

Reinforcement Value of Gustatory Stimuli Determined by Progressive Ratio Performance

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REILLY, S. *Reinforcement value of gustatory stimuli determined by progressive ratio performance*. PHARMACOL BIOCHEM BEHAV 63(3) 301–311, 1999.—The progressive ratio schedule provides a means to determine reinforcement value that is independent of response rate. This is achieved by increasing the number of lever presses for each successive reinforcement until, eventually, the subject fails to respond within a designated time limit. The number of responses in the final completed ratio defines the break point. When tested with appetitive gustatory stimuli (sucrose and saccharin), rats showed a concentration-dependent increase in break point when food deprived (Experiment 1A and, for sucrose only, Experiments 1B and 1C) but not when water deprived (Experiment 1A). For aversive gustatory stimuli (sodium chloride, citric acid, and quinine) break point declined as concentration increased (Experiment 1A). In Experiment 1C, reinforcement duration had a significant, although relatively small, influence on break point for each of three concentrations of sucrose. Experiment 2 found a dose-dependent effect of the neuroleptic drug haloperidol (0.025, 0.05, and 0.1 mg/kg) on break point for sucrose reinforcement. The present study demonstrates that the progressive ratio schedule provides a valuable method to assess the influence of manipulations that might affect the perceived reinforcement value of gustatory stimuli. © 1999 Elsevier Science Inc.

Sucrose	Saccharin	Sodium chloride	Citric acid	Quinine	Reinforcement value	Progressive ratio
Haloperidol	Rat					

SCHEDULES of reinforcement have long been used to assess the reinforcing properties of gustatory stimuli. Within limits, lever-pressing rates increase in a concentration-dependent manner for appetitive tastants, and decrease for aversive tastants [e.g., (4,12–14,19,25)]. As noted by Hodos and Kalman (17), however, comparisons of the relative strength of different reinforcers sometimes may be problematic because rates of responding do not always provide an accurate index of reinforcement value. To overcome this type of interpretational difficulty, Hodos and Kalman advocated use of the progressive ratio (PR) schedule [(10,15); for a review, see (34)].

With the PR procedure, the number of responses required to obtain reinforcement is progressively increased for each successive reinforcement until eventually the subject fails to respond within a designated time limit. On a PR-3 schedule, for example, the subject would be required to make three responses for the first reinforcement, six for the second, nine for the third, etc. The number of responses emitted to obtain the final reinforcement is termed the “break point,” and is taken as an index of reinforcer value that is independent of rate of responding per se. By this method, different types of stimuli that support the same break point are, by definition, considered equally reinforcing. Progressive ratio schedules have been successfully used to assess the reinforcing efficacy of electrical brain stimulation [e.g., (16,20)] and of self-adminis-

tered drugs [e.g., (7,11,18,22,23,26,31,35); for reviews, see (1,30)]. Surprisingly, there have been few attempts to use the PR schedule as a technique to assess the influence of treatments thought to change the perceived value of reinforcers. Such treatments include drugs (e.g., dopamine agonists and antagonists) and brain lesions, particularly of the central gustatory system and the central reward system. This circumstance may, in part, derive from the paucity of data concerning the influence on PR performance of the types of natural rewards (e.g., gustatory stimuli) typically used in the aforementioned studies. Intended to rectify this omission, the present research examined PR performance supported by the four basic taste types (bitter, salty, sour, and sweet). Therefore, the influence of a neuroleptic drug (haloperidol) on PR responding for sucrose reward was examined.

Experiment 1A used a PR-3 schedule to obtain normative performance data for ascending concentration series of sucrose and saccharin under conditions of food deprivation, and for sodium chloride (NaCl), sucrose, citric acid, saccharin, and quinine hydrochloride (QHCl) following a switch to water deprivation. The next two experiments focused on magnitude of reinforcement effects for sucrose in food-deprived rats. Specifically, Experiment 1B replicated, with additional concentrations, the sucrose series from Experiment 1A, and Experiment 1C examined the effect of reinforcement duration

on PR performance across three concentrations of sucrose. To gain a more complete profile of PR performance, postreinforcement pause (PRP) and lever-response running rate were recorded as well as break point. Additionally, latency to the first lick and lick running rate were monitored to provide an assessment of consummatory behavior. Thus, the present study will determine if break point is sensitive to the reinforcement value of highly preferred stimuli such as sucrose that, by more conventional indices (e.g., level pressing rate or lick rate), may be prone to ceiling effects in performance.

Experiment 2 was undertaken to provide evidence of the utility of the PR schedule as a tool for investigating manipulations that might affect responding for gustatory stimuli. Dopaminergic neurons play an important role in food-related behavior [e.g., (9,37)]. Drugs that block dopamine receptors (e.g., haloperidol, *cis*-flupenthixol, pimozide) attenuate behaviors generated by appetitive reinforcers such as sucrose [e.g., (38); see also (36)]. Accordingly, Experiment 2 investigated the influence of haloperidol (0.025, 0.05, and 0.1 mg/kg) on PR responding for a highly valued reward, 1.0 M sucrose.

METHOD

Subjects

Seven Sprague–Dawley rats (Charles River Laboratories, Wilmington, MA) served as subjects in Experiment 1. They were individually housed in stainless steel hanging cages in a temperature-controlled (21°C) vivarium maintained on a 12 L:12 D cycle (lights on at 0700 h). At the outset of Experiment 1, the rats were approximately 120 days of age, and they were maintained at 80% of their free-feeding body weights (mean: 401 g; range: 400–406 g) by a daily feeding given 30–45 min after any experimental manipulations scheduled for that day. Water was continuously available in the home cage. At the completion of the food deprivation condition, the rats were given free access to food, but water was restricted to 15 min per day. Free feeding body weights were redetermined (mean: 529 g; range: 502–555 g), and thereafter the rats were maintained at 80% body weight by the method described above. In Experiment 2, 10 Sprague–Dawley rats obtained from the breeding colony maintained in the Department of Psychology at the University of Illinois at Chicago served as subjects. They were housed and maintained as described above at 80% body weights (range: 284–334 g). These subjects had prior experience responding on a PR-3 schedule for sucrose (0.01, 0.1, 0.3, and 1.0 M) reinforcement. All experimental manipulations and treatments were performed during the light phase of the cycle. Sessions were conducted 7 days per week.

