Scaling relative incentive value: Different adjustments to incentive downshift in pigeons and rats[☆]

Santiago Pellegrini [a,*], María Florencia López Seal [a,b], Mauricio R. Papini [c]

[a] Instituto de Investigaciones Médicas, Consejo Nacional de Investigaciones Científicas y Técnicas, Buenos Aires, Argentina
[b] Universidad de Buenos Aires, Buenos Aires, Argentina
[c] Department of Psychology, Texas Christian University, Box 298920, Fort Worth, TX 76129, USA

ARTICLE INFO

ABSTRACT

Previous research suggests that pigeons and rats show differences in their behavioral adjustments in spaced-trial, incentive-downshift situations. Also, Papini and Pellegrini [Papini, M.R., Pellegrini, S., 2006. Scaling relative incentive value in consummatory behavior. Learn. Motiv. 37, 357–378] and Pellegrini and Papini [Pellegrini, S., Papini, M.R., 2007. Scaling relative incentive value in anticipatory behavior. Learn. Motiv. 38, 128–154] showed that changes in the rat's lever-pressing performance, runway running, and consumption of sucrose solutions after downshifts in incentive magnitude were a function of the ratio of postshift/preshift incentive magnitudes. Here, two experiments using a Pavlovian autoshaping procedure studied the adjustment of pigeons and rats to changes in incentive magnitude. In Experiment 1, pigeons received light-food pairings, whereas in Experiment 2, rats received lever-sucrose pairings. As a result, key-pecking and lever-pressing developed in each experiment, respectively. Preshift incentive magnitudes were downshifted so as to obtain postshift/preshift ratios of 0.125 and 0.25. Pigeons responded during the postshift phase according to the preshift incentive value and independently of the ratio value. However, rats showed ratio constancy, responding during the postshift in accordance with the postshift/preshift ratio, rather than with the absolute magnitudes of either the preshift or postshift incentives. These results support the comparative hypothesis that the mechanisms underlying ratio constancy during incentive downshifts are unique to mammals.

1. Introduction

Psychophysical research has shown that psychological processes triggered by external stimulation (e.g., sensation and perception) are not a direct function of the physical attributes of stimuli, as measured by scaling methods (e.g., Laming, 1997; Luce and Krumhansl, 1988). Indeed, an organism's behavior is strongly influenced by other stimuli present in the environment (e.g., Lockhead, 1992; Sarris, 2006), by sequential effects (e.g., Lockhead and King, 1983), and possibly also by the effects of associatively reactivated past experience (e.g., Helson, 1964; Sarris, 2006). An important problem in the study of behavioral psychophysics is to determine the rules according to which the incentive properties of current stimuli are affected by the reinforcers experienced several hours or days earlier (i.e., "long-term memory"). Such interactions give rise to incentive relativity effects. Notice that incentive relativity effects that depend on long-term memory are not easily explained solely by reference to nonassociative perceptual mechanisms because these effects are generally assumed to dissipate within a few minutes after the experience.

Incentive relativity phenomena involving long-term memory have been extensively studied in rat subjects using the successive negative contrast (SNC) preparation (Flaherty, 1996). SNC occurs when the postshift consummatory performance of a group trained in a $32 \rightarrow 4$ condition, drops below that of a $4 \rightarrow 4$ unshifted control group—with these numbers referring to the percentage concentration of sucrose solutions. In addition to this typical demonstration, a special case of SNC involves a comparison between, for example, $32 \rightarrow 4$ and $16 \rightarrow 4$ conditions. In this special case, groups with different preshift magnitudes are downshifted to the same magnitude; unlike in the typical SNC situation, the special case involves a downshift in both groups (i.e., there is no unshifted control). A lower postshift responding in the $32 \rightarrow 4$ condition than

in the $16 \to 4$ condition would indicate the occurrence of SNC. In both cases, the same postshift incentive magnitude controls different response levels depending on the magnitude received previously.

