

The Undermining Effect of Sucrose Reinforcement on Automatically-Reinforced
Operant Wheel Running in Rats

BY

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Abstract

The undermining effect can be defined as a decrease in levels of intrinsic motivation for a behaviour as a consequence of the delivery and subsequent removal of a contingent extrinsically-motivating reward. A well-documented phenomenon in humans, the present study investigated the potential presence of an undermining effect of extrinsic sucrose reinforcement on intrinsically motivated (automatically-reinforced) operant wheel running in eight female Long-Evans rats. In each session, rats ran for 20 min prior to and following operant wheel running on a fixed interval (FI) 60-s schedule. Across three conditions, water, sucrose, and water were delivered as outcomes for operant wheel running on the FI 60-s schedule. No undermining effect was observed for wheel running on the FI 60-s schedule following the removal of sucrose; nor was there a decrease in running during the 20-min post-operant running period. However, wheel running during the 20 min period prior to operant running significantly decreased. Contrary to previous findings, this result suggests that an undermining effect can occur in rats. Explanations for the presence of this effect as well as suggestions for future research investigating this effect in non-human species are discussed.

Table of Contents

Title Page.....	i
Abstract.....	ii
Table of Contents.....	iii
Table of Figures.....	iv
Acknowledgements.....	v
Introduction.....	1
The Undermining Effect.....	1
Meta-Analyses.....	5
Operant Wheel Running and the Undermining Effect in Rats.....	9
The Present Study.....	16
Method.....	17
Subjects.....	17
Apparatus.....	18
Procedure.....	18
Results.....	20
Discussion.....	29
References.....	34
Appendix.....	42

Table of Figures

Figure 1.....	21
Figure 2.....	21
Figure 3.....	22
Figure 4.....	27
Figure 5.....	28

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The Undermining Effect of Sucrose Reinforcement on Automatically-Reinforced Operant Wheel Running in Rats

An intrinsically motivated behaviour is one that is completed for its own sake. That is, no external motivator is required for the behaviour to occur; it is intrinsically motivated. When an external motivator, such as a reward, is delivered for engaging in an intrinsically motivated behavior and then subsequently discontinued, the level of the intrinsically motivated behavior is diminished relative to its level of occurrence prior to the application of an extrinsic reward. This effect has come to be known as the undermining effect. The undermining effect occurs because individuals attribute their behavior to the extrinsic incentive which undermines the intrinsic value of the behavior. Substantive research on this effect has been undertaken with human participants (e.g., Cameron & Pierce, 1994; Deci et al., 1999; Lepper et al., 1973; Murayama et al. 2010; Tang & Hall, 1995; Wiersma, 1992); however, to date there are very few published studies of this effect in animals. The present study sought to generalize this effect to operant wheel running in rats. Running in a wheel is a behavior that is considered self-reinforcing or intrinsically reinforcing (Sherwin, 1998) and as such, may be suitable for the demonstration of an undermining effect.

The Undermining Effect

The undermining effect originated from the results of a study by Deci (1971). Deci found that under most conditions, when an intrinsically motivated behaviour was reinforced with a material reward, the intrinsic motivation for that behavior was subsequently decreased. This was determined by observing participants in three different studies using ABA designs with three conditions; initially measuring the

baseline rate of occurrence for an automatically-reinforced behaviour, subsequently reinforcing that behaviour extrinsically, and then removing the extrinsic reinforcement to observe changes to the baseline in a third condition. The first study measured changes in intrinsic motivation for the completion of plastic block puzzles. Participants were initially determined to be intrinsically motivated if, when left alone in the experimental space (a laboratory) for eight minutes and told they could do whatever they liked, they chose to focus on the puzzle rather than magazines placed in the room as distractor items. This intrinsic motivation was also measured via self-reported interest. Individuals in the experimental group were rewarded with \$1.00 USD for each puzzle completed during the 13-minute sessions. The second study measured changes in a field experiment, where intrinsic motivation for headline-writing was manipulated in headline-writers of a college newspaper who were unaware of the study. Motivation was measured as the time spent in writing headlines that met publishing standards, reasoning that quicker writing suggested higher motivation. Participants in the experimental condition were rewarded with \$0.50 USD for each headline, led to believe that the money was coming from leftover newspaper budget, and instructed not to discuss this payment with their colleagues because not all writers were receiving it. The third study intentionally replicated the first, with the only difference being the use of verbal praise as a reward for puzzle completion rather than the material reward used in the first study. This was to isolate potential differences between the effects of material and immaterial rewards on intrinsic motivation.

