OPERANT WHEEL RUNNING BY RATS ON FIXED RATIO SCHEDULES OF SUCROSE REINFORCEMENT

BY

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Abstract

Prior studies have shown that operant wheel running in rats is reinforced by sucrose on fixed ratio (FR) schedules, but wheel running also occurs at a high frequency without experimentally-arranged consequences. Findings that scheduled reinforcement exerts only limited control on operant wheel running served as the basis for the current study. Eight female Long-Evans rats were exposed to a series of FR schedules (FR 5, 15, 40, and 80) for 0.1 ml of 20% sucrose solution and again with 0% sucrose (water). Wheel revolutions at each ratio size produced outcomes (sucrose or water), and wheel running rates were assessed for each scheduled reinforcement rate (FR size). Results showed significantly higher wheel-running rates for sucrose reinforcement than water; however, the difference in rates by outcome was modest and independent of the control exerted by FR size alone. For both outcomes, wheel-running rates decreased, and latency to initiate running increased as FR size increased and the reinforcement rate decreased. The lack of variation in the reinforcing effect of sucrose as the FR size varied differs from findings with operant behaviours such as key pecking and lever pressing. This finding suggests that automatic reinforcement and constraint on the opportunity to run might help explain these differences, but further research is required to substantiate these findings.

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Wheel running is a behavior that can function as both reinforcement for operant behavior, and as operant behavior that produces reinforcement. While wheel running as a reinforcing consequence has been extensively investigated (e.g., Belke, 1996, 1997, 2000, 2006a, 2006b; Belke & Pierce, 2009, 2016; Collier & Hirsch, 1971; Iversen, 1993; Kagan & Berkun, 1954; Premack, 1962; Premack, Schaeffer, & Hundt, 1964), there have been few studies of wheel running as an operant behavior (Belke & Pierce, 2014, 2015; Belke, Pierce, Fisher, & LeCocq, 2017; Belke, Pierce, & Welsh, 2018; Belke, Mann, & Pierce, 2015; Iso, 1996; Skinner & Morse, 1958). An important difference between wheel running as an operant behavior and more conventional operant responses, such as lever pressing and key pecking, is that wheel running generates reinforcement automatically, simply by doing it. The automatic reinforcement function of wheel running results in a high operant level (Belke et al., 2015), and limits the control exerted by scheduled (experimentally arranged) reinforcement (Belke et al., 2017). The objective of the current study was to further investigate the control exerted by scheduled sucrose solution reinforcement on operant wheel running on a series of fixed ratio (FR) schedules that varied the rate of scheduled (programmed) reinforcement.

"A fixed-ratio (FR) schedule is programmed to deliver reinforcement after a fixed number of responses have been made" (Pierce & Cheney, 2017, p . 146). This schedule of reinforcement produces a pattern of responding known as "break and run." Following reinforcement, there is a period of no responding, the break, or postreinforcement pause (PRP), then comes a rapid run of responses until the ratio requirement is met (Pierce & Cheney, 2017). As the ratio requirement increases, the duration of the PRP increases (Felton & Lyon, 1966; Schlinger, Derenne, & Baron, 2008). Response rate, however, has not always decreased, as expected (Crossman, Bonem, & Phelps, 1987). As the response requirement increases, the rate of reinforcement would decrease, and although the decrease can be overcome by an increase in the rate of responding initially, eventually it would decline.

Skinner and Morse (1958) were the first to investigate wheel running as an operant behavior. The study showed that the nature of control exerted by schedules of food reinforcement on operant wheel running deserves further investigation. A comparison of cumulative record slopes for unreinforced versus reinforced wheel running showed lower rates of wheel-running in the absence of a contingency of food reinforcement. The inference from this comparison is that the schedule of food reinforcement exerted some control on operant wheel running. However, as this early study examined reinforcement of wheel running by food on fixed interval (FI) schedules, it is not directly relevant to the current investigation of wheel-running on FR schedules.

Iso (1996) investigated operant wheel running on both FR and FI schedules. Three 12-week-old rats ran on a FR schedule, and three rats ran on a FI schedule. Three rats were yoked to the FR rats, and three were yoked to the FI schedule rats. Operant wheel running of the rats on the FR schedule is relevant to the current research. The operant response was a ¼ of a wheel turn for a 45 mg food pellet reinforcement. Yoked rats received food pellets whenever FR rats completed the schedule requirement, independent of wheel running. Furthermore, ratio requirements were increased across sessions during training until the FR rats were on a FR 40 schedule, and rats remained on this schedule for 10 sessions before being placed on extinction for five sessions.

Cumulative records showed that reinforcement on FR schedules produced break-and-run patterns in which rats paused after reinforcement, and then increased and maintained the rate of wheel revolutions to the moment of reinforcement. While cumulative records showed evidence of schedule effects, there was no significant difference in running reinforced on FR schedules compared to that of yoked rats. However, yoked rats showed a different pattern of running than rats reinforced on schedules, which included a bout of running after reinforcement followed by a pause in running before the next food delivery. Iso suggested that this pattern may reflect a schedule-induced or adjunctive behavior, as suggested by earlier research (Falk, 1961, 1969).

In a second experiment, Iso (1996) exposed rats to the same FR schedules, but maintained the rats at 91%, rather than 75% of original body weight. Iso noted that there was no significant difference in wheel running by body weight for rats on the FR schedule. Rats on the FR schedules once again showed break-and-run patterns in the cumulative records. Interestingly, Iso observed that the running rates of these rats did not decrease on extinction in either experiment. Based on this observation, Iso suggested that wheel running was likely influenced by reinforcing stimuli other than food reinforcement, because the wheel-running rates during extinction sessions were similar to those when food reinforcement was provided.

Belke and Pierce (2014) investigated operant wheel running on FR schedules arranged on a two-component multiple schedule. Wheel running served as reinforcement for operant lever pressing in one component, and as the operant behavior that produced sucrose reinforcement in the other component (Belke & Pierce, 2014). In the wheel running as reinforcement component, rats pressed a lever on a variable ratio (VR) 10 response schedule for the opportunity to run 15 revolutions as reinforcement. In the operant wheel-running component, rats ran on a FR 15schedule for the delivery of 0.1 ml of a 15% sucrose solution. Each component was signaled by a distinctive stimulus and the components were separated by a 10 s intercomponent interval, and remained in effect until rats obtained 10 reinforcements of each type (sucrose or wheel-running).