The learning mechanisms implicated in behavioral adjustments to incentive downshifts, and in general, those of paradoxical reward-schedule effects (Amsel, 1992), can be analyzed by means of comparative studies (Bitterman, 1975; Papini, 2002, 2006). Studies involving incentive downshifts with a variety of vertebrate species have consistently shown SNC effects only with mammalian species, including rats (Crespi, 1942; Elliot, 1928; Vogel et al., 1968), mice (Mustaca et al., 2000), didelphid marsupials (Papini et al., 1988), and human babies (Kobre and Lipsitt, 1972). Analogous experiments with nonmammalian vertebrates have produced evidence of discrimination of various reward magnitudes and of a gradual behavioral change after incentive downshifts, but no evidence of SNC. This outcome, called a reversed SNC, has been obtained in fish (Couvillon and Bitterman, 1985; Lowes and Bitterman, 1967), amphibians (Papini et al., 1995), reptiles (Papini and Ishida, 1994; Pert and Bitterman, 1970), and pigeons (Papini, 1997), all trained under analogous, spaced-trial conditions with food or water as the incentive. For example, pigeons downshifted from a large to a small incentive (number of food pellets) show no evidence of SNC, but a gradual behavioral adjustment to the postshift incentive value (Papini, 1997). Similarly, a downshift from either a large or a small incentive magnitude to extinction (i.e., zero magnitude—another special case of SNC) yields more responding in extinction after large-reward acquisition than after small-reward acquisition (Papini, 1997; Papini and Thomas, 1997; Thomas and Papini, 2003). Experiments with rats trained under analogous conditions demonstrate that extinction is actually faster after acquisition with large rather than small incentives (Hulse, 1958; Papini et al., 2001; Wagner, 1961).

In rats, the amount of conditioned behavior after a surprising reward downshift is determined by the relative change in incentive value involved in the downshift, rather than absolute incentive magnitude (Papini and Pellegrini, 2006; Pellegrini and Papini, 2007). For example (Pellegrini and Papini, 2007), in an autoshaping situation, the change in lever-pressing performance was similar in rats that experienced a $32 \to 8$ or $16 \to 4$ downshift in sucrose concentration (a postshift-to-preshift downshift ratio of 0.25), and in those that experienced a $32 \to 4$ or $16 \to 2$ downshift in sucrose concentration (downshift ratio of 0.125). Conditioned performance during the downshift phase was also significantly more depressed in the 0.125 downshift ratio groups than in the 0.25 ratio groups. Analogous results were observed in a runway experiment in which anticipatory running responses were reinforced with various numbers of food pellets (Pellegrini and Papini, 2007), and in a consummatory response experiment in which rats drank sucrose solutions of various concentrations (Papini and Pellegrini, 2006), when the incentives were downshifted by the same two ratios (0.125 and 0.25). In all these cases, the degree of behavioral change was determined by the downshift ratio, rather than the absolute magnitudes involved in the downshift.

In these experiments, the preshift incentive magnitude is referred to as the training incentive, the postshift magnitude as the test incentive, and the relevant ratio as the test/training ratio. In a consummatory response experiment (Papini and Pellegrini, 2006, Experiment 1), several additional test/training ratios were tested using a within-subject design. Under such conditions, the degree of consummatory responding during incentive downshift was similar with equal test/training ratios, with six ratio values ranging between 0.0625 and 1. However, in an analogous between-subject experiment (Papini and Pellegrini, 2006, Exper-

iment 2), performance tended to deviate from ratio constancy when the sucrose concentration of the preshift and postshift solutions were very low in absolute terms (e.g., $2 \to 0.5$ and $4 \to 1$, for a series of groups trained under a 0.25 test/training ratio). All together these results imply the applicability of Weber's law to conditioned responses in spaced-trial incentive-downshift situations, since observed responding was constant at a constant proportion of stimulus change, at least within limits.

Although the scaling properties of behavior in animals exposed to incentive downshifts was initially observed in procedures that induce SNC, subsequent experiments demonstrated that constant proportionality emerges even under conditions that do not produce behavioral evidence of SNC. One such condition involves the reinforcement of anticipatory responses with sucrose solutions in rats (see Flaherty, 1996). For example, rats trained in a runway situation with sucrose solutions yield no evidence of instrumental SNC (iSNC) in the main section of the runway—a measure of conditioned anticipatory responding. However, the same animals show clear evidence of consummatory SNC (cSNC) in the goal box of the runway, where they consume the solution (Sastre et al., 2005). Yet, rats trained in a lever-pressing autoshaping situation with sucrose solutions as the incentive (another example of anticipatory responding) exhibit no evidence of SNC, but change their behavior in proportion to the test/training ratio (Pellegrini and Papini, 2007). Furthermore, these conditions of training also failed to promote the special case of iSNC described above (i.e., different preshift magnitudes downshifted to the same magnitude). Given that ratio scaling does not depend on the presence of SNC in rats, would it be present in species that do not usually exhibit SNC?