Based on the results of these three studies, Deci (1971) noted that the undermining effect was not observed with an immaterial reward, namely verbal praise,

for which reinforcement did not significantly affect the automatic reinforcing effect. It is worth noting that while this study was foundational in research on an undermining effect, the results found were only significant at an alpha level of $p = .10$.

Following the results of this study and others (Cameron & Pierce, 1994; Deci et al., 1999; Lepper et al., 1973; Murayama et al. 2010; Tang & Hall, 1995; Wiersma, 1992; etc.), it was suggested that the undermining effect may be the result of an undermining of self-determination and agency —aspects considered critical to motivation within the framework of self-determination theory and the subsequent cognitive evaluation theory (Deci & Ryan, 1980; Deci et al., 1999). Therefore, according to cognitive evaluation theory, the undermining of intrinsic motivation by extrinsic rewards may be due to a perceived loss of self-determination and agency (Deci et al., 1999). If one is being given a reward to encourage a behaviour, this could be perceived as an attempt to control the individual, changing the behaviour from one that is self-determined and voluntary to one that is compulsory. The cognitive evaluation theory was supported by the results of Deci et al. (1999) meta-analysis, and is considered one of two primary possible cognitive explanations for the undermining effect.

An alternative explanation is the overjustification hypothesis (Cameron & Pierce, 1994; Deci et al., 1999; Lepper et al., 1973). According to the overjustification hypothesis, when an intrinsically motivated behaviour becomes additionally motivated extrinsically, intrinsic motivation for that behavior can be undermined. Specifically, the individual is thought to be over-justified in their completion of the target behaviour, and

they are theorized to begin to perceive the behaviour as something that requires a reward in order to be worthwhile (Cameron & Pierce, 1994; Lepper et al., 1973).

Lepper et al. (1973) provided an example of a study demonstrating the undermining of intrinsic motivation that was attributed to overjustification. Researchers measured the effect of extrinsic reward on the intrinsic motivation of children to draw with magic markers. The 55 participants (40 - 64 months of age) had been determined to be interested and intrinsically motivated to draw with magic markers through three days of observation during free-periods with several play options. They were said to be intrinsically motivated if they met a minimum standard duration of time spent sitting and/or holding markers during these periods. Two weeks after this baseline measurement, the intrinsically-motivated participants were tested individually by being brought to a room and lightly prompted to draw with markers for approximately six minutes. This procedure was repeated for one to four days, varying by participant as a result of uncontrollable scheduling confounds. Each participant was a member of one of three conditions: those who received no reward for drawing, those who received a reward unexpectedly, and those for whom the reward was expected. Motivation was measured as a function of the time spent drawing during these sessions. The reward was a small, decorated certificate entitled "Good Player Award," with the participant's name on it, which would be publicly displayed to the class along with the other students' awards on a bulletin.

The results showed that participants in the group that both expected and received the reward had lower observable intrinsic motivation over the course of the experiment compared to the initial baseline, while participants in the no-reward and unexpected-

reward conditions had no significant change in intrinsic motivation (Lepper et al., 1973). Based on these results, Lepper et al. (1973) suggested that an undermining effect due to the overjustification hypothesis had occurred; with the addition of an expected reward over-justifying the activity such as to undermine the pre-existing intrinsic motivation for drawing.

Meta-Analyses

Cameron and Pierce (1994) compiled a comprehensive meta-analysis of 96 studies on the relationship between intrinsic motivation and rewards in human participants. Specifically, Cameron and Pierce measured the effects of rewards on intrinsic motivation categorized by reward type, reward expectancy, and reward contingency. Cameron and Pierce's primary analysis was across studies using between-subjects designs.

