

Running head: WHEEL-RUNNING DISRUPTION AND OPERANT LEVER PRESSING

EFFECT OF DISRUPTION IN WHEEL-RUNNING REINFORCEMENT ON RATES
OF WHEEL RUNNING AND OPERANT LEVER PRESSING IN RATS

BY

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WHEEL-RUNNING DISRUPTION AND OPERANT LEVER PRESSING

Abstract

The current study investigated the effects of interruptions in wheel running on operant responding for a fixed bout of wheel-running reinforcement. Interruptions in the fixed bout of reinforcement occurred after rats completed different numbers of wheel revolutions and were designed to vary the local constraint on wheel running, while holding constant the total number of revolutions per session, the overall constraint. Eleven female Long-Evans rats responded on response-initiated variable interval 15-s schedules for the opportunity to run for 30 revolutions, with a 4.5-s wheel-brake asserted after 2, 5, 10 or 15 revolutions. After the brake disruption, rats had to complete the remainder of the 30-wheel turns required for the bout of wheel-running reinforcement. Results showed that wheel-running rates and overall lever-pressing rates followed a bitonic, inverted-U function for wheel revolutions completed before the 4.5-s interruption. These results suggest that interruptions of wheel-running within a reinforcement opportunity systematically altered wheel-running rates and lever-pressing rates. Notably, similar effects have been obtained when local constraint is manipulated as the number of wheel revolutions per reinforcement. Interruptions of wheel running within fixed bouts of wheel-running reinforcement, however, produced weaker effects than local constraint based on the number of revolutions per reinforcement, likely due to the wheel revolutions after the disruption which were required to complete each reinforcement. In sum, these results support an account based on local constraint on an automatically reinforced behavior rather than reinforcement magnitude to explain how wheel-running and lever-pressing rates change with revolutions per reinforcement.

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Effect of disruption in wheel-running reinforcement on the rates of wheel running and operant lever pressing in rats

Running in a wheel is a behavior that can serve as reinforcement for operant responding (e.g., Belke, 1997; Collier & Hirsch, 1971; Iversen, 1993; Kagan & Berkun, 1954). Considerable research has been conducted comparing the properties of wheel running as reinforcement to more conventional, consummatory reinforcement, such as a piece of food or a drop of sweetened solution (Belke, 1997; Belke & Dunbar, 1998; Belke & Hancock, 2003; Collier & Hirsch, 1971). Similar to consummatory reinforcement, withholding the opportunity to run (i.e. a deprivation manipulation) increases operant responding for wheel running (Belke & Heyman, 1994). Also, providing the opportunity to run freely in a wheel, prior to responding for wheel-running reinforcement (i.e. a satiation effect), decreases operant responding for wheel running (Belke, 2006b; Belke & Pierce, 2014). Furthermore, using the opportunity to run as a reinforcing consequence produces schedule effects similar to those observed with food reinforcement on fixed interval (Belke & Dunbar, 1998), fixed ratio (Collier & Hirsch, 1971), variable interval (Belke & Heyman, 1994), and variable ratio (Belke, Kervin, Kervin, Craig, Ferdinand, & Henry, 2014) schedules. And like operant responding for food reinforcement, responding for the opportunity to run increases as body weight decreases (Belke, 1996, 2004; Belke & Pierce, 2009, 2016; Belke, Pierce, Magee & Laffoley, 2016).

One principle that does not appear to generalize to wheel-running reinforcement is that of reinforcement magnitude. With conventional, consummatory reinforcement, the value of reinforcement is assumed to increase with reinforcement magnitude (Bonem &

Crossman, 1988). That is, larger amounts of reinforcement, longer durations of access to reinforcement, higher concentrations of a sweetened solution, and larger volumes of a sweetener are assumed to be of greater value than smaller amounts, shorter durations, lower concentrations, and smaller volumes. On single-operant schedules, reinforcement of greater magnitude would be predicted to maintain higher response rates than reinforcement of lower value. On concurrent schedules, alternatives leading to a higher magnitude of reinforcement should be preferred over those leading to reinforcement of lesser magnitude. And on progressive-ratio schedules, reinforcements of greater magnitude should produce higher breakpoints. In their review of the reinforcement-magnitude literature, Bonem and Crossman (1988) found inconsistencies in the findings but concluded that generally there is a positive relation between reinforcement magnitude and reinforcement value.