Apparatus

The rats were trained in one of two identical modular operant chambers (MED Associates, Inc., Georgia, VT), measuring $30.5 \times 24.0 \times 29.0$ (l \times w \times h) cm. Both chambers had clear Plexiglas front and back walls, the end walls were made of aluminum, and the ceilings of stainless steel. The grid floors consisted of 19 4.8-mm (diameter) stainless steel rods spaced 1.6 cm apart (center to center). Each chamber was equipped with a retractable lever located to the left of a retractable sipper tube. In the extended position, the tip of the sipper tube was aligned in the center of a 1.3-cm diameter hole, flush with the right end wall. A lickometer circuit was used to monitor licking. A shaded bulb, which reflected light off the ceiling, was located directly above the cage speaker on the end wall opposite the lever and sipper tube. Each chamber was housed

in a light- and sound-attenuating cubical fitted with a ventilation fan and white noise source providing a background noise level of 75 dB(A).

Control of events in the chambers and collection of the data were carried out on line by a 66-MHz 80486 computer (Dell Computer Corp., Austin, TX). Programs were written in the Medstate notation language (MED Associates, Inc.).

Procedure

The rats were trained to drink 0.1 M sucrose from the sipper tube and then shaped to press the lever to gain access to the sucrose. Thereafter, the number of lever presses required to receive the reinforcement (50 per session) was increased over sessions from one to five, culminating in five sessions of fixed ratio 5. This was followed by PR-5 for two sessions and then PR-3 for six sessions of baseline training. As stated previously, on the PR-3 schedule the response requirement increases by a factor of 3 for each successive reinforcement. In the present experiments, each PR session terminated when 3 min (the designated time limit) elapsed without a lever press.

Experiment 1A began the day following the final session of pretraining. Gustatory stimuli were tested in ascending concentration series with each series repeated three times (cycles) in succession. To prevent neophobia from distorting performance, scores from the first cycle of each taste type were discarded. The scores for each dependent measure were computed as the mean of cycle 2 and cycle 3 for each concentration series. Solution concentrations are given as molarity except for saccharin, which, to maintain comparability with previous research, is expressed as percentage (weight/volume) concentration. When food deprived, the rats were tested with sucrose (0.01, 0.1, and 1.0 M) and then sodium saccharin (0.1, 0.15, and 0.30%). Following the switch to water deprivation, the rats received five sessions of baseline training with water as the reinforcement. They were then tested with NaCl (0.01, 0.1, and 1.0 M), sucrose (0.01, 0.1, and 1.0 M), citric acid (0.0003, 0.003, and 0.03 M), sodium saccharin (0.1, 0.15, and 0.30%), and QHCl (0.00003, 0.0003, and 0.003 M). Reinforcement was available for 2 s, timed from the first lick to maximize the likelihood of constant access duration. In summary, Experiment 1 tested seven concentration series, each series lasted 9 days. Thus, gustatory stimuli were tested for a total of 63 days. During Experiment 1B, which began following a return to food deprivation, the rats were tested with an expanded series of sucrose concentrations (0.01, 0.1, 0.3, 1.0, and 2.0 M) for a total of three cycles over 15 days. Experiment 1C examined the influence of reinforcement duration on performance. Four access times (1, 2, 4, and 8 s) were tested (one per session) for three cycles using 0.1 M sucrose (stage 1). The same test procedure was repeated with 0.3 M sucrose (stage 2) and then with 1.0 M sucrose (stage 3). Thus, gustatory stimuli were tested for 36 days in Experiment 1C.

Experiment 2 examined the influence of the dopamine antagonist haloperidol (Sigma, St. Louis, MO) on PR-3 responding for 2-s access to 1.0 M sucrose in a new set of rats. Haloperidol was injected subcutaneously 30 min before testing on day 11 (0.05 mg/kg), day 15 (0.025 mg/kg), and day 24 (0.1 mg/kg); vehicle (30% propylene glycol) was administered via the same route on the day preceding each drug test.

Dependent Measures

Break point, the conventional index of performance on the PR schedule of reinforcement, served as the primary depen-

dent measure in the present study. Break point was defined as the number of lever presses in the final completed (i.e., reinforced) ratio before session termination. To further characterize PR performance, two additional scores were computed for each completed ratio. Postreinforcement pause was timed from the end of the reinforcement period to the first lever press of the next ratio. By definition, the latency to the first lever press at the beginning of a session does not constitute a PRP, and this score was excluded from the overall session mean PRP value. Lever-press running rate also was computed for all completed ratios as the number of responses divided by run time (measured from the first to the last response within a ratio). Finally, latency to the first lick and lick running rate (response rate exclusive on initial lick latency of the trial) also were recorded. Postreinforcement pauses, lick latencies, and run times were recorded with a resolution of 0.1 s.

RESULTS

Experiment 1A

As noted previously, the concentration series of each tastant was repeated three times in succession. For each dependent measure, data from cycle 2 and cycle 3 were collapsed together, and statistical analyses were conducted on the resultant means.

Food deprivation condition. Figure 1 (left column) shows mean scores for the five dependent measures from the sucrose concentration series. It will be apparent from inspection of the results summarized in the top panel of the figure that the break point increased as concentration increased. Indeed, break point doubled with each increment in sucrose concentration. It is, then, no surprise that the analysis of variance (ANOVA) found a significant main effect of concentration, $F(2, 12) = 22.41, p < 0.001$. Subsequent analysis with Fisher's least-significant difference (LSD) test revealed that each of the three pairwise comparisons was significant ($ps < 0.05$). There was, however, no effect of sucrose concentration on PRP ($F < 1$) or lever-press running rate ($F < 1$). Latency to the first lick remained constant (approximately 1.48 s) across the three concentrations ($F < 1$). Similarly, although there was a suggestion that lick rate increased with concentration (see Fig. 1, left column, bottom panel), there was no significant effect on performance, $F(2, 12) = 2.66, p > 0.10$; lick rate, collapsed across concentrations, was 6.2 licks per second.

The performance scores from the saccharin concentration series are summarized in Fig. 1 (right column). It can be seen that the saccharin results are comparable to those observed when sucrose served as the reinforcer. Indeed, the same pattern of statistical significance was obtained for both types of appetitive taste stimuli. Thus, an LSD test conducted on the significant main effect of saccharin concentration, $F(2, 12) = 12.44, p < 0.01$, revealed that the break point at each level was significantly different from the other two (all $ps < 0.05$). As with sucrose, there was no significant influence of saccharin concentration on PRP ($p > 0.25$) or lever press running rate ($F < 1$). Similarly, there was no effect of concentration on either the latency to the first lick ($F < 1$; overall mean 1.52 s) or lick rate ($p > 0.25$; overall mean 6.3 licks per second) for the saccharin reinforcer.

Water deprivation condition. The stimuli were tested in the following order: NaCl, sucrose, citric acid, saccharin, and QHCl. For presentational purposes, however, the aversive (NaCl, citric acid, and QHCl) and appetitive (sucrose and saccharin) tastants are grouped separately.