For the primary analysis, Cameron and Pierce (1994) required studies to meet specific inclusion criteria. Published studies were only included if they used a between-groups experimental design with intrinsic motivation as the dependent variable; and if the experimentally rewarded and control groups were kept separate. Studies also needed to not demonstrate any notable trend of pre-experimental differences in participants between the reward groups and control groups. Additionally, any unpublished studies were excluded from the analysis.

Cameron and Pierce (1994) organized the included studies into categories based on how they measured the dependent variable (intrinsic motivation). These categories included measures of intrinsic motivation such as free time spent on a task after the removal of an administered reward, self-reports of interest in the task, measurements of

contingent performance during a free-time period, and the extent to which one was inclined to participate in a target task again in the future (without reward). Data was analyzed on several levels, with the most broad level comparing all reward types generally, and other levels comparing reward types independently of others.

Cameron and Pierce (1994) observed an undermining effect only when a reward type was tangible, as opposed to an immaterial reward such as verbal praise, noted to have a positive influence on intrinsic motivation (Cameron & Pierce, 1994; Deci, 1971); when a reward type is expected; and when a reward is contingent on behaviour without criteria, such that the action of simply performing a behaviour was sufficient to receive a reward rather than performing to a standard. In a secondary analysis, across within-subjects designs, no undermining effect was found.

Cameron and Pierce's (1994) meta-analysis was criticized by several researchers on theoretical and methodological bases. Deci and Ryan (1996), Lepper et al. (1996), and Kohn (1996) all published direct responses to the meta-analysis questioning methodological choices such as the oversimplification of concepts that were suggested to be far more nuanced (Deci & Ryan, 1996). Deci and Ryan (1996) and Lepper et al. (1996) independently argued that Cameron and Pierce (1994) found little evidence of an undermining effect because their method of analysis did not make important distinctions between different categories of rewards during comparison. In a rebuttal, Cameron and Pierce (1996) countered that their "oversimplification" of the undermining effect was an attempt made to dispel what they felt to be over-generalized beliefs about the harmful nature of rewards in educational contexts drawn from publications such as that by Kohn (1993) (Cameron & Pierce, 1996). Moreover, while they made statements about the

undermining effect generally, Cameron and Pierce's (1994) rebuttal also discuss the phenomenon at increasing levels of specificity. While their analysis did find select conditions under which an undermining effect was observed (in agreement with previous results by Deci (1971)), the general conclusion drawn from comparing results of studies with different reward categories was that there was not a significant undermining effect. Deci et al. (1999) further criticized Cameron and Pierce (1994) for drawing a conclusion contrary to at least three other meta-analyses on the subject (Rummel & Feinberg, 1988; Wiersma, 1992; Tang & Hall, 1995). Of the meta-analyses cited by Deci et al. (1999), only the later meta-analysis co-written by the same author (Eisenberger & Cameron, 1996) yielded results in agreement with Cameron and Pierce (1994). One response by Cameron and Pierce (2001) to concerns that their analysis was flawed due to collapsing across reward types to draw conclusions (Deci et al., 1999; 2001) was that the method of Deci et al., collapsing instead across measures of intrinsic motivation, over-generalized what undermining effect could be observed.

Deci et al. (1999) published their own meta-analysis of 128 studies of the undermining effect in human participants, coming to a different general conclusion than Cameron and Pierce (1994). Where Deci et al. (1999) agree with Cameron and Pierce (1994), as well as with the authors of several other meta-analyses, is that there is an undermining effect under the conditions of a behaviour reinforced with a tangible, expected, task-contingent reward. Measurement of how often participants would engage in a target behaviour in a free-choice period was the main measure of intrinsic motivation used. Like Cameron and Pierce (1994), the studies in this meta-analysis were coded on the basis of reward categories, with distinctions drawn based on tangibility,

expectancy, and contingency of the reward administered. Unlike Cameron and Pierce (1994), findings were not collapsed on the basis of the type of measurement used, as this was a criticism of that analysis made by Deci and colleagues (Deci & Ryan, 1996; Deci et al., 1999). By contrast, the results of the Deci et al. (1999) meta-analysis found a significant undermining effect on intrinsic motivation when tangible rewards were used and a positive effect on motivation by verbal rewards.