Extension of the analysis of reinforcement magnitude to wheel-running reinforcement would suggest that long durations of wheel access enable more revolutions and would be of higher value than short durations of access, assuming that a wheel revolution is the unit of value. Thus, on single-operant schedules, wheel-running reinforcement intervals of long durations should maintain higher rates of operant responding than intervals of short durations. Previous research, however, has failed to confirm this predicted relation. Belke (1997) investigated the effect of 30 s, 60 s, and 120 s wheel-running reinforcement durations on operant responding on a tandem FR1 VI 30-s schedule (response initiated VI 30-s schedule). Results showed that, contrary to expectation, lever-pressing rates decreased as duration of access to wheel running increased. Belke (1997) also found that, as with lever-pressing rates, wheel-running rates

varied inversely with duration; wheel-running rates on the 30 s opportunity to run were higher than on the 60 and 120 s opportunities. Furthermore, Belke and Dunbar (1998) replicated these findings by manipulating the duration of wheel-running access from 15 s to 90 s on an FI 60-s schedule. Again, operant lever-pressing rates varied inversely with reinforcement duration, as did wheel-running rates that covaried with the rates of lever-pressing (Belke & Dunbar, 1998).

Subsequently, Belke and Hancock (2003) used a wider range of wheel-access durations, between 5 s and 90 s, arranged on an FI 30-s schedule of reinforcement as part of a multiple schedule that alternated between wheel running reinforcement in one component and sucrose reinforcement in the other. The results showed a bitonic relationship between operant responding and wheel-running reinforcement duration. Specifically, the operant rate initially increased with the duration of reinforcement (up to 15 s), then decreased over longer reinforcement durations. Additionally, a similar bitonic relation described the rate of wheel running that increased to 10 s, then decreased over longer durations. This finding suggested that the rate of wheel running influences the rate of operant lever-pressing.

More recently, Pierce, Belke, and Harris (2018) provided additional evidence of the bitonic relationship by manipulating the number, rather than the duration, of wheel-running revolutions. Manipulation of duration enabled more revolutions with greater access; however, rats running at different speeds generate different numbers of revolutions for a given duration. By contrast, defining wheel-running reinforcement by number of revolutions ensures that rats obtain the same number of revolutions per reinforcement opportunity; however, in this case the time taken to complete those

revolutions varies with the speed of running. Based on this realization, Pierce, Belke, and Harris (2018) investigated the effect of reinforcement magnitudes that varied between 2 and 40 revolutions on operant responding, using a response-initiated VI 15-s schedule. Results showed that lever-pressing rates initially increased as the number of revolutions increased from 2 to 10 wheel turns, but operant rates decreased as revolutions continued to increase to 40 revolutions, explaining the puzzling results of previous research (Belke, 1997; Belke & Dunbar, 1998). Specifically, the wheel-access durations investigated in past studies would have generated decreasing response rates on the descending limb of the bitonic function linking wheel-access durations and response rates. Only with the inclusion of short durations, such as those investigated in Belke and Hancock (2003), would the bitonic relation begin to emerge.

The bitonic relation between operant lever-pressing and wheel-running revolutions appears at odds with a reinforcement magnitude account that predicts a monotonic function; however, bitonic relations have been observed in other literature (Conrad & Sidman, 1956; Guttman, 1953; Schrier, 1965). In these studies, the decrease in operant responding as reinforcement magnitude increased beyond certain values was attributed to additional variables such as satiation or reduced sensory effects from reinforcement. However, Pierce, Belke, and Harris (2018) argued for an alternative account based on the constraints imposed on wheel running as an automatically reinforced behavior and the covariation between lever-pressing and wheel-running rates. As the duration of an opportunity to run decreases, rate of wheel-running increases as does the automatic reinforcement value of an opportunity to run. This effect of constraint increasing the reinforcement value continues until the constraint is so great that few

revolutions can occur, leading to a decline in the value of an opportunity to run as well as wheel-running rate. This conceptualization of wheel-running reinforcement as constraint on the automatic-reinforcement value of the wheel activity is related to Timberlake and Allison's (1974) response-deprivation hypothesis; when animals experience constraint on baseline level of wheel running, presumably the reinforcement value of wheel activity increases relative to baseline level, and lever pressing for wheel running increases as animals attempt to reinstate the baseline level of wheel activity.