The present experiments were designed with this comparative question in mind. The goal is to determine whether ratio constancy scaling is observed under analogous training conditions in two species that have demonstrated differences in their propensity to exhibit SNC, rats and pigeons. Training conditions that do not normally produce SNC in rats (i.e., lever-pressing autoshaping procedure with sucrose solutions as the incentive) were chosen to increase the comparability of data across species. Latency to the first response after CS onset was taken as the dependent measure. Because this measure might be less affected by response topography (as compared to response level), it was assumed to be more comparable between species. Two experiments using an autoshaping procedure with rats and pigeons suggest that whereas anticipatory behavior after incentive-downshift changes as a function of the test/training ratio in rats, it is a function of the preshift incentive magnitude in pigeons.

2. Experiment 1

On the basis of previous comparative studies (Papini, 1997), it was anticipated that the autoshaping key-peck performance of pigeons would not exhibit SNC, thus allowing for an evaluation of Weber's law using a response measure that does not reflect incentive contrast effects as traditionally measured (see Section 1). Twelve pigeons received autoshaping training in a four-stage *A-X/A-Y* design, where *A* represents the preshift amount of food pellets (either 16 or 8 food pellets for independent groups), and *X* and *Y* represent two different amounts of food pellets chosen so as to generate test/training ratios of 0.125 and 0.25 for both groups. Therefore, each subject experienced four successive training stages, only one preshift amount (*A*), but two ratios of downshift (*X* and *Y*). The order of *X* and *Y* was counterbalanced across subjects, so that half of the subjects experienced first the 0.125 downshift ratio while the rest experienced first the 0.25 downshift ratio.

2.1. Method

2.1.1. Subjects

The subjects were 12 adult pigeons (*Columba livia*) obtained from Ruthardt Pet and Feed (Fort Worth, TX). 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 was 415.6 g (range: 363–519 g). The colony was under a 12:12 h light:dark cycle (lights on at 07:00 h). Animals were maintained in wire-bottom individual cages with water freely available. All these pigeons had participated previously in an experiment involving progressive ratio schedules reinforced with either 1 or 5 food pellets per trial. Pairs matched for weight and previous reward magnitude experience were randomly assigned to the two conditions of the present experiment (see below). Seven months spanned between the end of the previous experiment and the start of the present experiment. During that time, pigeons were maintained on free food.

2.1.2. Apparatus

Training was carried out in three standard operant-conditioning chambers that were 32.2 cm wide, 29.9 cm long, and 32.2 cm high, each enclosed in a sound-attenuating chamber. Each chamber was equipped with a fan that provided air circulation and masking background noise. The front wall, back wall, and ceiling of the boxes were made of Plexiglas, whereas the two lateral walls were made of aluminum. One of the lateral walls contained a lamp (General Electric 1820) providing diffuse illumination from the upper left corner, and the response key that could be illuminated with a green light from behind (1.8 cm in diameter, 18.5 cm above the floor, and in the center of the wall). There was also a feeder cup located 3 cm above the floor and in the center of the wall. This cup was made of opaque Plexiglas and was 4.5-cm wide, 5.5-cm long, and 4-cm high. Noyes precision pellets (pigeon formula, 45 mg) were automatically delivered into this cup. A computer located in an adjacent room controlled all the stimuli and recorded response latencies in 0.01-s units.