Examination of Fig. 2 (left column, top panel) shows and statistical analysis confirms that break point declined as NaCl concentration increased, $F(2, 12) = 5.98, p < 0.05$. Further analysis (LSD test) revealed that this effect was due to a decrease in the break point at 1.0 M NaCl compared to 0.1 M NaCl ($p < 0.05$). The break point at 0.1 M NaCl did not differ from that at 0.1 M NaCl ($p > 0.50$). Although the duration of the PRP lengthened somewhat with ascending NaCl concentration, this tendency was not significant ($p > 0.15$). Lever running rate did, however, decline as concentration was increased, $F(2, 12) = 10.82, p < 0.01$. Subsequent analysis found that running rate was lower at 1.0 M than at 0.1 M ($p < 0.05$) or 0.01 M ($p < 0.01$), and that the rate at the two latter concentrations did not differ ($p > 0.10$). Sodium chloride concentration exerted no influence on the latency to the first lick ($F < 1$), but lick rate declined as concentration increased, $F(2, 12) = 8.04, p < 0.01$, an effect that was again confined to the high concentration of NaCl. That is, there was no difference ($p > 0.20$) between the rates supported by 0.01 M and 0.1 M NaCl (6.9 vs. 6.7 licks per second, respectively), but the rate at 1.0 M (5.9 licks per second) was significantly lower than that at 0.1 M NaCl ($p < 0.05$).

As illustrated in Fig. 2 (center column, top panel), break point declined as the concentration of citric acid increased, $F(2, 12) = 6.07, p < 0.05$. Further analysis (LSD test) revealed a significant difference between break point at the highest concentration relative to the middle ($p < 0.05$) but not the lowest concentration ($p < 0.07$), and that break points at the latter two concentrations did not differ from each other ($p > 0.25$). Neither PRP nor lever running rate were influenced by citric acid concentration (both $F < 1$). There was, however, a significant effect of concentration on the latency to lick the citric acid reinforcer, $F(2, 12) = 7.61, p < 0.01$. Again, the effect was due to performance at the highest concentration. That is, there was no difference ($p > 0.50$) between scores at 0.0003 and 0.003 M citric acid (1.52 vs. 1.55 s, respectively) but the response latency at 0.03 M citric acid (1.72 s) was significantly longer than each of the other two concentrations ($ps < 0.05$). Finally, there was no influence of concentration on lick rate for citric acid reinforcement ($Fs < 1$).

As can be seen in Fig. 2 (right column), QHCl concentration exerted a profound influence on the PR performance of water deprived rats. Post hoc analysis (LSD test) of the significant main effect of concentration, $F(2, 12) = 25.12, p < 0.001$, revealed that each increment in QHCl concentration produced a significant decline in break point (all $ps < 0.05$). As QHCl concentration increased PRP increased, but not significantly ($p > 0.10$). Lever running rate declined as concentration increased, $F(2, 12) = 5.09, p < 0.05$, an effect that was primarily due to the difference between the two highest concentrations ($p < 0.05$); running rate at the two lowest QHCl concentrations was not significant ($p > 0.35$). The latencies to make the first lick for the QHCl reinforcer lengthened as concentration was increased, $F(2, 12) = 4.38, p < 0.05$. Subsequent analysis revealed only a significant difference between latencies at the lowest vs. highest concentrations ($p < 0.05$). The rate of licking decreased as concentration increased, $F(2, 12) = 47.46, p < 0.0001$, an effect that was significant for each of the three pairwise comparisons (all $ps < 0.05$).

Sucrose performance scores are displayed in Fig. 3 (left column). It can be seen that sucrose concentration exerted little influence on break point, PRP, or lever running rate when the subjects were water deprived ($Fs < 1$). There was, however, a significant effect of concentration on the latency to the