One issue that has not been addressed is that previous studies of wheel-running reinforcement changed the magnitude of reinforcement (i.e., duration or number of revolutions) while holding constant the number of reinforcement opportunities in a session (Belke, 1997; Belke & Dunbar, 1998; Belke & Hancock, 2003; Pierce, Belke & Harris, 2018). This procedure confounds the duration of an opportunity to run with the total time available to run over the entire session. For example, in Belke's (1997) study, 20 reinforcements were completed in each session at each of the 30 s, 60 s, and 120 s wheel-running reinforcement durations. This means that over the entire 20 reinforcements rats had 600 s, 1200 s, and 2400 s to run, respectively across the three reinforcement durations. Thus, variation in the local duration of an opportunity to run is confounded with overall time to run per session. As such, the unique contributions of the local duration (or number) of revolutions and the overall session duration (or number) to the bitonic relation cannot be determined. To understand this, the overall duration (or number) of revolutions per session must be held constant while the local duration (or number) of revolutions per reinforcement is varied; also, the local duration (or number) of revolutions per reinforcement must be held constant while the overall duration (or

number) of revolutions per session is varied. However, in both of these cases, the number of reinforcements per session would still vary. An alternative procedure is used in the current study to vary local constraint on wheel running while holding the overall constraint of number of revolutions, and reinforcement opportunities, per session constant. We established a fixed number of revolutions per reinforcement (30 revolutions/reinforcement) and reinforcements per session (20 reinforcements/session), and thereby held the overall constraint constant at 600 total revolutions per session. To generate local constraint, we interrupted the fixed bout of 30 revolutions for each reinforcement after rats had completed different numbers of revolutions (ranging from 2 to 15).

This distinction between local and overall constraint appears similar to a distinction between response patterns and total responding in Gawley, Timberlake, and Lucas' (1986) investigation of drinking contingent on wheel running. A response pattern with respect to drinking refers to the duration of a burst of drinking while total responding refers to the total time spent drinking within a session. According to the authors, the constraint imposed by a reinforcement schedule affects both local response patterns as well as total responses. That is, "if a schedule reduces the average burst length, it also produces an a priori deficit in total drinking interval" (Gawley, Timberlake, & Lucas, 1986, p. 78).

In Gawley, Timberlake and Lucas' (1986) first experiment, wheel-running served as the operant response and water-drinking as contingent reinforcement. Subsequent to establishing baseline durations of wheel running and drinking, constraint on operant wheel running and water-drinking reinforcement was created by adjusting the absolute

durations of water-drinking and wheel running, while maintaining the ratio of operant wheel-running to drinking. For example, if the rats ran for 200 s at baseline to obtain 100 s of drinking, each rat was exposed to a running opportunity of 300 s for 150 s of drinking (1.5 times baseline durations), 150 s running to 75 s drinking (0.75 times baseline duration), 100 s running to 50 s drinking (0.5 times baseline durations), and 50 s running to 25 s drinking (0.25 times baseline durations). With this manipulation of constraint on both operant and reinforcement behaviors, rats responded by maintaining the total time spent drinking and wheel-running within a session but increased the rate of occurrence of the behaviors as the duration of both behaviors decreased. In a second experiment, this effect was replicated with the two behaviors similarly manipulated, but in terms of revolutions and licks rather than time spent running and time spent drinking. In summary, the effect of increasing rates of the operant behaviour of wheel running and the consequent behaviour of drinking appears equivalent to the increase in wheel-running and lever-pressing rates observed in studies of wheel-running reinforcement magnitude, that manipulated the duration of the opportunity to run as reinforcement for lever pressing (Belke, 1997; Belke & Dunbar, 1998; Belke & Hancock, 2003). It would also suggest that local schedule constraints may impact the automatic reinforcement value of wheel-running (Pierce, Belke, & Harris, 2018).

Accordingly, the current study examined operant lever-pressing and wheel-running reinforcement rates given changes in local constraints on wheel-running reinforcement. Due to the confounding of local and overall constraints (Belke, 1997; Belke & Dunbar, 1998; Belke & Hancock, 2003; Pierce, Belke & Harris, 2018), rats were required to press a lever on a response-initiated VI 15-s schedule in which the total

number of revolutions per reinforcement as well as overall revolutions for each session were held constant (i.e., 20 reinforcements by 30 revolutions/reinforcement = 600 revolutions). We also began the experiment without the wheel brake (or disruption) to obtain the operant rate on the VI 15-s schedule with 30 revolutions per reinforcement. To create local constraint, we disrupted or interrupted the bout (30 revolutions) of wheel-running reinforcement with the onset of a brake for 4.5 s after different numbers of the 30 revolutions per reinforcement had been completed. Specifically, the brake was engaged after 2, 5, 10, or 15 revolutions. Once the brake released, the rats had to complete the remaining number of the 30 revolutions per reinforcement. For example, if a disruption occurred after 2 revolutions, rats had to complete the remaining 28 revolutions once the brake was released. If the disruption occurred after 5 revolutions, the rats completed 25 revolutions after the break, and so on. This procedure allows for the assessment of localized constraint while holding overall constraint (in the total number of revolutions in a session) constant; a method not done in previous studies. If rats are sensitive to varying local constraint without the impact of overall constraint, then the rates of wheel running prior to the brake disruption should vary, as well. Since wheel running generates its own reinforcement effect that is determined by the rate of running (Belke, 2006a), the variance in wheel-running rate should similarly determine the automatic-reinforcement value. This will be translated into similar changes in operant lever-pressing rates. Ideally, but depending upon the range of values investigated, bitonic trends for wheel running and lever pressing should be observed.