2.1.3. Procedure

Pigeons were matched for weight and previous experience with reward magnitudes. Pair members were randomly assigned to two groups ($n = 6$) that differed in the training incentive magnitudes. All animals experienced four phases according to an *A-X/A-Y* sequence. The first and the third phases (*A*) were considered preshift training phases, and pigeons received autoshaping with the training incentive (either 16 or 8 food pellets for different groups). Within each group, pigeons were further divided into two subgroups on the basis of the order of the downshift phases (*X* and *Y*), thus yielding four conditions: 16-4/16-2, 16-2/16-4, 8-2/8-1, or 8-1/8-2. The first number (16 or 8) refers to the number of food pellets administered during preshift training phases, whereas the second number (4, 2, or 1) refers to the number of food pellets administered during the postshift phases. Thus, the order in which the animals experienced each of the two test/training ratios (0.125 and 0.25) was counterbalanced for each training magnitude group. At the end of the first training phase, pairs of animals in each of the two preshift conditions (16 or 8 pellets) were matched in terms of their performance during the last 10 preshift sessions and randomly assigned to one of the ratio subgroups (ratio 0.25 or 0.125). During the second and fourth training phases (*X* and *Y*), pigeons experienced the incentive-downshift manipulation. The food amounts for these phases were chosen so as to generate test/training ratios similar to those used in previous experiments with rats (e.g., Papini and Pellegrini, 2006, Experiment 1). These ratios also allowed for an assessment of the special case of SNC by comparing groups exposed to different incen-

tive magnitudes during preshift sessions, but the same incentive magnitude during postshift sessions: Groups 16-2 and 8-2.

There were 25 preshift training sessions (*A*) followed by 21 postshift test sessions (*X* or *Y*). In each session, a pigeon was placed in the conditioning box where it received five trials per session. Each trial consisted in a 10-s light presentation (the conditioned stimulus, CS) followed by the response-independent administration of the corresponding number of food pellets (the unconditioned stimulus, US). At the start and end of each session, and between successive trials, there was an average interval of 100 s (range: 70–130 s). The running order of four-pigeon squads was counterbalanced across groups and days. At the end of each session, animals were returned to their home cages and the chambers cleaned with a damp paper towel.

The dependent measure taken was the latency (measured in 0.01-s units) to the first response after CS onset. Latency measures were transformed to $\log_{10}$ scores to improve normality and allow for the use of parametric statistics. Transformed scores were subjected to conventional analysis of variance (ANOVA). The alpha value was set at the 0.05 level in all analyses.

2.2. Results

One animal became ill during the experiment and its data were discarded. Two other subjects failed to develop key-pecking during the last five preshift sessions of the first phase, and their data were also discarded from the experiment. The final group sizes were $n = 4$ for the 16-pellet condition and $n = 5$ for the 8-pellet condition. All the data used in statistical analyses and figures were blocked by five sessions. Due to experimental error, an extra session was run in each postshift phase (*X* and *Y*); however, the results of this last session were not included in the analyses and figures.

Fig. 1 presents the results in terms of the absolute latency scores for each group in each phase of training (see Table 1). Latencies were generally lower for pigeons responding for a large incentive than for those responding for a low incentive. After the downshift, groups remained segregated by the magnitude of the preshift incentive, rather than by the postshift magnitude or their ratio. Two separate mixed-model ANOVAs were computed on these data, one for preshift and one for postshift, with Preshift Magnitude (16 vs. 8) as the between-subject factor, and Session Block (1–5) and Ratio (0.25 vs. 0.125) as within-subject factors. The preshift results indicated no significant effects during acquisition for any of the factors or their interactions, $Fs < 2.92$, $ps > 0.13$. Postshift results indicated a significant session effect, $F(3, 21) = 5.49$, and a significant preshift

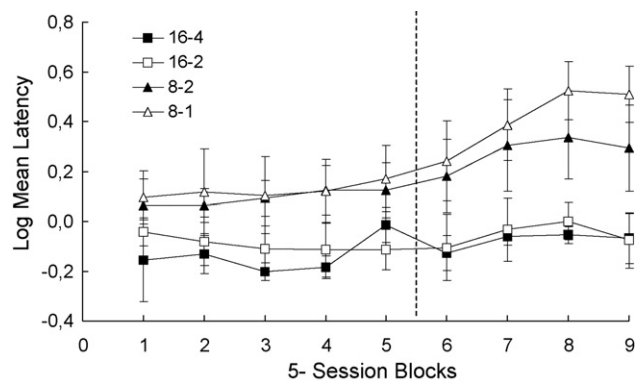**Fig. 1.** Mean $\log_{10}$ latency (s) to the first key-peck response for the four experimental conditions representing two different preshift incentive values (16 or 8 food pellets) and two downshift ratios (0.125 or 0.25). Subjects were trained in a four-stage *A-X/A-Y* design. Preshift data are averaged across both *A* phases. The vertical dashed line separates preshift (right) from postshift (left) data. Error bars depict S.E.Ms.