Deci et al. (1999) had a number of inclusion criteria that potential studies needed to meet. Most simply, they chose only to include studies that had been performed in a lab or equivalent location. Field studies were excluded. Studies also needed to have utilized a between-subjects design with separate experimental and control groups (where the control group received no reward manipulation of any kind). Additionally, when intrinsic motivation was measured in the experimental group, it needed to have been measured after the complete removal of the extrinsic motivator. Studies were also excluded when the target behaviour task was determined to be uninteresting to participants, and this lack of interest was determined in two ways. Firstly, studies wherein the researchers explicitly declared the task as uninteresting were excluded. Secondly, in studies that involved a measurement of interest in a task, interest must have been found to be at least equal to the middle-point of the scale used (interest below neutral was deemed insufficient).

To summarize, research on the presence of an undermining effect of intrinsic motivation by extrinsic reward has been divisive. One perspective argues that an undermining effect can be broadly observed across reward type and administration as a rule (Deci et al., 1999). The other argues that an undermining effect is present only

under specific conditions; that being when a reward is tangible, expected, and task-contingent (Cameron & Pierce, 1994). To date, the controversy with respect to which conclusion is more valid remains unresolved.

Operant Wheel Running and the Undermining Effect in Rats

In a behaviourist paradigm, intrinsically motivated behaviours can be conceptualized as behaviours that are “automatically-reinforced”. That is, operant behaviours with an automatic effect of reinforcement value intrinsic to the behaviour itself (Belke & Pierce, 2015). Automatically-reinforced behaviours have some unique characteristics; such as enduring over time self-sufficiently (Belke & Pierce, 2015), and showing resistance to extinction (Belke & Pierce, 2014; Iso, 1996). Most relevant to the present analysis is that as a behaviour that seems to be intrinsically “motivated,” automatically-reinforced behaviours are those which can be studied as an operant with extrinsic reinforcement to determine the presence of an undermining effect.

Previous research has demonstrated that wheel running in rats is an automatically-reinforced behaviour (Belke & Pierce, 2014; 2015; Belke et al., 2017). That is, rats will run without any external reinforcement, seemingly out of an intrinsic “motivation” for the wheel running itself. According to Belke and Pierce (2015):

Rats run in their wheels based on the automatic reinforcement that follows— plausibly emanating from the sensory feedback of the activity (sight, sound, and kinesthetic feedback of the wheel, Weasner et al., 1960), from the upward angular momentum and speed of self-generated wheel activity (Sherwin, 1998), something akin to the fun and thrill of going on a roller coaster as a child, or

from physiological changes in neural centers of the brain associated with reinforcement (Monroe et al., 2014) (p. 2).

Due to this automatic reinforcement effect, wheel running is a behaviour that can serve as a reinforcing consequence for an operant behavior such as lever-pressing, or as an operant behaviour that produces an extrinsic reinforcement such as sucrose. As a reinforcing consequence, wheel running has been extensively investigated (Belke, 1996, 1997, 2000, 2004, 2007; Belke & Hancock, 2003; Belke & Pierce, 2016; Belke et al., 2004; Belke & Wagner, 2005; Collier and Hirsch, 1971; Iversen, 1993; Kagan & Berkun, 1954; Premack, 1962; Premack et al., 1964). As an operant behavior, there has been less investigation (Belke & Pierce, 2014, 2015; Belke et al., 2015, 2017, 2018; Iso, 1996; Skinner & Morse, 1958), and only two previous investigations of an undermining or overjustification effect; a questionable study by Garland and Staff (1979), and a very recent master's thesis (Sunde, 2021).