Method

Subjects

Twelve female Long-Evans rats were used as the subjects of this study. The animals were obtained from Charles River Laboratories in Saint-Constant Quebec and were approximately 15 months of age at the start of the experiment. Rats had previous experience in classical and operant-conditioning procedures, as part of an undergraduate course and/or other experimental research. The rats were housed individually in polycarbonate cages (48.3 cm x 26.7 cm x 20.3 cm), with heat-treated beta chips and paper towel as bedding. The lighting in the housing room followed a 12 h light/dark cycle (lights on a 0730). The rats were fed Prolab R-M-H 3000 lab chow, and were maintained at body weights of 260 +/- 10 g. This weight was 87% of the average female weight for this strain (300 g; Long-Evans Rat, Growth Chart, Charles River Laboratories, 2018). In addition, unlimited distilled water was provided in home cages, throughout the study. This research was conducted in accord with the guidelines of the Canadian Council on Animal Care, under a protocol reviewed and approved by the Mount Allison Animal Care Committee.

Apparatus

The experimental and training sessions used four activity wheels; one Wahmann (circumference of 110 cm) and three Lafayette wheels (circumference of 112 cm). The length and width of the wheel opening was 10 cm x 7 cm. The floors of the wheels were wire mesh, 1 cm x 1 cm grids for the Lafayette wheels and 0.7 cm x 0.7 cm grids for the Wahmann. Each wheel was equipped with a retractable lever mounted to a plate that covered the opening to the wheel (next to a liquid receptacle, which was not used in this

study), a solenoid-operated brake, two 24 VDC lights attached to the wheel frame (17 cm from the base of the wheel) that lighted the wheel chamber, and two LED lights above the lever (2.5 cm above the lever). The retractable lever was 5 cm long and extended 2 cm into the wheel chamber. A solenoid was attached to the base of the wheel and when activated, a rubber tipped metal shaft contacted the outer edge of the wheel, acting as a brake that prevented the wheel from turning. Wheel revolutions were recorded by a microswitch attached to the wheel frame. Each wheel was enclosed in a sound-attenuating shell 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.

Procedure

Training

Each rat was placed in a running wheel that was free to turn for 30 min each day over 12 sessions to adapt the animals to running in the wheel. Next, for three sessions, rats began operant training for wheel-running on a fixed ratio (FR) 1 schedule. That is, the rats were required to make a single lever press for the opportunity to run for 60 s in the wheel. After 60 s of wheel-running, the wheel brake and the LED lights above the lever came on. When the rats pressed the lever, it retracted, the brake disengaged, and the 24 VDC chamber lights came on, allowing wheel running for another 60 seconds. This cycle was repeated until 30 wheel-running reinforcements were completed, which terminated the experimental session. Subsequently, the rats were placed on a variable ratio (VR) 3 schedule for three sessions. In this procedure, 60 s of running was made contingent upon an average of three lever presses, for 30 wheel-running reinforcements.

Lastly, the rats completed four training sessions on a VR 5 schedule in which 60 s of running was contingent on an average of 5 lever presses. For each of the training and experimental conditions, the LED lights were on only when the rats were required to press the lever, and the chamber lights were on only when the rats were allowed to run in the wheel, acting as cues for lever-pressing and wheel-running, respectively.

Experiment

Following the training schedules, the rats remained on the response-initiated VI 15-s schedule but were assigned to each of the five experimental conditions, with order of the conditions partially varied over rats (see Table 1). Each of the five conditions terminated after 20 reinforcement opportunities, and completion of 30 revolutions per reinforcement (30 revolutions x 20 reinforcements = 600 total revolutions per session). Initially, the rats completed 20 sessions on the VI 15-s schedule for 30 uninterrupted revolutions (revolutions without brake). In the next condition, a brake was activated for 4.5 s after 15 revolutions and when the brake retracted the rats had to complete the remaining 15 revolutions. Considering the number of revolutions required before the onset of the brake (15 revolutions), we designate this condition as low constraint on wheel-running and lever-pressing responses. Thus, the 15-revolution condition served as a baseline to ascertain whether adding a wheel brake changed the rats' behavior. Following this baseline condition, the onset of the break was adjusted to occur after 2, 5 or 10 revolutions in a counterbalanced order according to the rat; again, once the brake released rats had to complete the remainder of the 30 revolutions (28, 25, or 20 revolutions).