Following 50 sessions under these baseline conditions, two manipulations were carried out. In the first manipulation, 15% sucrose solution was replaced by 0% sucrose solution (water), then reinstated. For the second manipulation, rats ran for 1 hour prior to responding on the multiple schedule. Results showed, contrary to expectation, that the operant wheel-running rate reinforced by 15% sucrose solution was not significantly higher than the wheel-running rate of rats reinforced for lever pressing with an opportunity to run (Belke & Pierce, 2014). In other words, as was the case for Iso's (1996) study, there was no evidence that sucrose reinforcement increased the operant wheel-running (Belke & Pierce, 2014).

Interestingly, removal of 15% sucrose solution for operant wheel running decreased wheel-running rates in both components, but to a greater extent in the operant wheel-running component than in the wheel running as reinforcement component. Reinstatement of sucrose restored both wheel-running rates to their previous level. By contrast, pre-running the rats for 1 hour prior to the multiple schedule reduced wheel-running rates in the wheel-running reinforcement component more than it did in the operant wheel-running component. Based on these findings, Belke and Pierce (2014) concluded that "operant wheel running is controlled by the intrinsic reinforcement of the activity and the extrinsic reinforcement of the situation." (p. 41)

Belke and Pierce (2015) also manipulated the presence or absence of 15% sucrose solution as reinforcement for operant wheel running on a two-component multiple schedule. Wheel running functioned as reinforcement for lever pressing in one component, and as the operant for sucrose reinforcement in the other component; however, unlike their earlier multiple schedule study, the components advanced based upon time rather than behavior. Lever pressing for wheel-running reinforcement remained on a VR 10 schedule and operant wheel running remained on a FR 15 schedule. Wheel-running reinforcement remained as 15 wheel revolutions. Components were 8 minutes in duration with a 30 s intercomponent interval. Sessions ended when each component had been experienced twice.

As before, manipulation of the presence/absence of 15% sucrose solution as a consequence for operant wheel running systematically affected wheel-running rates in both components. However, advancement of the two components no longer depended on behavior. With the components unlinked, operant wheel-running rate reinforced by sucrose was higher than that of the wheel-running reinforcement component (Belke & Pierce, 2015). Furthermore, the initial removal of sucrose reduced operant wheel-running rates by 26.40% while the rate for wheel-running reinforcement declined by 10.56%. Thus, in contrast to Belke and Pierce (2014), wheel-running rates in the operant component were significantly higher than those in the wheel running as reinforcement component.

Belke and Pierce (2015) concluded that their findings confirmed the effect of an extrinsic reinforcement (sucrose) on a behavior (wheel running) that generates its own reinforcement just by doing it. Thus, unlike previous studies with operant wheel running, Belke and Pierce demonstrated control of operant wheel running by scheduled sucrose reinforcement and, in line with Iso's (1996) assumption, that wheel running generates its own automatic reinforcement that functions as an alternative source of reinforcement. The automatic reinforcement function of wheel running would account for why operant wheel running still remained high when the experimentally-arranged reinforcement (food, sucrose solution) was removed. Moreover, the results also suggested that scheduled sucrose reinforcement and the automatic reinforcement generated by wheel running are additive for the multiple schedule contingencies arranged in these studies.

Automatic reinforcement may be defined as reinforcement that is not mediated by the deliberate action of another person (Vaughn & Michael, 1982). Automatic reinforcement emanates from engaging in the behavior itself. It can be seen as a high operant level of a behavior prior to scheduled reinforcement as well as a high level of responding during extinction (Belke et al., 2015; Iso, 1996). Iso's (1996) finding that wheel-running rates continued at a high rate despite an extinction manipulation is indicative of the automatic reinforcement function of wheel running. Furthermore, any control exerted by experimentally-arranged sucrose reinforcement should be additive to the automatic reinforcement of wheel running (Belke & Pierce, 2015).

In another study of multiple schedules and wheel running, Belke et al. (2015) investigated the differential effect of sucrose reinforcement on rates of operant wheel running and operant lever pressing. Specifically, rats were exposed to two different multiple schedules. In both multiple schedules, one component involved lever pressing on a VR 10 schedule for the opportunity to run for 15 revolutions. However, in the alternating component of one multiple schedule, operant wheel running on a FR 15 schedule produced 15% sucrose, and in the alternating component of the other, lever pressing on a FR 15 schedule produced 15% sucrose. On each of these multiple schedules, the manipulation involved replacing the 15% sucrose solution as reinforcement for operant responding with water (i.e., 0% sucrose). Belke et al. found that operant wheel-running rates for sucrose solution decreased by only 24% when placed on extinction (water). By comparison, lever pressing decreased by 90%. Thus, the study demonstrated control by sucrose reinforcement on operant wheel running as well as the difference in automatic-reinforcement value between wheel running and lever pressing as operant behaviors.

Subsequently, Belke et al. (2017) investigated control by sucrose reinforcement on operant wheel running of rats under ad-lib and deprived feeding conditions. Rats were initially trained on an FR 30 schedule of operant wheel running for 20 reinforcements of 15% sucrose solution. Rats were then divided into two groups – one that experienced progressively higher concentrations of sucrose reinforcement (0%, 2.5%, 5%, 10% and 15%), and another that experienced progressively lower concentrations (15%, 10%, 5%, 2.5%, and 0%). Under ad-lib conditions, only wheel-running rates reinforced by 10% and 15% were significantly higher than those at 0%. Under conditions of deprivation, however, wheel-running rates increased for all concentrations higher than 0%, and the wheel-running rates increased with concentration. Although wheel-running rates increased with concentration, the increase in wheel-running rates relative to those at 0% was limited. Collapsed across both deprivation levels, the highest concentration (15%) increased the wheel-running rates by 7 revolutions/min relative to wheel-running rates at 0%, indicating that the automatic reinforcement of wheel running limited the control by scheduled sucrose reinforcement.

Belke et al. (2017) showed that on an FR schedule the reinforcing effect of sucrose on operant wheel running varied with sucrose concentration – a reinforcement magnitude effect. Another variable that usually controls operant responding is the rate of reinforcement. Iso (1996) investigated the effect of food reinforcement on operant wheel running on a FR 40 schedule while Belke and Pierce (2014, 2015) and Belke et al. (2015) arranged a FR 15 schedule of 15% sucrose solution for operant wheel running. Belke et al. (2017) investigated the effect of sucrose reinforcement on operant wheel running using a FR 30 schedule with wheel revolutions as the operant. To date, there are no studies that systemically varied the rate of reinforcement (FR size) under a series of FR schedules for operant wheel running.