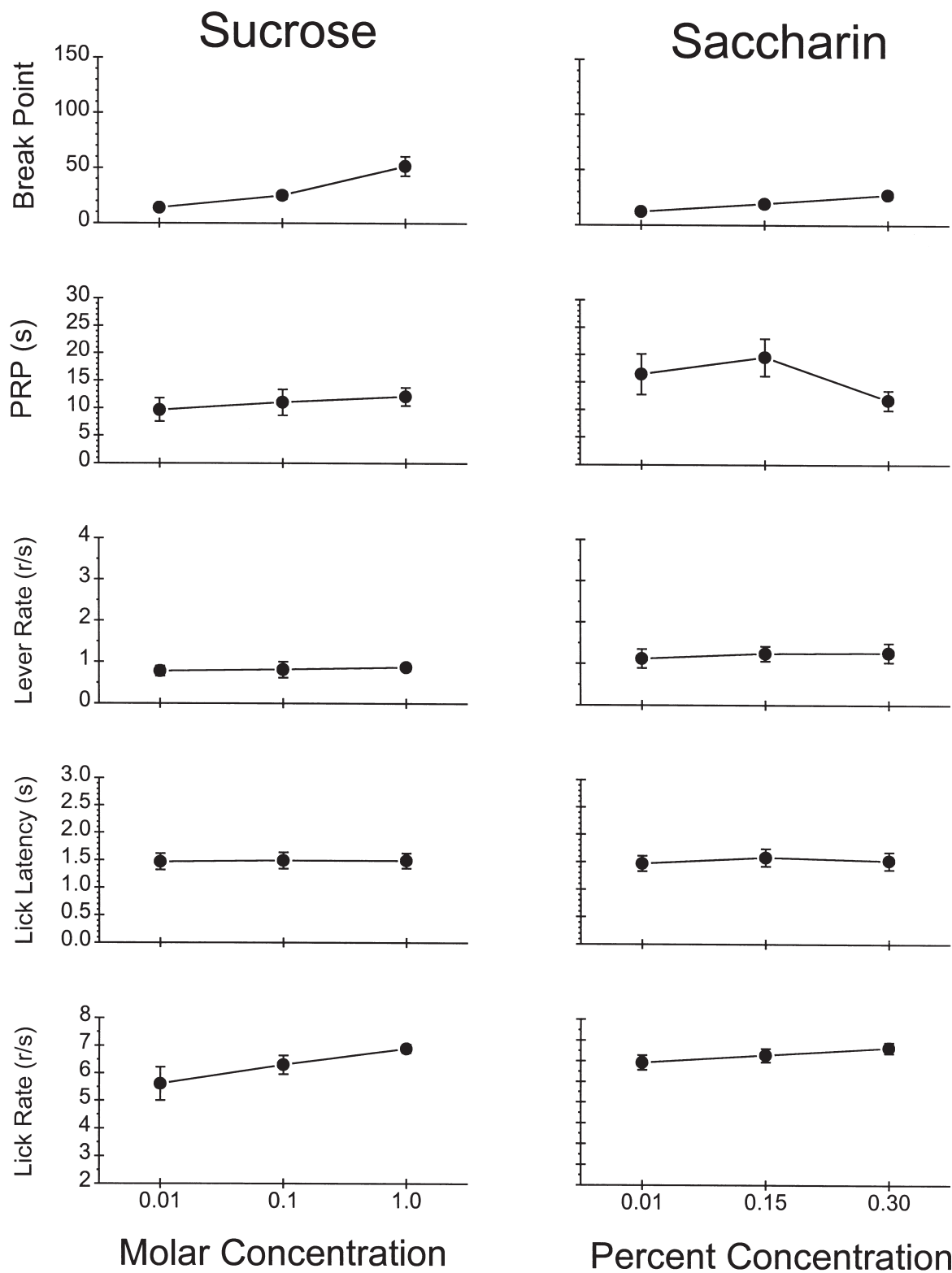


FIG. 1. Mean (\pm SE) performance scores for sucrose and saccharin when the rats were food deprived. From the top of the figure the dependent measures are break point, postreinforcement pause (PRP; in seconds), lever-running rate (lever rate; in responses per second), lick latency (in seconds), and lick running rate (lick rate; in responses per second).

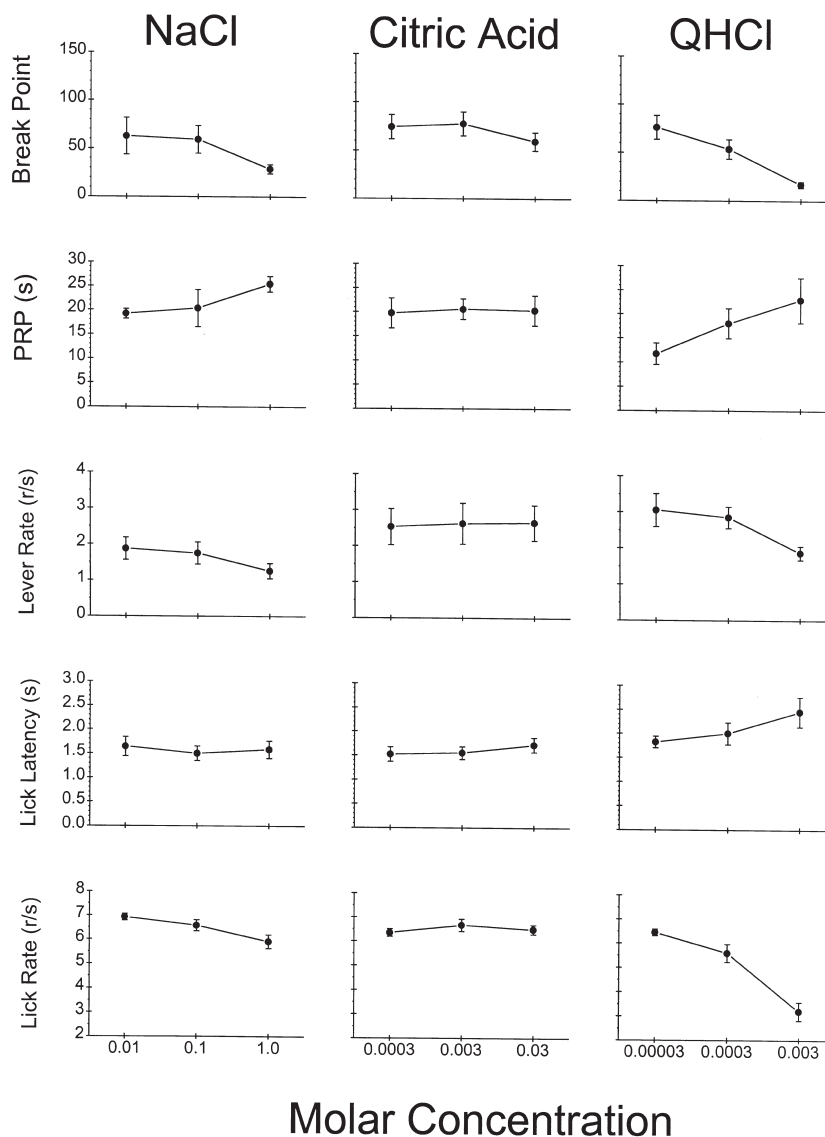


FIG. 2. Performance scores (mean \pm SE) for sodium chloride (NaCl), citric acid, and quinine hydrochloride (QHCl) when the subjects were water deprived. From the top of the figure the dependent measures are break point, postreinforcement pause (PRP; in seconds), lever-running rate (lever rate; in responses per second), lick latency (in seconds), and lick running rate (lick rate; in response per second).

first lick, $F(2, 12) = 5.29$, $p < 0.05$. Subsequent analysis (LSD test) found no difference in lick latencies for 0.01 and 0.1 M sucrose ($p > 0.20$), but revealed that response latencies were longer for 1.0 M relative to 0.1 M sucrose ($p < 0.01$). The rate of licking was not influenced by sucrose concentration ($p > 0.35$). Thus, although the rats displayed a longer latency to initiate licking for 1.0 M sucrose, there was no concomitant effect on lick rate.

The performance scores for saccharin when water deprived are summarized in Fig. 3 (right column). Examination of the figure suggests that saccharin concentration had little influence on any index of responding. This view was substantiated with statistical analyses that found no significant effect

of concentration on breakpoint, PRP, lever response rate, lick latency, or lick rate (all $F < 1$).

Experiment 1B

Following a return to food deprivation the rats were tested on an expanded series of sucrose concentrations (0.01, 0.1, 0.3, 1.0, and 2.0 M). The scores for each dependent measure were computed as the mean of cycle 2 and cycle 3. These data are summarized in Fig. 4. As is apparent from inspection of the top panel of the figure, there was a significant effect of concentration on break point, $F(4, 24) = 20.40$, $p < 0.0001$. Post hoc analysis revealed that break point was lower at 0.01 M