Table 1

The order of experimental conditions for each rat (N = 12)

Rat	Revolutions (no break)	Revolutions before break onset			
NU14	30	15	2	5	10
NU15	30	15	2	5	10
NU16	30	15	10	5	2
NU13	30	15	10	5	2
NV4	30	15	10	5	2
NV6	30	15	10	5	2
NV7	30	15	2	5	10
NU17	30	15	2	5	10
NU18	30	15	2	5	10
NW9	30	15	2	5	10
NW5	30	15	10	5	2
NW7	30	15	10	5	2

Dependent measures

Lever-presses, time spent lever-pressing, number of reinforcements, number of wheel revolutions, time spent wheel-running and post-reinforcement pause (PRP) were recorded for each reinforcement opportunity and cumulated for each session. Time spent lever-pressing was measured as the interval between the first lever press following reinforcement and the offset of the wheel brake that marked access to wheel running. PRP duration (or latency to initiate wheel running) was measured as the time between the termination of the previous reinforcement (marked by the onset of the brake after 30 revolutions) and the first lever-press. Time spent running was measured as the time between the offset and onset of the wheel brake, minus the time the brake was activated (4.5 s). Total wheel-running rate was calculated by dividing the number of total wheel revolutions (30) by the time taken to complete them, expressed in revolutions per minute. In addition, local lever-pressing rate was calculated by dividing the number of presses by the time spent pressing, not including the PRP. The mean PRP was calculated by dividing

the cumulative PRP durations by the number of reinforcements. Lastly, the overall lever-pressing rate was calculated by dividing the number of presses by the time spent pressing, including the PRP.

Data analysis

Total wheel-running rates (30 revolutions/min), pre-brake wheel-running rates (pre-brake revolutions/min), overall lever-pressing (total lever presses/min), PRP duration and local lever-pressing rates (lever presses/min) averaged over the last five sessions for each revolutions/reinforcement condition were used for analysis. Paired sample t-tests were conducted between the conditions with no-break (30 revolutions) and 15 revolutions to the brake condition, to determine the effect of adding the 4.5 s wheel-brake on the operant and dependent measures. Repeated measures ANOVAs were conducted for order effects (among the 2-, 5- and 10 revolutions conditions) and for placement of the wheel brake, to determine whether differing numbers of revolutions to onset of the brake influenced the rate or duration of each measure. Before the statistical analysis, we decided to exclude the 15 revolutions condition if order effects were detected but include this condition if order was not statistically significant. Following analysis by ANOVAs, post-hoc pairwise comparisons using Tukey HSD analysis were conducted. Lastly, contrast analyses with weights of -1, 0, 2, -1 were conducted for the local lever-pressing rates, overall lever-pressing rates and wheel-running rates (before brake onset) to determine bitonic trends. With PRP duration, weights of 1, 0, -2, and 1 were used to assess for an inverted-U shaped trend.

Results

The initial ANOVA (order by brake placement without the 15-revolutions condition) showed no order effects for total wheel-running rates, $F(1,9) = 1.63, p = .23$, pre-brake wheel-running rates, $F(1,9) = .07, p = .80$, overall lever-pressing rates, $F(1,9) = .40, p = .54$, PRP, $F(1,9) = .06, p = .82$, and local lever-pressing rates, $F(1,9) = 1.92, p = .20$, respectively; nor were there any significant interactions of order with brake placement. In the absence of order effects, the 15-revolutions condition was included in subsequent analyses of brake placement.

Figure 1 shows the mean values for all dependent measures (+SE) as a function of the number of pre-break revolutions per reinforcement. Note that due to the absence of order effect or order by break placement interactions, the mean values were calculated for the last five sessions of the 2, 5, 10 and 15 revolution conditions.

The top panel of Figure 1 shows total wheel-running rates. A paired sample t-test revealed that the addition of a 4.5 s interruption after 15 revolutions significantly increased total wheel-running rate relative to the no-brake condition, $t(10) = -5.11, p < .001$. A repeated measures ANOVA analysis revealed that the total wheel-running rate did not differ by brake placement across the 2, 5, 10, and 15 revolution conditions, $F(3,30) = 1.21, p = .32$.