Variation in the FR size for sucrose reinforcement provides a way to assess the reinforcement value of sucrose on operant wheel running, as response rates should decrease on large ratios. As wheel running occurs at a high operant level in the absence of reinforcement due to its generation of an automatic reinforcement effect, a no-reinforcement (0% sucrose) condition is required to discern the effect of varying rate of scheduled reinforcement (FR size) on operant wheel running. That is, scheduled sucrose reinforcement must increase the wheel-running rate above its operant level, and the rate of operant wheel running should decrease with increases in FR size (i.e., low rates of wheel running on high fixed ratios).

The present study assessed the control by scheduled sucrose reinforcement on operant wheel running and whether this control varies with the rate of sucrose reinforcement. Rats were placed on a series of FR schedules (FR 5, FR 15, FR 40, and

FR 80) that varied FR size with wheel revolutions as the operant for delivery of 0.1 ml of a 20% sucrose reinforcement. We also required rats to wheel run for water (0% sucrose) on each of the FR schedules to assess the operant level of wheel running at each ratio size. Wheel-running rates were expected to be higher for sucrose reinforcement than water and to decrease as the ratio requirement reached the lowest rate of sucrose reinforcement (FR 80).

Method

Subjects

Eight female Long–Evans rats obtained from Charles River Breeding Laboratories in St. Constant, Quebec, served as subjects. The rats were naïve, and approximately 17 weeks old at the start of the experiment. In their colony room, the rats were individually housed in polycarbonate cages (48 cm × 27 cm × 210 cm). Heat-treated beta chips and paper towel were used in the cage as bedding. Lighting in the colony room was on a 12-h light/dark cycle (lights on at 0730) while the temperature was maintained at ~20˚ C. Distilled water was freely available at all times within the home cage. Rats were fed Prolab-R-M-H 3000 standard rat chow daily. Food was restricted to an amount that would maintain the rats at 255 +/- 5 g, that is approximately 85% of an adult female ad-lib body weight for this strain. This research was conducted in accord with the guidelines set forth by the Canadian Council on Animal Care under a protocol approved by the Mount Allison Animal Care Committee.

Apparatus

Training and experimental sessions occurred in eight activity wheels. One set of four wheels consisted of three Lafayette wheels and one Wahmann wheel. The other set consisted of two Wahmann and two Lafayette wheels (circumference of 112 cm). Length and width of the wheel opening was 9 cm x 7 cm. The floors of the wheels were wire mesh 1 cm x 1cm grids. Each wheel was equipped with a solenoid-operated brake and two 24 VDC lights attached to the wheel frame (17 cm from the base of the wheel) that illuminated the wheel chamber. A solenoid attached to the base of the wheel was part of a brake that prevented the wheel from turning. When activated, the solenoid pulled a metal shaft with rubber tip against the outer edge of the wheel gradually stopping it from turning. Wheel revolutions were recorded by a microswitch attached to the wheel frame. Each wheel was enclosed in a sound-attenuating cubicle, equipped with fans to mask extraneous noise and to provide ventilation. Control of experimental events and recording of data were handled by a Borland Turbo Pascal 4.0 program run on PC computers interfaced to the wheel through the parallel port.

Each set of four wheels had a different panel attached to the opening of the wheel. For the first set (three Lafayette, one Wahmann), a metal panel (170 mm high by 170 mm wide by 2 mm thick) equipped with a retractable rat lever, two yellow LED stimulus lights, and a liquid receptacle was attached to the 9 cm by 7 cm opening on each wheel frame using Velcro strips. For the current study, neither the retractable lever nor the LED lights over the lever were used. The liquid receptacle (55 mm by 32 mm by 37 mm) was located to the left of the retractable lever and the base of the receptacle opening was 75 mm above the base of the panel. Sucrose solution was contained in a cylindrical dispenser and delivered into the receptacle by a solenoid valve controlled by a computer. The dispensers were 37 mm in diameter, 106 mm long, and held in place by a metal clamp above the liquid receptacle.

For the second set of wheels (two Lafayette, two Wahmann), a metal panel (180 mm by 185 mm by 2 mm) containing a liquid receptacle, two yellow LED stimulus lights, and two openings for levers was attached to the 9 cm by 7 cm opening of each wheel. Neither the stimulus lights nor the levers were used in the current study. The liquid receptacle (60 mm by 30 mm by 35 mm) was situated 160 mm from each side of the panel and 40 mm from the base of the panel to the base of the liquid receptacle. A cylindrical dispenser attached to a solenoid valve was situated above the liquid receptacle.

Procedure

Initial training of the rats in the wheels was conducted over 24 days to habituate the rats to the wheels. Rats were placed in the wheels and given 30 min of free access to wheel running on each daily session. Subsequently, the rats were given free access to sucrose by replacing water bottles with 15% sucrose solution for two 1-hour sessions in home cages to habituate the digestion of sucrose, which was used as reinforcement in the experiment.

Following initial training, eight rats were selected from the 16 that completed initial training. The eight remaining rats were used for an undergraduate course in conditioning. Of the two rats that were trained in each of the eight running wheels, the rat that consistently had more revolutions during the 30 min of free access to the wheel over the last 5 days of the initial training in each wheel was selected for the current study. This selection procedure maintained rats in the wheels in which they initially trained, but also took into consideration the high number of wheel revolutions that would be required in the experiment.

The eight rats were then randomly assigned to an ascending or descending order of FR schedules that varied the size of the ratio. One schedule order progressed with an ascending ratio size (FR 5, 15, 40, and 80), and the other progressed with a descending ratio size (FR 80, 40, 15, and 5). Two levels of sucrose concentration (0% and 20%) were delivered in 0.1 ml drops on each of the schedules. Half of the rats (NX 2, 8, 9, and 6) first received 20% sucrose, and half (NX 3, 7, 12, and 13) received water (0%). Thus, of the four rats assigned to the ascending order of ratio size, two (NX 2, and 8) first experienced 20% sucrose concentration for operant wheel running while the other two (NX 7, and 12) experienced water. Of the four rats assigned to the descending order of ratio size, two (NX 6, and 9) first experienced 20% sucrose concentration for operant wheel running, and two (NX 3, and 13) experienced water. Upon completion of the assigned order (ascending or descending) of FR size, the concentration (sucrose or water) was reversed; rats that first experienced sucrose were changed to water, and rats initially on water were changed to sucrose. Each rat now repeated the order of ratio size as originally assigned at the alternative level of concentration (sucrose or water).