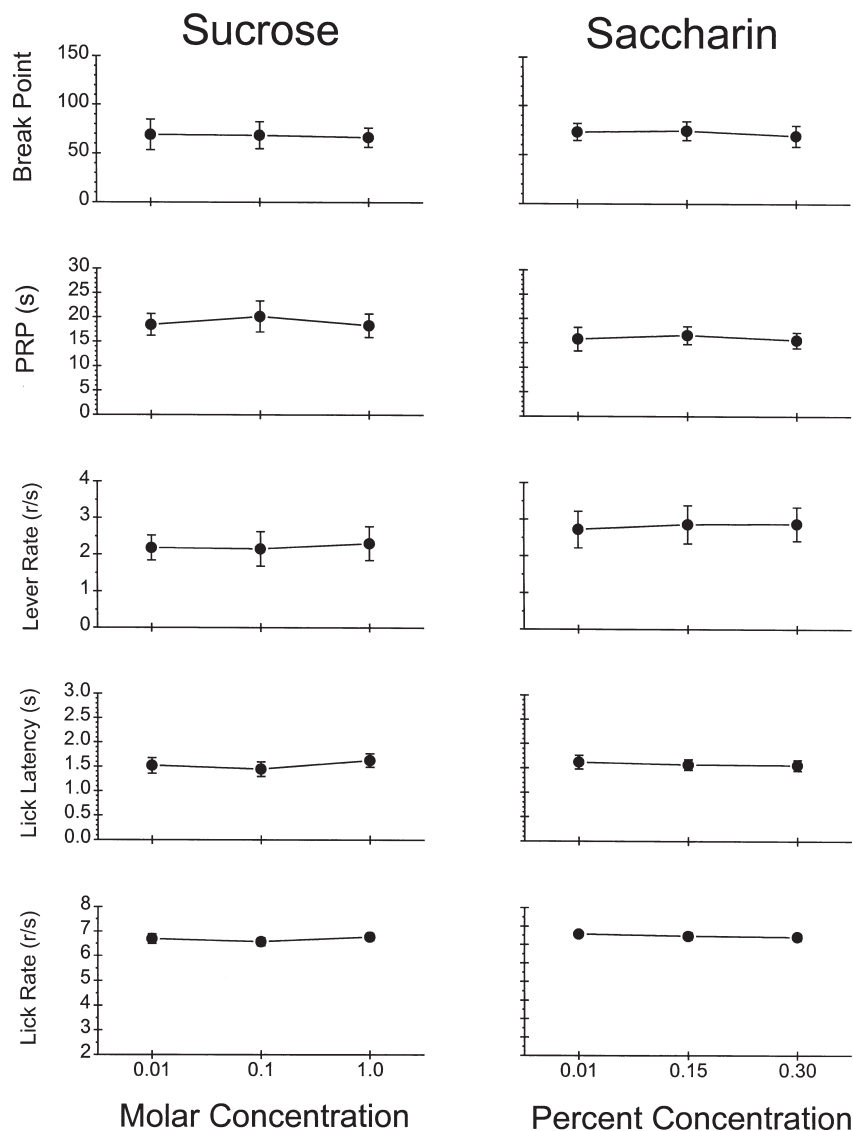


FIG. 3. Mean (\pm SE) performance scores for sucrose and saccharin when the rats were water deprived. From the top of the figure the dependent measures are break point, postreinforcement pause (PRP, in seconds), lever-running rate (lower rate; in responses per second), lick latency (in seconds), and lick running rate (lick rate; in responses per second).

than at each of the four higher concentrations ($p < 0.01$). Similarly, break point at 0.1 M was significantly lower than at each of the three higher concentrations ($p < 0.05$). Break point at 0.3 M was lower than at 2.0 M ($p < 0.05$) but the difference between 0.3 and 1.0 M narrowly failed to achieve acceptable levels significance ($p < 0.06$). Finally, there was no significant difference between break points at 1.0 and 2.0 M ($p > 0.50$). There was no influence of sucrose concentration on the duration of the PRP ($F < 1$; overall mean 13.3 s). Lever running rate showed an inverted U-shaped function that peaked at 0.3 M sucrose with a rate of 2.89 responses per second. Subsequent analysis of the main effect of concentration, $F(4, 24) = 3.80$, $p < 0.02$, revealed that running rate was lower at 0.01 M than each of the four higher concentrations ($p < 0.05$). However, no other comparisons were significant ($p >$

0.10). Examination of Fig. 4 suggests, and analysis confirmed, that there was no significant influence of sucrose concentration on lick latency ($p > 0.35$; overall mean 1.7 s) or on lick rate ($p > 0.35$; overall mean 6.3 responses per second).

Experiment 1C

In this experiment, the influence of reinforcer duration (1, 2, 4, and 8 s) was examined for 0.1 M (stage 1), 0.3 M (stage 2), and 1.0 M (stage 3) sucrose. The performance scores (means of cycle 2 and cycle 3) during each of the three stages of Experiment 1C are summarized in Fig. 5. Results from each stage were analyzed separately.

Stage 1. A repeated-measures ANOVA conducted on break points obtained when 0.1 M sucrose served as the reinforcer

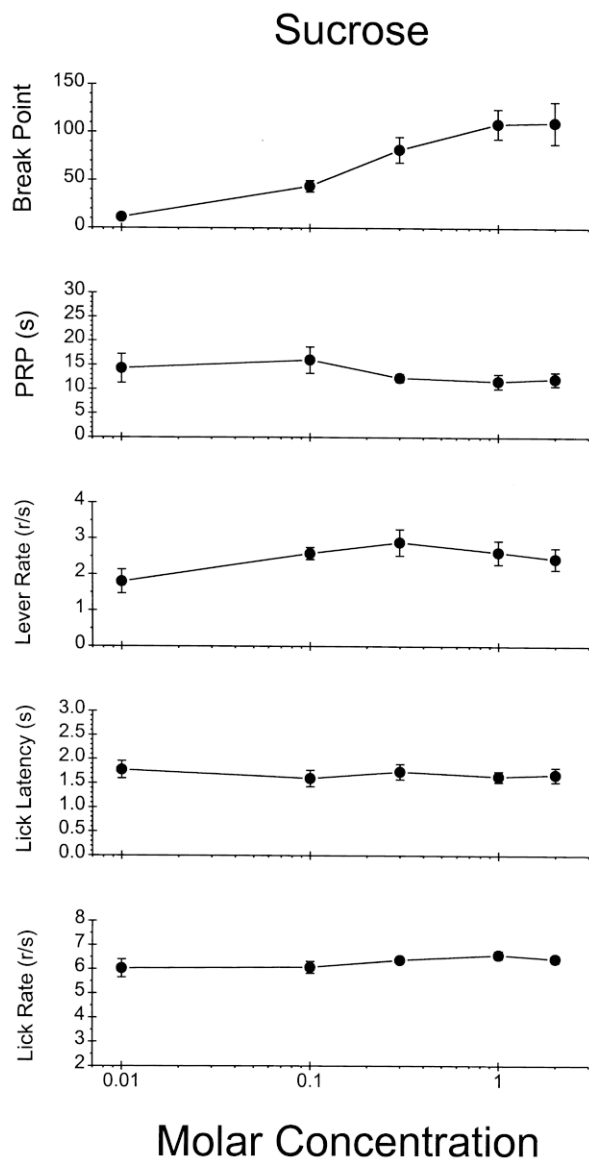


FIG. 4. Semilogarithmic plot of the performance scores (mean \pm SE) for an expanded series of sucrose concentrations when subjects were food deprived. From the top of the figure the dependent measures are break point, postreinforcement pause (PRP; in seconds), lever-running rate (lever rate; in responses per second), lick latency (in seconds), and lick running rate (lick rate; in responses per second).