By contrast, a repeated measures ANOVA analysis revealed that the pre-brake wheel-running rate, shown in the second panel from the top in Figure 1, differed significantly with brake placement, $F(3,30) = 4.11, p = .01$. Specifically, Tukey HSD comparisons showed that the pre-brake wheel-running rate in the 2-revolutions condition was significantly lower than in the 5-revolutions condition, $p < .05$. No significant

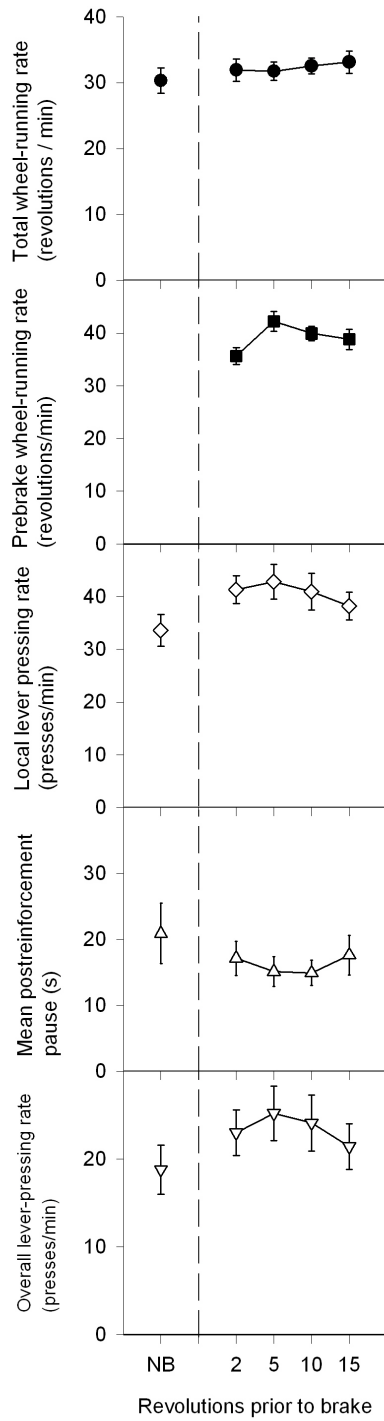


Figure 1. The mean total wheel-running rate, pre-brake wheel-running rate, local lever-pressing rate, PRP duration, and overall lever-pressing rate for all five brake placement conditions (no brake [NB], 2-, 5-, 10- and 15-pre-brake revolutions), averaged over the last five sessions in each condition.

differences in rate occurred between any other brake placements. Contrast analysis revealed that the pattern of pre-brake wheel-running rates conformed to the inverted U-shape, $F(1,10) = 6.17, p = .03$.

With respect to the operant measures, a paired sample t-test conducted between no-brake and the 15-revolutions conditions for local lever-pressing (Figure 1 middle panel) revealed the addition of the 4.5 s interruption significantly increased the rate of local lever-pressing, $t(10) = -2.51, p = .03$. A repeated measures ANOVA analysis showed no significant difference in local lever-pressing rates generated by different placements of the wheel-brake, $F(3,30) = 2.05, p = .13$. Analysis for an inverted-U shape showed no significant trend, $F(1,10) = 3.37, p = .10$.

Unlike wheel-running rates and local lever pressing rates, PRP duration or latency to initiate lever pressing for wheel running (Figure 1 second panel from the bottom) did not differ between the no brake and the 15 revolution brake conditions, $t(10) = 1.17, p = .27$. Additionally, the repeated measures ANOVA analysis also yielded no significant effects of brake placement on PRP duration, $F(3,30) = 1.95, p = .14$. Analysis for the U shape trend again found no significant results, $F(1,10) = 2.44, p = .15$.

Overall lever-pressing rates, shown in the bottom panel of Figure 1, significantly increased when the 15-revolutions condition was compared to the no-brake condition, $t(10) = -2.74, p = .02$. The repeated measures ANOVA indicated a significant effect of brake placement on overall lever-pressing rate, $F(3,30) = 3.33, p = .03$. Tukey's HSD comparisons revealed that lever-pressing rate in the 15-revolutions condition was significantly lower than the rate in 5-revolutions condition, $p = .025$, but no other comparisons between conditions yielded significant differences. As with pre-brake

wheel-running rates, the contrast analysis revealed that the trend for overall lever-pressing rates conformed to an inverted U-shape, $F(1,10) = 8.28, p = .02$.

Discussion

Pre-brake wheel-running rates and overall lever-pressing rates were controlled by the placement of the 4.5-s interruption, and inverted-U shaped trends were observed for both measures. That is, the rate of wheel running initially increased from 2-revolutions to 5-revolutions and then decreased from 10-revolutions to 15-revolutions—showing the predicted bitonic relationship with constraint on wheel running operationalized as the placement of 4.5-s wheel-brake disruption. Total wheel-running rates (30 revolutions/min) showed no change with brake placements, while local lever-pressing rate and PRP duration covaried with changes in the pre-brake wheel-running rates but did not differ consistently across rats to be statistically reliable.