Each of the four FR sizes was in effect for 15 sessions for both the 20% sucrose reinforcement and 0% water condition for a total of 120 sessions. Each session began at 0800 with the release of the wheel brake allowing the running wheel to turn freely in an unlit chamber. Meeting the FR ratio requirement for wheel revolutions resulted in the activation of the brake, illumination of 24 VDC lights at the front and back of each wheel, and concurrent delivery of the scheduled solution (sucrose or water). After 4 s elapsed, the 24 VDC lights were extinguished, the brake released, and the next FR requirement came into effect. Each session terminated when 20 outcomes (sucrose, water) were completed on the schedule of reinforcement in effect. On the FR 5, 15, 40, and 80 schedules, this required that the rats run 100, 300, 800, and 1600 revolutions to complete a session, respectively.

Dependent measures

During each session, the number of revolutions, the number of reinforcements, time spent wheel running, and the latency to initiate running following termination of the 4-s outcome interval were recorded by the computer for each reinforcement as well as cumulatively for the session. Local wheel-running rate, expressed as revolutions per minute, was calculated by dividing the number of revolutions required to complete 20 reinforcements on a schedule by the time taken to complete that number of revolutions; completion time was measured from the first revolution of the wheel to the revolution that completed the FR ratio requirement. With water as an outcome, postreinforcement pause (PRP) is referred to as latency to initiate wheel running. PRP and latency to initiate running were measured as the time between the end of the 4-s outcome delivery interval, and the first wheel turn; the mean latency was then calculated by dividing the cumulative latency over the entire session by 20 outcomes.

Data analysis

Wheel-running rates and mean latencies to initiate running for each FR schedule were averaged over the last five sessions and analyzed using a two-way repeated-measures ANOVA with outcome (water, sucrose) and FR size (FR 5, 15, 40, and 80) as within-subjects factors. Post-hoc pairwise comparisons were conducted using Tukey HSD tests. Effect sizes of pairwise comparisons were calculated using Hedges *g*. In addition, wheel-running rates and latencies were assessed for linear trends using a linear contrast analysis.

Results

Figure 1 shows local wheel-running rates as a function of FR size for water and sucrose outcomes for each individual rat. Rats that experienced the FR-size values in ascending order are shown on the left of Figure 1, while rats that experienced the descending order are on the right. In general, regardless of whether the outcome was water or sucrose, local rates of wheel running decreased as the FR size increased. This relation was consistent across rats, although for NX 3, 7, and 13, local rates appear to decline more steeply with sucrose as the outcome. Less consistent is the difference in local wheel-running rates for sucrose versus water, particularly on the low ratio sizes (i.e., FR 5 and 15). On the FR 5 schedule, NX 3, 7, and 13 show higher wheel-running rates for sucrose, NX 6 and 9 show higher wheel-running rates for water, and NX 2, 8, and 12 show roughly the same local rates for both water and sucrose. On the FR 15 schedule, NX 2, 3, 7, 8, 12, and 13 show higher local wheel-running rates for sucrose, and only NX 6 and 9 show slightly higher rates for water. On the FR 40 schedule, rates for sucrose were higher for NX 2, 3, 7, 8, and 13, slightly lower for NX 12 and the same for NX 6 and 9. Finally, on the FR 80 schedule, rates for sucrose were greater for NX 3, 6, and 9, marginally higher for NX 2 and 7, and approximately the same for NX 8, 12, and 13.

One other observation in Figure 1 is that there was greater inconsistency between wheel-running rates for water and sucrose on the FR 5 schedule for rats experiencing the FR sizes in descending order (NX 6, 9, 3, and 13 on the right side of Figure 1) than for rats experiencing these schedules in ascending order (NX 2, 8, 7, and 12 on the left side