found a significant main effect of access time, $F(3, 18) = 5.46$, $p < 0.01$ (see Fig. 5, left column, top panel). Post hoc analysis revealed that the break point at 1 s was lower than at 4 s ($p < 0.05$) or 8 s ($p < 0.05$) but not 2 s ($ps < 0.08$); no other break point comparisons were significant ($ps > 0.10$). The duration of the PRP lengthened as access time to 0.1 M sucrose increased, $F(3, 19) = 3.60$, $p < 0.05$. More specifically, PRP was shorter at 1 s than at 4 or 8 s ($ps < 0.05$); no other PRP comparisons were significant ($p > 0.10$). There was no significant influence of access time on lever running rate ($F < 1$) or latency to the first lick ($p > 0.25$). There was, however, a main effect of reinforcement duration on lick rate, $F(3, 18) = 6.26$,

$p < 0.01$ (see Fig. 5, left column, bottom panel). Subsequent analysis revealed that a higher lick rate was obtained at 1 s relative to 2, 4, or 8 s access time ($ps < 0.05$); no other pairwise comparisons were significant ($ps > 0.10$).

Stage 2. When 0.3 M sucrose was the reinforcer, there was a significant effect of access time on break point, $F(3, 18) = 6.68$, $p < 0.01$ (see Fig. 5, center column, top panel). Post hoc analysis revealed no significant differences between break points obtained at the two shortest durations (1 vs. 2 s; $p > 0.50$) or at the two longest durations (4 vs. 8 s; $p > 0.40$). Break points were, however, lower at each of the shorter durations relative to each of the longer access periods ($ps < 0.05$). The duration of the PRP increased as the duration of access time increased, $F(3, 18) = 4.34$, $p < 0.05$. Subsequent analysis (LSD test) found that PRP was shorter at 1 s relative to 4 or 8 s access time ($ps < 0.05$); no other PRP comparisons were significant ($ps > 0.10$). Again, there was no effect of reinforcement duration on lever running rate ($F < 1$) or latency to the first lick ($p > 0.30$) and a highly significant effect of access time on lick rate, $F(3, 18) = 15.74$, $p < 0.0001$. Further analysis revealed that lick rate was higher at 1 s than at 2, 4, or 8 s ($ps < 0.01$). The lick rate at 2 s relative to 4-s access duration approached but did not achieve acceptable levels of significance ($p < 0.06$). The 2-s rate of licking was, however, higher than the rate at 8 s ($p < 0.01$). Finally, there was no significant difference in the lick rate at 4 s relative to the 8 s reinforcement duration ($p > 0.20$).

Stage 3. Inspection of Fig. 5 (right column, top panel) shows that break point increased and then decreased as access time to 1.0 M sucrose increased. There was, however, no significant effect of access time on break point ($p > 0.35$). The duration of the PRP increased with increments in reinforcer duration, but this tendency failed to achieve acceptable levels of significance, $F(3, 18) = 2.66$, $p < 0.08$. Lever running rate was not influenced by access time ($F < 1$; overall mean 2.9 s). There was, however, a highly significant effect of reinforcement duration on the latency to make the first lick, $F(3, 18) = 22.82$, $p < 0.0001$. Subsequent analysis revealed that the lick latency at 1-s access time was significantly longer than at each of the three longer access times ($ps < 0.001$); no other latency comparisons were significant ($ps > 0.35$). There also was a significant effect of access time on lick rate, $F(3, 18) = 40.45$, $p < 0.0001$ (see Fig. 5, right column, bottom panel). Except for the rate at 1 s relative to 2-s access time that failed to achieve an acceptable level of significance ($p = 0.08$), every other pairwise comparison was highly significant ($ps < 0.001$).

Experiment 2

Figure 6 shows the influence of haloperidol (0, 0.025, 0.05, 0.1 mg/kg) on the five dependent measures for a new group of rats responding on a PR-3 schedule to obtain 2-s access to 1.0 M sucrose. Each dose of the neuroleptic was tested once. The scores for the 0 mg/kg dose were obtained by collapsing the data obtained on each of the vehicle injection days that preceded each drug test day. It will be apparent from inspection of the top panel of the figure, that the neuroleptic attenuated break point in a dose-dependent manner, $F(3, 27) = 34.17$, $p < 0.00001$. Post hoc analysis revealed that all pairwise comparisons were significant ($p < 0.05$), except the difference between 0.05 vs. 0.1 mg/kg narrowly failed to achieve acceptable levels of significance ($p < 0.06$). Similarly, PRP decreased as haloperidol dose increased, $F(3, 27) = 9.22$, $p < 0.001$. Again, all pairwise comparisons except one (0.025 vs. 0.05 mg/kg; $p < 0.09$) were significant ($p < 0.05$). There was a significant effect