Table 1
Mean (and S.E.M.) latency to the first response

Group	Preshift	S.E.M.	Postshift	S.E.M.
Experiment 1				
16-4	1.15	0.57	0.97	0.49
16-2	0.84	0.42	1.02	0.51
8-2	1.54	0.69	3.02	1.35
8-1	1.88	0.84	4.10	1.83
Experiment 2				
32-8	1.78	0.63	1.82	0.64
32-4	1.45	0.51	2.06	0.73
16-4	2.08	0.73	1.88	0.66
16-2	2.06	0.73	2.85	1.01

Note: Mean latency (seconds) to the first response and standard error of the mean (S.E.M.) in the last five session blocks of the preshift and postshift phases.

magnitude effect, $F(1, 7) = 5.77$. None of the other main effects and interactions were significant, $Fs < 2.18$, $ps > 0.18$. Also clear in Fig. 1 is the absence of the special case of SNC in the data. Thus, postshift performance in the $16 \rightarrow 2$ and $8 \rightarrow 2$ conditions remained separate without any evidence of crossing over. Statistically, a Preshift by Block analysis for these two conditions indicated nonsignificant effects, $Fs < 2.71$, $ps > 0.71$.

The data were transformed to difference scores according to the same procedure used by Pellegrini and Papini (2007). Briefly, for each pigeon and preshift phase, a baseline score was computed by obtaining the average latency for sessions 21–25. Then, the latency for each session was subtracted from the baseline score. Fig. 2 plots the average per group and downshift value of these difference scores. The fifth five-session block used as a baseline was not included in any statistical analysis. With a transformation that reduces the influence of individual differences the preshift scores tend to be closer together than with absolute scores, but the postshift scores still show a somewhat greater consistency as a function of preshift incentive magnitude than in relation to the test/training ratio. An ANOVA conducted on preshift data indicated no significant main effect or interactions, $Fs < 2.79$, $ps > 0.14$. However, an ANOVA conducted on postshift data indicated a significant main effect of session blocks, $F(3, 21) = 5.60$, and a significant preshift magnitude effect, $F(1, 7) = 10.12$. No other main effect or interaction was significant, $Fs < 2.05$, $ps > 0.20$. Notice that relative transformations may yield the appearance of the special case of SNC, even in the absence of the effect in absolute response levels. Thus, the difference scores of the $16 \rightarrow 2$ and $8 \rightarrow 2$ conditions were here not compared.
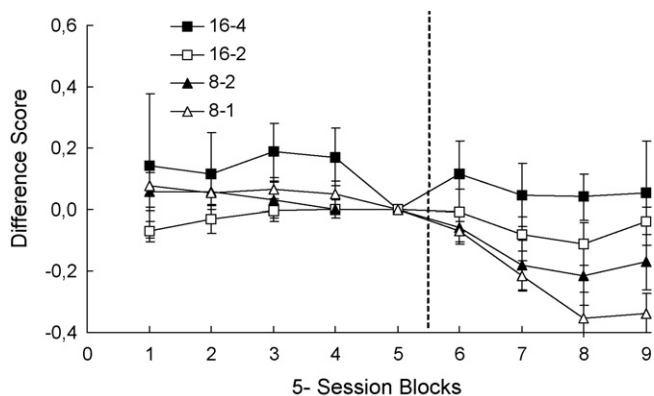

Fig. 2. Difference scores ($\log_{10}$ latency to the first key-peck response on session *n* minus mean $\log_{10}$ latency on sessions 21–25) for the four experimental conditions. The vertical dashed line separates preshift (right) from postshift (left) data. Error bars depict S.E.Ms.

These results provide no support for constant proportionality during incentive downshifts in pigeons. The latency to the first peck after a downshift was a function of preshift incentive magnitude, rather than of the test/training ratio of incentive magnitudes. The larger preshift incentive value produced shorter pecking latencies than the smaller value regardless of the test/training incentive ratio. This conclusion was supported by both absolute and relative analyses of latency data.