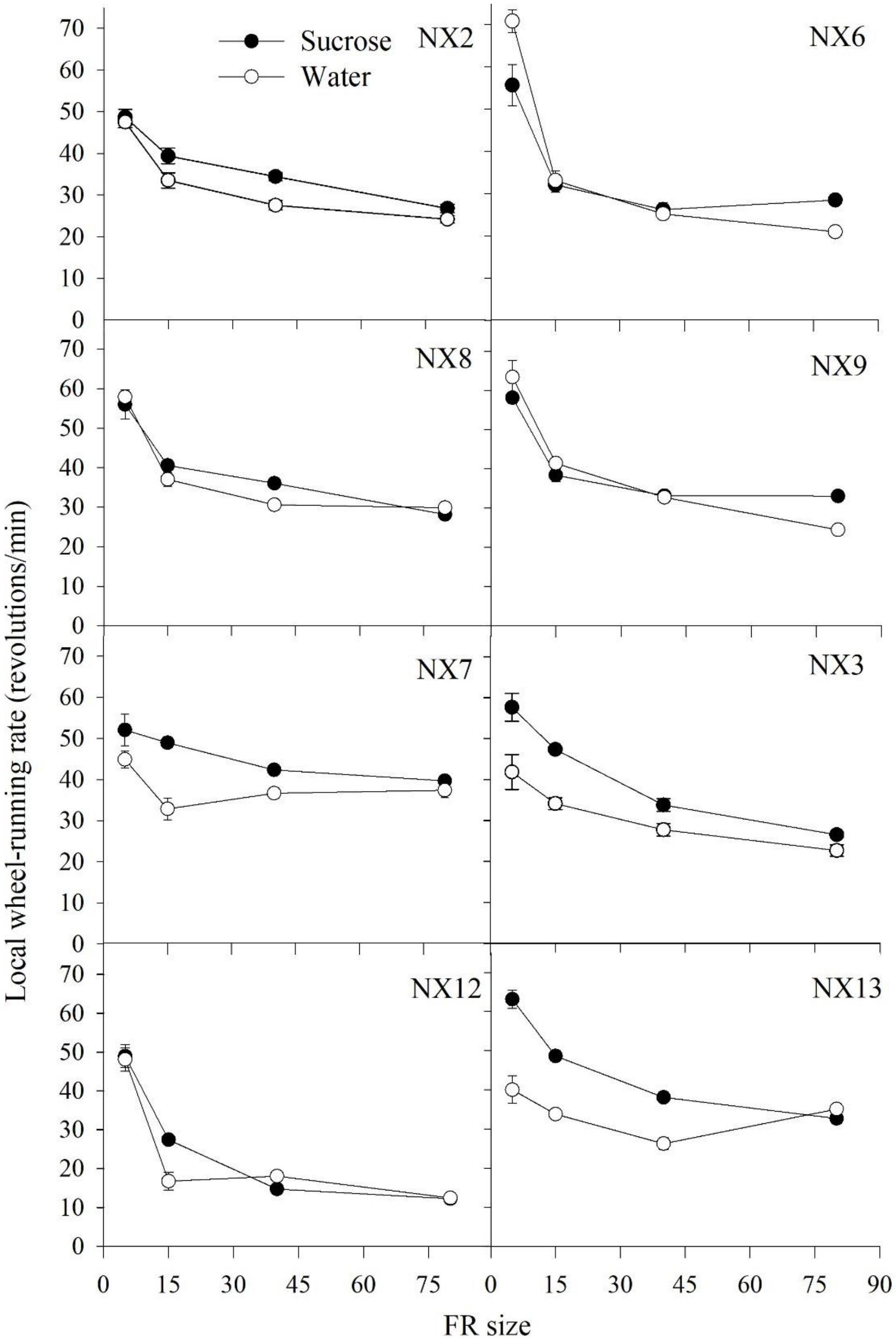

Figure 1. Mean local wheel-running rates as a function of fixed ratio (FR) size for water and sucrose as outcomes. Rats that experienced the series of FR schedules in an ascending order are on the left while rats that experienced them in a descending order are on the right. Standard error bars are plotted for each mean.

of Figure 1). For rats experiencing the descending order, local wheel running rates were higher for outcomes experienced the second time with the same order of FR size. For example, NX 6 and 9 experienced sucrose on the first exposure to these schedules and water on the second exposure. By contrast, NX 3 and 13 experienced water first then sucrose. As seen in Figure 1, on the FR 5, NX 6 and 9 had higher local rates for water while NX 3 and 13 had higher local rates for sucrose. This pattern is not observed for rats on the ascending order.

Figure 2 displays mean local wheel-running rates as a function of FR size and outcome (sucrose or water) for the group. A two-way repeated measures ANOVA on local wheel-running rate showed a significant main effect of outcome, $F(1,7) = 6.43$, $p = .038$, $\eta_p^2 = .48$, a significant main effect of FR size, $F(3,21) = 47.55$, $p < .001$, $\eta_p^2 = .87$, but no interaction, $F(3,21) = 0.85$, $p = 0.48$. For the main effect of outcome, mean local

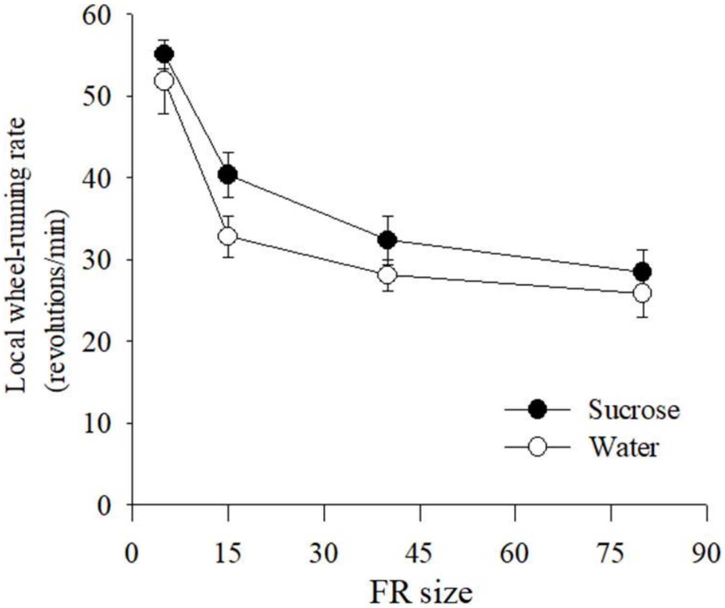

Figure 2. Mean local wheel-running rates as a function of fixed ratio (FR) size for water and sucrose as outcomes for the group. Standard errors bars are plotted for each mean.

wheel-running rate for sucrose and water were 39.04 and 34.65 revolutions/min, respectively. A post-hoc Tukey HSD comparison showed that wheel-running reinforced by sucrose occurred at a significantly higher rate, $p = .039$, $g = 0.29$. Mean local wheel-running rates on the FR 5, 15, 40, and 80 schedules were 53.43, 36.59, 30.22, and 27.16 revolutions/min, respectively. A post-hoc Tukey HSD analysis showed that local wheel-running rates on the FR 5 schedule were significantly higher than those on all other schedules of reinforcement, all p-values <.001, $g = 1.11$, 1.53, and 1.73 under the FR 15, 40, and 80 schedules, respectively, and rates on the FR 15 were significantly higher than those under the FR 80, $p = .004$, $g = 0.62$. Linear contrast analyses of local wheel-running rates as a function of ratio size using weights of 2, 1, -1, and -2 showed a significant linear relationship for sucrose reinforcement, $F(1,7) = 103.62$, $p < .001$, and for water $F(1,7) = 23.97$, $p = .002$.