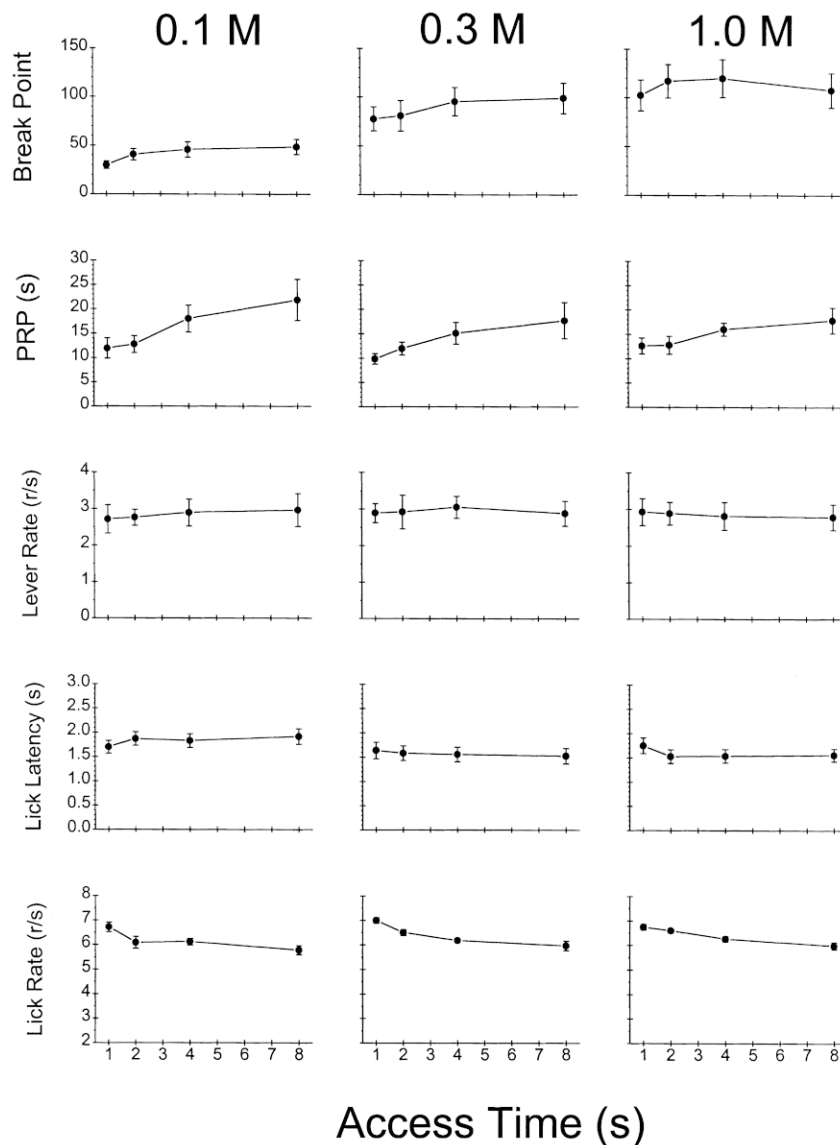


FIG. 5. Performance scores (mean \pm SE) for 0.1, 0.3, and 1.0 M sucrose when the rats were food deprived. From the top of the figure the dependent measures are break point, postreinforcement pause (PRP; in seconds), lever running rate (lever rate; in responses per second), lick latency (in seconds), and lick running rate (lick rate; in responses per second).

of haloperidol on lever running rate, $F(3, 27) = 5.53$, $p < 0.01$. As inspection of the figure (middle panel) shows, lever running rate declined following administration of the low and medium doses of haloperidol but, anomalously, appeared unaffected by the highest dose of the drug. This characterization of the data was confirmed by post hoc analysis, which found that all pairwise comparisons were significant ($p < 0.05$), except those between 0 (the vehicle) vs. 0.1 (high dose), and 0.025 mg/kg (low dose) vs. 0.05 mg/kg (medium dose). Although lick latency varied in a dose-dependent manner, the magnitude of the increase failed to attain significance, $F(3, 27) = 2.40$, $p < 0.09$. There was, however, a significant effect of the neuroleptic drug on lick rate, $F(3, 27) = 31.50$, $p < 0.0001$. Subsequent analysis revealed that this effect was entirely due to a decrease in lick rate at 0.1 mg/kg relative to each of the

other doses (all $ps < 0.001$); no other comparison achieved significance.

DISCUSSION

Normative performance scores from rats responding on a PR schedule when examples of four prototypic taste types served as reinforcement were obtained in Experiment 1A. Two sweet tasting stimuli, sucrose and saccharin, served as positive reinforcers. These stimuli, which differ in terms of caloric content, produced virtually identical patterns of behavioral effects. In both cases, break point reliably increased in a concentration-dependent manner when the rats were food deprived, an effect that was more pronounced for sucrose than saccharin (see Fig. 1). Because of the relatively low number of

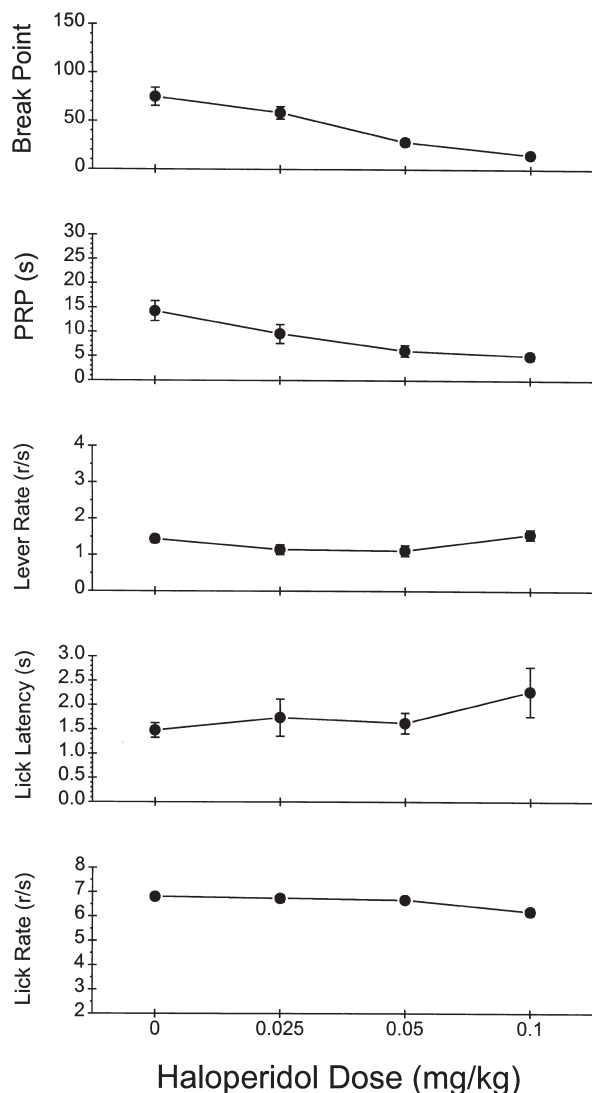


FIG. 6. Effect of haloperidol or its vehicle (0 mg/kg) on performance scores (mean \pm SE) for 1.0 M sucrose. From the top of the figure the dependent measures are break point, postreinforcement pause (PRP; in seconds), lever running rate (lever rate; in responses per second), lick latency (in seconds), and lick running rate (lick rate; in responses per second).

reinforcers obtained and the brief duration (2 s) of each reinforcement, postingestive consequences [including caloric, mechanical, and osmotic properties; see (6)] may have exerted only a minor influence on the response levels supported by sucrose and saccharin. It is likely, then, that performance was determined primarily by the orosensory stimulation (i.e., taste) of these stimuli. Given that the break point (mean \pm SE) for 0.1 M sucrose was comparable to that of 0.30% saccharin (25.1 ± 3.43 vs. 27.4 ± 4.05 , respectively), the taste of these two stimuli, by definition of break point, appear to be equally reinforcing for the food deprived rats in Experiment 1A. Because saccharin's bitter taste becomes more apparent as concentration increases (8), it seems improbable that a higher concentration of saccharin could support the same level of responding as, say, 1.0 M sucrose. No other dependent measure was sensitive to

variations in concentrations of either sucrose or saccharin for food-deprived rats.