3. Experiment 2

The results of Experiment 1 suggest that pigeons adjust to a downshift in incentive magnitude by responding during the postshift phase according to the preshift incentive value. That is, the higher the preshift incentive, the stronger the conditioned responding during postshift sessions, regardless of the postshift incentive value. Previous experiments with rats, using a similar autoshaping procedure, but with a retractable lever as the CS, lever-pressing as the sign-tracking response, sucrose solution as the reward, and a between subject design with only 15 preshift sessions, indicated that the postshift behavior of rats is controlled by the test/training ratio, rather than by the preshift incentive value, as in pigeons (Pellegrini and Papini, 2007). In order to enable a more direct comparison between species, Experiment 2 assessed the behavior of rats under the same within-subject design used in Experiment 1 with pigeons. Sucrose solutions were used as incentives, rather than solid food, because this type of reinforcer is ineffective to induce SNC in rats. This characteristic makes the behavioral outcomes of these two experiments more similar to each other.

3.1. Method

3.1.1. Subjects

The subjects were 16 adult Wistar rats (*Rattus norvergicus*), approximately 120 days old at the start of the experiment. 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 was 343 g (range: 282–389). Animals were housed in individual wire-bottom cages with water continuously available. The colony was under a 12:12 h light:dark cycle (light on at 07:00 h).

3.1.2. Apparatus

Rats received training in four operant-conditioning chambers (MED Associates, VT), each enclosed in a sound-attenuating cubicle. Each box was 29.2-cm wide, 24.1-cm long, and 21-cm high. 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 opening 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 the opening. 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 tap water (w/w) (e.g., the 32% solution was prepared by mixing 32 g of sugar for every 68 g of tap water). Solutions were prepared the day before and presented at room temperature.

3.1.3. Procedure

Rats were randomly assigned to one of four experimental conditions (32-8/32-4, 32-4/32-8, 16-4/16-2, or 16-2/16-4) defined by the sucrose concentration administered during preshift training phases (either 32% or 16% sucrose) and by the order in which the animal experienced each of the two test/training ratios (0.125 and 0.25). As in Experiment 1, all animals experienced 4 training phases according to an *A-X/A-Y* sequence. There were 25 preshift training sessions (*A*) followed by 21 postshift test sessions (*X* or *Y*). In each session the rat was placed in the conditioning box, where it received five trials each consisting of a 10-s lever presentation followed by the response-independent administration of 1 ml of the corresponding sucrose solution delivered with the liquid dipper. The running order of four-rat squads was randomized across groups and days. At the end of each session, animals were returned to their cages and the chambers cleaned with a damp paper towel. The time (latency) to compute the first response in each trial was recorded and transformed to $\log_{10}$ score, as described in Experiment 1. Statistical analyses and all other aspects were the same as in Experiment 1.

3.2. Results

Fig. 3 shows the results of Experiment 2 in terms of the absolute latency measure across groups and phases (see Table 1). A Preshift Magnitude (32% vs. 16% sucrose) by Session Blocks (1–5) by Ratio (0.25 vs. 0.125) analysis indicated only a significant session effect during the preshift phase, $F(4, 56) = 37.98$. None of the other main effects and interactions was significant, $Fs < 0.77$, $ps > 0.39$. A similar analysis for the postshift data indicated a significant effect of the downshift ratio, $F(1, 42) = 5.87$, and a significant ratio by session block interaction, $F(3, 42) = 4.13$. None of the other main effects or interactions were significant, $Fs < 2.50$, $ps > 0.73$. Given this ratio by session interaction, separate analyses were computed for each postshift session block. These analyses indicated significant ratio effects on session blocks 8 and 9, $Fs(1, 14) > 7.61$. No other significant effect or interaction was detected, $Fs < 4.41$, $ps > 0.054$.