Figure 3 shows latency to initiate running as a function of FR size for water, and PRP for sucrose as outcomes for individual rats. Rats that experienced the FR sizes in ascending order (low to high ratio size) are shown on the left while rats that experienced a descending order (high to low ratio size) are shown on the right. Generally, the latency or time to initiate wheel running increased as ratio size increased for both outcomes. However, time to initiate running increased only slightly for NX 13 as the ratio requirement for sucrose increased from FR 15 to FR 80, and likewise for NX 7 and 2 for water. Latency to initiate running was also consistently longer for sucrose than for water for all rats on the lower ratio schedules (i.e. FR 5 and 15), but less consistently so at higher ratios. On the FR 40 schedule, NX 2 and 13 paused longer for water than for sucrose. On the FR 80 schedule, NX 6, 9, and 12 paused longer for water than for

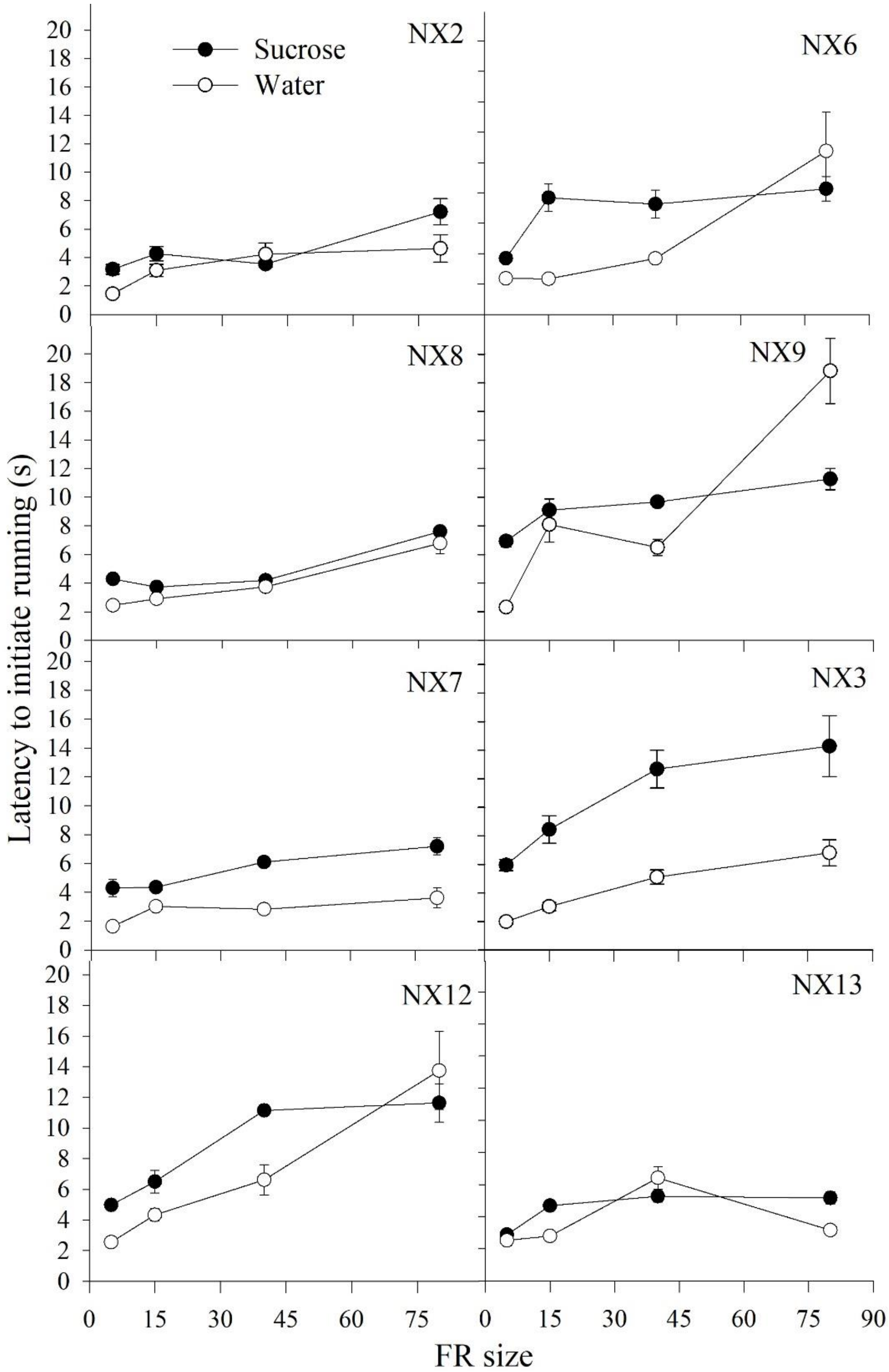

Figure 3. Mean latency to initiate running as a function of fixed ratio (FR) size for water and sucrose as outcomes. Rats that experienced the series of FR schedules in an ascending order are on the left while rats that experienced them in a descending order are on the right. Standard error bars are plotted for each mean.

sucrose.

Figure 4 displays mean latency to initiate running as a function of FR size for water and sucrose as outcomes for the group. With the exception of the upward trends, the group functions display greater consistency than is represented by the individual rat functions. A two-way repeated measures ANOVA showed a significant main effect of outcome (sucrose or water) on PRP/latency to initiate running, $F(1,7) = 9.30$, $p = .019$, $\eta_p^2 = .57$, a significant main effect of FR size, $F(3,21) = 18.24$, $p < .001$, $\eta_p^2 = .72$, but no interaction, $F(3,21) = 1.03$, $p = 0.40$. For the main effect of outcomes, mean PRP for sucrose and latency to initiate running for water were 6.80 and 4.82 s, respectively.

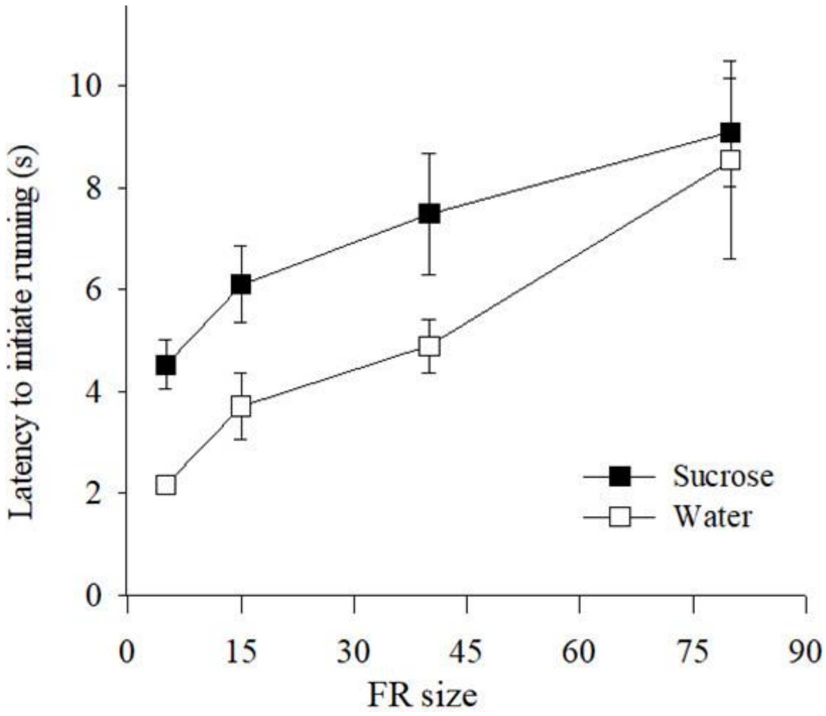

Figure 4. Mean latency to initiate running as a function of fixed ratio (FR) size for water and sucrose as outcomes for the group. Standard errors bars are plotted for each mean.