Previous studies have reported a bitonic relationship between the duration or number of wheel-running revolutions per reinforcement and operant lever-pressing rate (Belke & Hancock, 2003; Pierce, Belke, & Harris, 2018). Pierce, Belke, & Harris (2018) suggested that as the number of wheel-running revolutions per reinforcement decreased from 40 revolutions, the rate of wheel-running and corresponding lever-pressing rates increased to a point (10 or 15 revolutions), indicating the rising constraint on the automatic-reinforcement value of wheel running. As the number of revolutions per reinforcement continued to decrease, the constraint on wheel running became too restrictive to provide automatic reinforcement and the rate of responding for wheel running decreased—resulting in the bitonic relationship (Pierce, Belke, & Harris, 2018).

As suggested by Pierce, Belke, and Harris, (2018), this account based on constraint on automatically reinforced behavior builds on Timberlake and Allison's (1974) response deprivation hypothesis. According to the response-deprivation, a reinforcement schedule establishes a contingent relation between the instrumental and contingent behaviors and the more restricted contingent behavior should reinforce the other, instrumental response. Beyond the reinforcement contingency that restricted lever pressing for wheel-running, in the present study an additional constraint on wheel running involved the number of revolutions prior to the brake which affected the rate of running. And, we suggest that the automatic-reinforcement value of wheel running varied with changes in the rate of running, which in turn regulated the rate of lever pressing (Belke & Pierce, 2015).

The results of the current study are inconsistent with a reinforcement magnitude account of value. According to the reinforcement magnitude account, a wheel revolution is the unit of value rather than the rate of wheel running. Thus, opportunities to run that enable more revolutions would be of greater value than opportunities that enable few revolutions. As the total number of revolutions per reinforcement remained constant (30 revolutions) in the current study, a reinforcement magnitude analysis would predict no change in value and therefore no change in operant response rates within the bout of wheel-running reinforcement. Clearly this was not the case, as overall lever-pressing rates varied with changes in the brake placement.

Instead, we propose that the disruption of the 30-revolutions bout of wheel-running reinforcement functioned as a constraint on the automatic-reinforcement value of wheel running (Belke & Pierce, 2015), resulting in a bitonic relationship with operant

measures. Notably, a bitonic relationship for operant measures and constraint typically occurs by manipulating number (or duration) of wheel revolutions per reinforcement, a between reinforcement constraint (Belke & Hancock, 2003; Pierce, Belke, & Harris, 2018). As a bitonic relationship describes both between and within constraints on wheel-running reinforcement, we conclude that local constraint on automatic wheel-running reinforcement is a critical determinant of operant responding rather than the overall constraint involving total wheel-revolutions per session (Belke, 1997; Belke & Dunbar, 1998; Belke & Hancock, 2003; Pierce, Belke, & Harris, 2018). The confounding of local and overall constraint on automatic reinforcement by the manipulation of revolutions per reinforcement (Belke, 1997; Belke & Dunbar, 1998; Belke & Hancock, 2003; Pierce, Belke, & Harris, 2018), was rectified by the manipulation of local constraint (4.5 s interruption) within a bout of wheel-running reinforcement.

In previous studies, overall lever-pressing rate typically covaried with local lever-pressing rate due to the inverse relationship between the local rate and PRP duration (Belke, 1997; Belke, & Hancock, 2003; Pierce, Belke, & Harris, 2018). For the current study, although neither local lever-pressing rates nor PRP duration showed a bitonic trend with pre-brake disruptions, when the separate measures were combined as overall lever-pressing rates, we detected a reliable bitonic (inverted-U shape) relation. One interpretation is that the local constraint imposed by the 4.5-s brake disruption was reduced in effectiveness by the requirement to complete the remainder of the 30-wheel revolutions after the interruption. One possibility is that completing the remainder of the bout of wheel-running reinforcement introduced a delay in the opportunity to respond for the next bout of wheel-running reinforcement. Alternatively, the effect of local constraint

on subsequent operant responding may have been weakened by a direct effect of the wheel revolutions following the break. For example, previous research shows that shorter wheel-running reinforcement durations lead to shorter subsequent PRP durations and vice versa (Belke & Hancock, 2003). So, a small number of pre-brake wheel revolutions should lead to a short PRP duration to the next reinforcer; however, the greater number of post-brake revolutions would lead to a longer subsequent PRP duration. Such offsetting effects on PRP could have weakened the observed impact of constraint on pre-brake revolutions on subsequent PRP duration.