A comparison between the $32 \rightarrow 4$ and $16 \rightarrow 4$ conditions during the postshift phase could have provided evidence for the special case of iSNC. Statistically, a Preshift by Block analysis of these two conditions indicated a significant Preshift by Block interaction, $F(3, 42) = 6.96$. The main effects were not significant, $Fs < 1$. Four separate analyses for each five-Trial Block indicated nonsignificant effects of Preshift in any Block, $Fs < 2.29$ $ps > 0.15$. Thus, there was no evidence of the special case of contrast in these data.
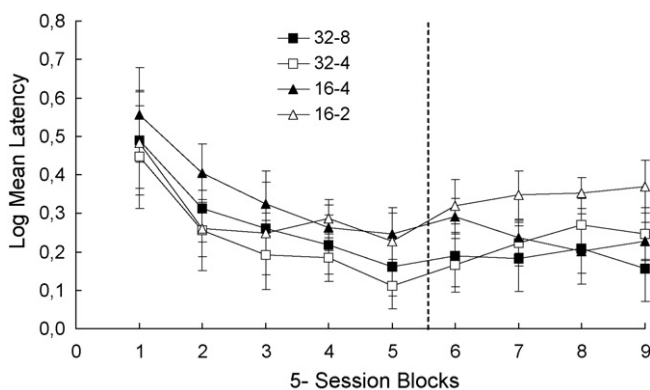

Fig. 3. Mean latency (s) to the first lever-press response for the four experimental conditions representing two different preshift incentive values (32% or 16% sucrose solution) and two downshift ratios (0.125 or 0.25). Subjects were trained in a four-stage *A-X/A-Y* design. Preshift data are averaged across both *A* phases. The vertical dashed line separates preshift (right) from postshift (left) data. Error bars depict S.E.Ms.
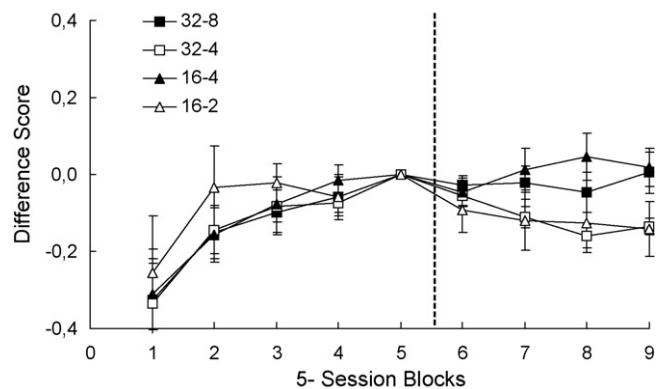

Fig. 4. Difference scores ($\log_{10}$ latency to the first lever-press response on session *n* minus $\log_{10}$ latency on sessions 21–25) for the four experimental conditions. The vertical dashed line separates preshift (right) from postshift (left) data. Error bars depict S.E.Ms.

The transformation of $\log_{10}$ latencies into difference scores according to the same rule used for Experiment 1 is presented in Fig. 4. When individual differences are reduced, preshift performance was very similar across groups and downshift conditions, but the postshift performance is clearly segregated according to the test/training ratio. An ANOVA conducted on preshift data indicated a significant session effect during acquisition, $F(3, 42) = 35.82$, but no other main effect or interaction, $Fs < 1.08$, $ps > 0.32$. A similar ANOVA conducted on postshift data indicated a significant main effect of ratio, $F(1, 42) = 7.03$, and a significant ratio by session block interaction $F(3, 42) = 4.13$. None of the other main effects or interactions were significant, $Fs < 2.50$, $ps > 0.073$. A separate analysis of each session block indicated a significant ratio effect on session blocks 7, 8, and 9, $Fs(1, 14) > 6.16$. No other significant main effect or interaction was found, $Fs < 1.11$, $ps > 0.31$.

Unlike the pigeons of Experiment 1, rats did show an incentive relativity effect in terms of latency to the first lever response, whether in absolute or relative terms. These results are in accordance with the prediction of Weber's law and with previous experimental results cited above.

4. General discussion

The present results suggest that rats and pigeons adjust differently to situations involving downshifts in appetitive incentives. In the case of rats, Experiment 2 extended previous results that pointed to a behavioral adjustment characterized by its dependence on the test/training ratio of incentive magnitudes. Such ratio constancy is especially strong for the intermediate ratio values used in the present experiments (Papini and Pellegrini, 2006) and is consistent with Weber's law as studied in the context of sensory judgments (e.g., Luce and Krumhansl, 1988). Pigeons also modify their behavior after downshifts in incentive magnitude, but their output depends on the magnitude experienced before the change, rather than on the ratio of the two magnitudes or on the postshift magnitude. These species differences in scaling do not reflect differential SNC effects, as shown by the absence of the special case of SNC in these experiments.