A post-hoc Tukey HSD analysis showed that latency to initiate running for water was significantly shorter than the PRP for sucrose, $p = .019$, $g = 0.35$. For the main effect of schedule, mean latencies to initiate running for both outcomes on the FR 5, 15, 40, and 80 schedules were 3.34, 4.90, 6.19, and 8.81 s, respectively. A post-hoc Tukey HSD analysis showed that mean latency to initiate running was significantly lower on the FR 5 schedule than it was on FR 40 (p = .006, g = 0.51), and FR 80 (p < .001, g = 0.97) schedules, lower on the FR 15 than FR 80 schedules (p < .001, g = 0.70), and lower on the FR 40 than FR 80 (p = .012, g = 0.47) schedules. Linear contrast analyses using weights of -2, -1, 1, and 2 showed that both PRP for sucrose, F(1,7) = 27.21, p = .001, and latency to initiate running for water, F(1,7) = 15.78, p = .005, increased linearly as a function of ratio size.

Discussion

In the current study, sucrose reinforced operant wheel running on FR schedules, but the effect on wheel-running rate was modest, and the reinforcement effect of sucrose did not vary as a function of ratio size. Wheel-running rate decreased in a linear manner as the FR size increased. Notably, this relation was also observed when sucrose reinforcement was absent (water), indicating that it may not represent a reinforcement schedule effect. Although postreinforcement pause (PRP) duration following 20% sucrose reinforcement was longer than latency to initiate running for 0% sucrose (water) at smaller ratio requirements (FR 5, 15, and 40), it was similar on the FR 80. Thus, PRP following sucrose reinforcement increased as FR size increased as expected, but latency to initiate running for 0% sucrose increased in a similar way, suggesting that this trend may also be due to something other than a schedule effect.

Specifically, the current study showed that 20% sucrose reinforced wheel-running rate by 4.40 revolutions/min (13% higher), on a series of FR schedules (FR 5, 15, 40, and

80), relative to no scheduled or programmed reinforcement 0% sucrose (water) on these schedules. The reinforcement effect of sucrose, however, was modest relative to previous investigations. In Belke and Pierce's (2015) study using a two-component multiple schedule procedure, 15% sucrose reinforced operant wheel-running rate by 16.63 revolutions/min (37%) relative to 0% sucrose on an FR 15 schedule. Similarly, Belke et al. (2015), using the same multiple schedule procedure, showed that wheel-running rates for 15% sucrose were 14.7 revolutions/min (33%) higher than those for 0% sucrose on an FR 15 schedule. Belke et al. (2017) showed that wheel-running rates of food-deprived rats for 15% sucrose were 6.86 revolutions/min (21%) higher than those for 0% sucrose using an FR 30 schedule and exposing rats to series of sucrose concentrations between 0% and 15%. This comparison of sucrose reinforcement on operant wheel running across studies suggests that the reinforcement effect of sucrose may be greater on multiple than on single operant schedules due to contrast effects inadvertently arranged by multiple schedules (Reynolds, 1961; Nevin & Shettleworth, 1966; Williams, 2002). Future research should investigate this possibility.

Another possibility is that the difference observed in the reinforcement effect of sucrose is a function of sucrose concentration. Previous research suggests that the reinforcement effect of 20% sucrose solution for wheel running tested in the present experiment may be less than the effect of 15% sucrose tested in previous experiments. Increasing sucrose concentration may indeed decrease its reinforcement effect. The reinforcement effect of sucrose on responding under FR schedules appears to increase from 0% to 16%, but then to decrease at 32% sucrose (Guttman, 1953), and to be less at 32% sucrose than at 8% sucrose (Hurwitz, Walker, Salmon, & Packham, 1965, as cited in

Lowe, Davey, & Harzem, 1974, p. 558). However, other studies have found no consistent relationship between sucrose concentration and rate of responding (Meunier & Starratt, 1979). Thus, future research should investigate the possibility that the relatively modest increase in wheel-running rates observed in the present experiment might be explained by a decrease in the reinforcement value of sucrose as a function of its higher concentration in the present study.

Based on previous research with traditional operant behaviors such as lever pressing or key-pecking, it was expected that as FR size increased, the lower rate of reinforcement per response would produce a lower rate of responding. This results in a decreasing relationship between FR size and rate of response on FR schedules (e.g., inverse relationship). Across several experiments with pigeons, Bizo and Killeen (1997) demonstrated an inverse relation between response rate and FR size. Similarly, Felton and Lyon (1966) showed that local rates of key-pecking by pigeons decreased over FR 25 to 150 schedules. Furthermore, Mazur (1983) showed that local and overall rates of lever pressing on FR schedules for milk decreased as the ratio size increased from FR 10 to 80.

Not all studies, however, have shown the inverse relation. Barofsky and Hurwitz (1968) showed that the bar-pressing rate of rats increased up to FR 40 or FR 80, and then decreased as the ratio size increased. In part, this inconsistency may be due to procedural differences used to generate these response rate functions, or to how response rate was calculated (i.e., local versus overall response rates). In general, there does not appear to be a consistent answer as to how response rates with more conventional operant behaviors would be predicted to vary with reinforcement rate on FR schedules. For the purpose of comparison in the current study, it is assumed that an inverse relation is more commonly observed.