For water-deprived rats, break point remained constant as the concentration of sucrose or saccharin was increased (see Fig. 3). This is, of course, a further demonstration that the motivational state of the animal is an important determinant of the effectiveness of a reinforcer. Collier and Bolles (5) investigated this issue more thoroughly in a study that examined operant responding for sucrose in hungry, thirsty, and nondeprived rats in reference to total daily food and fluid intake. Comparable to the results obtained in the present experiment, hungry rats responded in a concentration-dependent manner for sucrose, whereas response rate was independent of sucrose concentration for water-deprived subjects. Collier and Bolles concluded that performance was determined by caloric requirements in food-deprived subjects and by water requirements in thirsty rats. In the present experiment, then, it is likely that the PR responding of water-deprived rats was governed by the water content of the sucrose or the saccharin solutions rather than by their sweet taste.

The water deprivation level used in Experiment 1A (15 min per day) was predicated on the need to obtain a baseline level of responding that would be sufficiently high so as to be sensitive to variations in performance occasioned by the use of the aversive stimuli, without being so high as to obscure these effects due to excessive thirst. The results displayed in Fig. 2 indicate that this goal was successfully achieved. Increases in the concentrations of NaCl, citric acid, or QHCl, all generated a concomitant decrease in break point, an effect that was most pronounced in the case of quinine. This concentration-dependent influence on lever-press break point conformed to the pattern of licking supported by the three aversive tastants (compare the upper and lower panels of Fig. 2). The absence of a similar effect for sucrose or saccharin when tested during food deprivation in Experiment 1A, likely is due to a ceiling effect in licking for these appetitive tastants. Thus, break point was sensitive to reinforcement value at times when a more traditional index, lick rate, was not. This dichotomy serves to highlight one of the benefits of using the PR schedule to assess the reinforcement value of highly preferred stimuli.

The results from the concentration study of Experiment 1B replicated the data obtained for sucrose in Experiment 1A when the rats were food deprived. Additionally, it was demonstrated that the break point for 0.3 M sucrose was intermediate between 0.1 and 1.0 M sucrose. There was, however, no significant difference between the break points at 1.0 M relative to 2.0 M sucrose (108.4 vs. 109.7, respectively). This absence of an effect is noteworthy. Because there was no difference in lick rate for these two stimuli and the reinforcer access time was fixed, the volume of 1.0 M sucrose ingested was about the same as that of 2.0 M sucrose (assuming that lick volume was constant across concentrations). So, despite the fact that there are twice as many calories in 2.0 M sucrose than 1.0 M sucrose, reinforcer magnitude failed to differentiate performance at these two concentrations. Given that total reinforcement access time was approximately 73 s (number of reinforcements obtained multiplied by reinforcement duration) temporally distributed in 2-s epochs for both concentrations of sucrose, it is difficult to believe that postingestive negative feedback could influence break point. It might be easier to accept that the taste of 1.0 M sucrose was not well discriminated from 2.0 M sucrose in the present experiment. Taste was, of course, sufficient to differentiate the lower concentrations from each other.

In Experiments 1A and B, the influence of magnitude of reinforcement on PR responding was investigated by varying the concentration of the tastant while holding reinforcer access time constant at 2 s (timed from the first lick to ensure comparability). In Experiment 1C, the opposite method was used. That is, concentration of sucrose was held constant (0.1, 0.3, or 1.0 M), and access time was varied (1 s, 2 s, 4 s, and 8 s). With regard to the primary dependent measure, there was a significant effect of reinforcement duration on break point when 0.1 or 0.3 M sucrose served as the reinforcer. There was, however, no significant influence of reinforcer access time on break point for 1.0 M sucrose. Moreover, it will be apparent from inspection of Fig. 5 that the effects of reinforcer access time were relatively small in magnitude. Thus, for 0.1 M sucrose, group mean break points were 29.8 and 48.4 at 1 and 8 s, respectively. These values represent a difference of six reinforcers. Similarly, the break points at these same reinforcement durations were 77.6 and 99.0, respectively, when 0.3 M sucrose was the reinforcer. This corresponds to a difference of seven reinforcers. By way of comparison, at 1 s access time the difference in the number of reinforcements obtained for 0.1 and 0.3 M sucrose was 16 and, for the 8-s reinforcer duration, 16.9. Although these numbers support the view that effects of reinforcement magnitude are more readily observed when concentration rather than access time serves as the independent variable, it should be noted that the range of these two variables (concentration and access time) may not have been functionally equivalent. Thus, although the present data provide good support for the view that variations in the magnitude of reinforcement produce changes in operant performance, they should not be taken as an endorsement of the view that reinforcer concentration is more effective than reinforcer access time in affecting that change. For further discussion of issues concerning reinforcement magnitude and behavior the reader should consult Bonem and Crossman (2), Killeen (21), and Reed (27).

Beginning with the original work of Hodos (15), break point has been used as the primary (sometimes only) dependent measure for assessing performance on the PR schedule. This is a reasonable approach, because break point proved to be the most sensitive index of reinforcer value. However, additional dependent measures do serve an important function [see (32,34)]. Although not emphasized in the foregoing discussion, these other measures are reported so as to provide a

more complete profile of performance not only in terms of lever pressing behavior but also with regard to the related consummatory responding. Analyses utilizing multiple dependent measures may allow for a more thorough understanding of the influence of experimental manipulations on PR performance.

As demonstrated in Experiment 1, break point varies in a concentration-dependent manner for sucrose reinforcement. These data provide the foundation for further studies that might profitably examine the effects on PR responding of treatments thought to influence the reinforcement value of gustatory stimuli. The utility of this approach was demonstrated in Experiment 2, which investigated the influence of haloperidol on PR performance for 1.0 M sucrose. The results of this experiment indicated that break point decreased as haloperidol dose increased. In addition to assessing the influence of drug treatments on food-reinforced behavior, PR schedule might also be used to evaluate the impact of brain lesions on the perceived reinforcement (or hedonic) value of gustatory stimuli. In particular, this schedule may provide a valuable addition to the repertoire of tasks used to determine the functional organization of the central gustatory system [for reviews, see (3,24,28,29,33)].

The results from the present study show that for both appetitive and aversive tastants an orderly relationship exists between stimulus concentration and break point on the progressive ratio schedule of reinforcement. A similar conclusion was reached when reinforcement (sucrose) access time served as the independent variable. As discussed above, analysis of PR performance provides a means by which manipulations that may influence the perceived reinforcement value of gustatory stimuli can be evaluated. This is especially true in those cases where motor impairments or altered patterns of behavior may lead to a reduction in the rate of responding. Or, it might be added, in those situations where a ceiling effect on the rate of lever pressing per se may otherwise obscure the influence of a highly valued reinforcer.

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