 446–454.

Woods, P. J. (1967). Performance changes in escape conditioning following shifts in the magnitude of reinforcement. *Journal of Experimental Psychology, 75*, 487–491.

Woods, P. J., Davidson, E. H., & Peters, R. J., Jr. (1964). Instrumental escape conditioning in a water tank: Effects of variations in drive stimulus intensity and reinforcement magnitude. *Journal of Comparative and Physiological Psychology, 57*, 466–470.