These species differences might reflect a fundamental divergence in the mechanisms responsible for assessing incentive value (Papini, 2002, 2003). Previous accounts of these differences were based on one of two different assumptions, namely, that the reversed SNC effect reflects that animals do not anticipate rewarding events or that they do not learn about the emotional reaction to the incentive downshift (Bitterman, 1975, 2000; Papini, 2003,

2006). The new evidence on ratio scaling, collected in the absence of SNC, introduces another potential explanation involving an incentive averaging rule (Pellegrini and Papini, 2007). According to this view, the value of a current incentive is compared to the memory of the average value of incentives experienced previously in the same (or similar) situation. At its core, ratio scaling of incentive value requires a comparison between the current incentive and the associatively reactivated memory of previously experienced incentives. Whereas this mechanism is not sufficient to produce SNC by itself, it may be necessary. Understanding the connection between ratio scaling and SNC would require a broader comparative description of the occurrence of ratio scaling, at least analogous to the available comparative data on SNC (Papini, 2006).

The same procedures used to study SNC can be applied to identifying the determinants of ratio scaling following incentive downshifts. For example, the asymptotic runway performance of toads (*Bufo arenarum*) responding for water reinforcement is an increasing function of the length of access to water between 20 and 1280 min (Muzio et al., 1992). Like pigeons, toads exhibit no evidence of SNC, but their behavior exhibits orderly changes either in the transition from large to small incentive magnitudes (Papini et al., 1995), or from large or small magnitudes to extinction (Muzio et al., 1992). These incentive magnitudes could be easily adjusted to determine whether toads respond to ratio scaling, to the preshift magnitude, or to the postshift magnitude. Similar experiments could be performed with goldfish and turtles, two other species for which there is evidence for reversed SNC (see Section 1 for references).

The suggested comparative studies have an interest of their own, but to the extent that these ideas are offered in the context of the current experiments, it may be appropriate to end with a word of caution about the conclusions favored here. Whereas care was taken to follow similar procedures, any one of several procedural discrepancies between the present experiments could account for the species differences reported here. Because rats have exhibited ratio scaling in other experiments, doubts may be raised about the replicability of the results reported in Experiment 1. For example, perhaps pigeons would show ratio scaling when incentives other than food pellets are used during training. A more typical incentive used in research on learning with pigeons involves the length of access to a hopper that offers mixed grain. It has occasionally been reported that this incentive manipulation does not yield magnitude-of-reinforcement effects on autoshaped key-pecking (Balsam and Payne, 1979), although pigeons do show magnitude effects in some training conditions (e.g., Osborne, 1978). Pigeons do show magnitude effects with pellets in widely spaced instrumental training situations (Papini, 1997). The extent to which the type of incentive and its delivery technique may affect ratio scaling remains to be determined.

The pigeons used in Experiment 1 also had prior experience, whereas the rats used in Experiment 2 were experimentally naïve. Assignment to the new magnitude conditions was done such that prior experience was matched across groups. Such matching reduces the possibility that specific aspects of the previous experience determine performance under the new incentive magnitudes, but it does not completely eliminate the general possibility that prior experience influences the incentive comparison process. After all, the incentive averaging mechanism described above could be sensitive to such variable.

It could also be argued that in these species autoshaping is only similar in terms of procedure, but not in terms of underlying processes. For example, the pigeon's key-pecking response seems to be less sensitive to omission contingencies than the rat's lever-pressing response (e.g., Davey et al., 1989; Williams and Williams, 1969). Perhaps pigeons would show constant proportionality if a

response with a more salient instrumental component were used, such as pedal pressing or runway running. The generality of ratio scaling across response systems in rats suggests that this may not be a relevant factor, but then this may not apply to other species.

The present results certainly encourage another look at the role of the test/training ratio in pigeons under other training conditions. These results also suggest that it may be worth studying other species that have failed to show evidence of SNC to determine their type of adjustment to incentive downshifts with systematic manipulation of the test/training ratio (see references in Section 1). A confirmation of the results of Experiment 1 with additional nonmammalian vertebrates would be consistent with the evolutionary hypothesis that the mechanisms underlying SNC are unique to mammals (Papini, 2002, 2003, 2006).

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