Notably, the total wheel-running rate over the 30-revolution reinforcement did not differ with the placements of the interruption. That is, the interruption after 2 revolutions did not reliably differ in total wheel-running rate from the interruption placed after 15 revolutions. One possibility is that the requirement to complete the remainder of the 30-wheel revolutions per reinforcement washed out the effect of the 4.5 s interruption on total wheel-running rate. As there is no precedent for our disruption procedure, it is not known whether partitioning the 30 revolutions by a brief interruption would equalize the wheel-running rates before and after the 4.5 s interruption. And, as there were significant alterations in pre-brake wheel-running rates (described by an inverted-U shape trend), it suggests that the pre-brake rate changes were offset by changes in wheel-running rate after the brief interruption, maintaining a stable total rate of running across brake placements. Future investigations should assess wheel-running rates that occur both prior to and following the occurrence of the interruption.

We assumed that the interruption after 15 revolutions would be sufficiently distant in time from operant lever-pressing that it would not control operant responding

and could be used as a manipulation check (control condition) for insertion of the wheel-brake. However, the onset of the brake after 15-wheel revolutions unexpectedly had a significant effect on operant responding. This observation has implications for previous accounts of wheel-running reinforcement magnitude on response rates (Belke, 1997; Belke & Dunbar, 1998; Belke & Hancock, 2003; Pierce, Belke, & Harris, 2018). Previous investigations of wheel-running reinforcement durations, utilizing single operant procedures, showed that operant responding was affected by the duration (reinforcement magnitude) of an opportunity to run and was based on an assumption that wheel running occurring throughout the interval of reinforcement affected operant responding (Belke, 1997; Belke & Dunbar, 1998; Belke & Hancock, 2003).

Investigations of wheel-running reinforcement duration using concurrent schedules, however, showed no preference for a larger duration (50 s) of reinforcement over one of shorter duration (10 s) (Belke, 2006a). Based on these results, Belke (2006a) suggested that rats would be indifferent between different durations of wheel-running reinforcement when difference between the durations occurred farther in time from the operant lever-pressing. That is, 10 s and 50 s wheel-running reinforcement durations do not differ until after 10 s has elapsed. For the 10 s opportunity to run, the brake is applied to terminate the wheel-running reinforcement after 10 s while for the 50 s opportunity to run, the wheel continues to be freely available. On the other hand, 2.5 s and 50 s opportunities to run differ after 2.5 s. In this latter case, the difference between the two wheel-running reinforcement durations occurred closer in time to the lever pressing, generating a preference for the 50 s wheel-running reinforcement. One possibility is that rats are sensitive to wheel-running rates occurring within the first few seconds of the

onset of the opportunity to run. However, in the current study, we found that a brief interruption after 15 revolutions changed operant lever-pressing, suggesting that rats are sensitive to wheel-running farther in time from operant responding. Further research on wheel-running reinforcement with brief interruptions is required to clarify the contradiction between results generated on single operant and concurrent operant procedures.

In the current study, the positioning of the 4.5 s brake disruption was only investigated during the first half of the 30-revolution reinforcement, but a complete assessment of brief interruptions of wheel-running reinforcement on operant lever-pressing should involve insertions of the interruption in the second half of the 30-revolution reinforcement. For example, in addition to investigating the effect of the brake occurring after 2, 5, 10, and 15 revolutions, brief interruptions should be positioned after 20, 25, and 28 revolutions. Such an assessment may provide a more complete assessment of bitonic relation between pre-break revolutions and operant measures. A more extensive assessment of brake placement would also provide insight on the effect of brake disruption closer to subsequent operant responding.

To conclude, the results from the current study suggest that constraint on local reinforcement, based on interrupting a fixed number of revolutions per reinforcement, generates a bitonic (inverted-U shape) relationship between wheel-running reinforcement and operant lever-pressing rates. These results suggest that local constraint on wheel-running alters the rate of wheel-running before the brake disruption, reflecting a change in the automatic-reinforcement value of wheel running. Changes in local constraint and automatic reinforcement, in turn, account for the bitonic relationship between local

constraint and overall lever-pressing rate. Notably, this bitonic relationship occurred when overall constraint remained constant, suggesting that operant lever-pressing rates in previous studies were a function of local, rather than overall, constraint on wheel-running reinforcement. Future research should include a greater range of break placements, that extend beyond 15 revolutions, to determine whether the bitonic relation generalizes beyond the halfway point of the bout of wheel-running reinforcement, how the revolutions that occur after the break regulate operant responses, and to further determine if the interruption of the bout wheel-running reinforcement operationalizes local constraint on the automatic reinforcement value of wheel running. Generally, this study is the first to show that local constraint, without the influence of overall constraint, impacts the automatic-reinforcement value of wheel-running and the rate of operant lever-pressing.

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