In addition, assessment of reinforcement of wheel running by sucrose as a function of ratio size must be considered in light of the high operant level of wheel running without sucrose. The inverse relationship observed for typical operant behaviors with a low operant levels suggests that higher response rates at lower FR sizes are due to their higher rates of reinforcement, and that lower response rates at higher FR sizes are due to lower reinforcement rates. The expectation that the strengthening effect of sucrose reinforcement on wheel-running rate would vary in this manner was not supported in the current study. With water as the outcome, there was no scheduled reinforcement for wheel running, yet wheel-running rate decreased as FR size increased—in a manner similar to wheel running reinforced by presentation of sucrose. Thus, this finding requires an explanation, and two factors seem to account for it: automatic reinforcement and constraint.

Automatic reinforcement, as described earlier, refers to reinforcement generated simply by engaging in a behavior, and provides the basis for a higher operant level for wheel running than observed with traditional operant behaviors, such as lever pressing, that have a near zero operant level of responding (Belke et al., 2015; Belke et al., 2017). Constraint refers to an increase in the rate of running when the opportunity to run is restricted to an increasingly shorter length of time, or number of revolutions (Pierce, Belke, & Harris, 2018). As the number of revolutions that produce water, or sucrose decreases, the constraint on running increases, and the rate of running increases. According to Pierce, Belke, and Harris (2018), wheel-running rate increases as the opportunity to run decreases due to the high automatic reinforcement value of running when constrained. Constraint theory accounts for increases in wheel-running and lever-pressing rates when wheel running serves as its own reinforcement and constraint increases. In this analysis, small FR sizes augment both the constraint on wheel activity, and the automatic reinforcement value of wheel running, while large FR sizes reduce both constraint, and the automatic reinforcement value. The present finding of change in wheel-running rate suggests that constraint can also be applied to wheel running as an operant behavior.

On the other hand, researchers typically find more consistency in changes in PRP than in rate of responding as ratio sizes increase (Lowe, Davey, & Harzem, 1974; Felton & Lyon, 1966). Results of the present study showed that both PRP and latency to initiate wheel running increased as the FR size increased for both sucrose and water. Longer latencies were observed for sucrose than water at the smaller ratios. It is a commonly known effect that PRP duration increases on FR schedules as the ratio requirement increases (Felton & Lyon, 1966; Powell, 1968; Schlinger, Derenne, & Baron, 2008). Thus, the increase in PRP duration of wheel running for sucrose reinforcement would be considered a confirmation of this well-known finding, but the same effect also occurred for latency to initiate running for water as the outcome.

If not a schedule effect, then what could be the cause of the shortened latency to initiate running at lower ratios for water as an outcome? One possibility is that it is affected by the same factors as local wheel-running rate for water as an outcome – namely automatic reinforcement and constraint. As described previously, automatic reinforcement and constraint provide an explanation for why wheel-running rate for water increased as the FR size decreased. As the number of revolutions prior to the onset of the brake decreased, constraint on the automatically-reinforced wheel running led rats to run faster, and to start running sooner. Thus, as the FR size decreased with water as an outcome, wheel-running rates would increase, while the latency to initiate running would decrease. A further implication of this effect is that it would not be possible to distinguish, with sucrose reinforcement present, to what extent the increase in PRP duration with FR size was due to a schedule effect, from that due to a decrease in constraint on wheel running.

The difference in duration of PRP for sucrose and latency to initiate running for water likely reflects a difference in consumption time, especially at the smaller FR sizes. The time taken to consume the sucrose solution delivered into the receptacle would have led to longer PRP durations than when water was the outcome. It was evident that the rats did not consume the water because at the end of these sessions, the base of the running wheel was wet and/or the paper towel beneath the wheel was soaked. In the absence of consumption, rats initiated running sooner following the release of the brake when water was delivered. Belke and Pierce (2015) noted this difference in their statement that, "in this context, the application of the brake and delivery of water served to temporarily withhold running. As a result, when the brake released, a momentary increase in the automatic reinforcement value of running led the rats to initiate running sooner. In contrast, with the addition of extrinsic reinforcement, rats ran faster to produce the sucrose solution, but took longer to initiate running because behavior was directed toward consuming the extrinsic reinforcer" (p. 6).

In terms of limitations, this is the first study with operant wheel running in which rats were exposed to a series of reinforcement schedules arranged in an ascending or descending order with the order repeated for sucrose and water. For rats that experienced FR size in descending order, local wheel-running rates by outcome (sucrose or water) on the FR 5 and FR 15 schedules were higher for whichever outcome they experienced second. This was not observed for rats that experienced FR size in ascending order. Although there was counterbalancing to mitigate this effect (i.e., half the rats experienced water second; half experienced sucrose second), this unexpected effect contributed variance to the differences between wheel running for sucrose and for water at the lower ratio schedules. Future studies of wheel running and FR size should assess the effect of sucrose and water as outcomes for operant wheel running on each FR size in turn before proceeding to the next FR value. This would eliminate experiencing the entire sequence of schedules with one outcome prior to assessing the effect with the other outcome. Thus, assessment of the effect of sucrose and water as outcomes would also be closer in time rather than separated by considerable time.

In summary, the present study examined how the rate of sucrose reinforcement (FR size) controlled operant wheel running compared to no reinforcement (water). Results showed that the wheel-running rates decreased as FR size increased independent of the outcome (sucrose or water). Although wheel-running rate showed a difference by outcome (sucrose or water) in the grouped data, the reinforcement effect of sucrose was modest relative to previous studies, and had a small effect size—suggesting that the reinforcement effect of sucrose on wheel running may be less on single operant schedules than on two-component multiple schedules.

Changes in wheel-running rates, latency to initiate running, and PRP across FR sizes, with and without sucrose, were generally consistent with the theories of automatic reinforcement and constraint (Belke & Pierce, 2015; Pierce et al., 2018). Wheel-running rates remained relatively high both with and without sucrose reinforcement (water). Results indicated that wheel-running rates decrease as the ratio requirement increases regardless of outcome (sucrose or water). That is, wheel-running rates, independent of solution, were high when constraint was increased by a low FR size, and low as the FR size increased. Finally, across FR schedules, both PRP, and latency to initiate running increased in duration with increased ratio requirements – an effect commonly known for FR schedules. While these trends in wheel-running rates and PRP (latency to run) are typically attributed to schedule effects, the current study suggests that with wheel running as an operant, constraint and automatic reinforcement effects play a more substantive role than the reinforcement schedule. As this is an initial study of varying a reinforcement schedule with operant wheel-running, further research is required to sort out the effects of schedule and constraint.

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