For the present study, prior investigations of wheel running as an operant are relevant given that an assessment of the undermining effect requires that an extrinsic reinforcement be made contingent upon an intrinsically motivated, or in this case, automatically-reinforced behaviour. The focus of prior investigations of wheel running as an operant were to determine if the extrinsic reinforcement served to strengthen wheel running (Belke & Pierce, 2014, 2015; Belke et al., 2015, 2017, 2018) or if a schedule of reinforcement produced a pattern of revolutions on that schedule consistent with patterns of responding observed with behaviors that do not have an automatic reinforcement effect (Iso, 1996; Skinner & Morse, 1958). The study by Skinner and Morse (1958) was the first published investigation of wheel running as an operant. Two

rats were exposed to a fixed interval (FI) five-minute schedule with wheel running as the operant and food as the reinforcement. During each experimental session, rats ran for 30 minutes prior to, and following, exposure to the FI five-minute schedule. During these free-running periods, the lights were turned off in the chamber where the wheel was located. While the FI schedule was in effect, the chamber was illuminated. Food as a reinforcement was only delivered when the FI five-minute schedule was in operation. No extrinsic reinforcement occurred during the 30-minute free-running periods. Skinner and Morse's objective was to determine if a pattern of responding consistent with that observed for FI schedules occurred when wheel running was the operant. Cumulative records of the revolutions on the FI schedules showed occasional instances of a pattern of pausing followed by accelerated running with a decline in running just prior to the delivery of food reinforcement. Although there was no direct assessment of a reinforcement effect of the food delivery on operant running, it was noted that running occurred at a higher rate while the FI schedule was in effect relative to that during the 30-minute free-running periods.

Similar to Skinner and Morse (1958), Iso (1996) investigated the patterns of operant wheel running on fixed interval (FI) and fixed ratio (FR) reinforcement schedules. Three rats were exposed to an FI 60-second schedule and three to an FR 40 response schedule. In this case, an operant response was defined as a quarter of a turn of a wheel and the reinforcement was a 45 mg food pellet. To assess the potential reinforcement effect of the food pellets, a rat was yoked to each experimental rat that ran on an FI or FR schedule. For yoked rats, the delivery of food pellets was not contingent on wheel running; instead, whenever the rat on the FI or FR schedule met the

requirement and produced a food pellet, a food pellet was also delivered to the yoked rat. In other words, for the rats on an FI or FR schedule, the delivery of food was contingent on wheel running; but for the yoked rat there was no contingent relationship between wheel running and food delivery. Following sessions of food delivery on the FI and FR schedules, Iso (1996) exposed the rats to five extinction sessions where food pellets were no longer delivered for wheel running. Cumulative records suggested a response pattern similar to that observed for FR schedules occurred for rats running on the FR 40 schedule; however, only one of the three rats on the FI 60-second schedule showed patterns of operant responses similar to that expected on an FI schedule. More importantly, Iso (1996) observed no difference in wheel-running rates between rats on the reinforcement schedules and the yoked rats. In other words, non-contingent delivery of food produced the same rate of wheel running as contingent delivery, suggesting no reinforcement effect. Moreover, running rates by the rats on the FI and FR schedules did not decrease in extinction when food pellets were no longer delivered. The lack of a decrease in running on extinction was attributed to running being reinforced by some other (automatic) reinforcement in the context.

Belke and Pierce (2014; 2015) investigated wheel running as both an operant behaviour and as reinforcement for lever-pressing on a multiple schedule. In one component of the multiple schedule, rats pressed a lever for the opportunity to run as reinforcement (i.e., wheel-running reinforcement component) and in the other component, rats ran a required number of revolutions to produce sucrose reinforcement (i.e., operant wheel-running component). In both studies, the 15% sucrose reinforcement for operant wheel running was removed and readministered. Across both studies, wheel-

running rates systematically decreased by approximately 25% when 15% sucrose was changed to 0% sucrose (water) and then increased by 25% when changed from 0% sucrose to 15% sucrose. These systematic changes demonstrated that sucrose as an extrinsic reinforcement successfully reinforced wheel running. The main difference between the two studies had to do with the operation of the multiple schedule. In a study by Belke and Pierce (2014), advancement of the multiple schedule between components depended on the rat's behavior; while in another study (Belke & Pierce, 2015), the multiple schedule advanced based on time, independent of the rat's behavior. The effect of this difference was that in Belke and Pierce (2014), the wheel-running rate in the operant component was not significantly different than that in the wheel-running reinforcement component; however, with the change to a more traditional multiple schedule, the wheel-running rate in the operant component was significantly higher than that in the wheel-running reinforcement component, as would be expected if sucrose reinforced wheel running. Thus, in contrast to the earlier studies, Belke and Pierce (2014; 2015) demonstrated that operant wheel running was reinforced by making it contingent upon an extrinsic reinforcement and that the increase added to the rate of running that was being maintained by the automatic reinforcement effect.

In a subsequent study using the same multiple schedule, Belke et al. (2015) compared the effect of changing from 15% sucrose to 0% sucrose in the operant component when the operant behavior was wheel running, and when it was lever-pressing. The results suggested that when the operant was lever pressing, there was a 90% reduction in lever-pressing rate from 229 presses/minute down to 19 presses/minute. By contrast, removal of sucrose only reduced operant wheel running

from 59 to 44 revolutions/minute. This comparison directly demonstrates a fundamental difference between wheel-running and lever-pressing behavior. Lever-pressing behavior, unlike wheel running, is not automatically-reinforcing, and therefore, in the absence of any extrinsic reinforcement, occurs at a very low level. Wheel running, in contrast, is automatically-reinforcing, and in the absence of any extrinsic reinforcement, occurs at 75% of the level that occurs when extrinsic reinforcement is administered (Belke et al., 2015). As stated previously, this property of wheel running makes it a suitable candidate for observing an undermining effect.

To date, very few investigations of the undermining effect with non-human animals have been undertaken. Garland and Staff (1979) tested the undermining effect of 0.45mg food pellets reinforcement on operant wheel running. They used an ABA design where 16 diet-restricted (80% ad libitum weight) female Holtzman albino rats were put on an FI 20-second reinforcement schedule to reinforce wheel running in three conditions; an un-reinforced baseline, a reinforced experimental condition, and a return to baseline (conceptualized as an extinction condition). A between-subjects design was used, with eight rats each in one experimental group and one control group. Garland and Staff hypothesized that any present undermining effect may be the result of “reward contrast,” a change in the perceived beneficial outcome(s) of a behaviour based on the discrepancy between its present reward and the rewards it elicited in the past. Although the authors explicitly avoided considering constructs of motivation, this explanation could suggest support for the aforementioned overjustification hypothesis; where intrinsic motivation for a behaviour decreases as a consequence of a change in perception of a behaviour as a consequence of this reward manipulation.

Garland and Staff (1979) did claim to find evidence of an undermining effect in their rats' rates of wheel running during the extinction trials. During extinction, rates of wheel running systematically decreased for the experimental condition, while increasing for the control condition. Notably, the extinction period was longer than most, 12 days in duration, and the authors observed a trend suggesting that the influence of the undermining effect faded over time following the conclusion of conditioning. These results represent (to our best knowledge) the first evaluation of an undermining effect in non-human animals; however, they must be interpreted with some caution. First and most notably, a significant increase in wheel running during the reinforcement period relative to the baseline period was not observed; which calls into question whether the trends observed during the extinction period were actually due to a reinforcement effect and subsequent removal of that effect. This is particularly questionable when considering that, for whatever reason, the wheel-running rate of the control group increased dramatically to a degree comparable to the decrease in rate of the experimental group. Additionally, the use of a between-subjects design with only eight subjects in each condition constitutes an issue in the validity and generalizability of the findings outside of the sample. These questionable results unfortunately limit the extent to which the 'undermining effect' observed during extinction can be considered a valid finding.

At least one other study of the undermining effect in non-human animals has also been conducted. For their recent master's thesis, Sunde (2021) investigated the relationship between intrinsic motivation and expected rewards in the context of the overjustification hypothesis (Lepper et al., 1973) using sucrose solution to reinforce

wheel running in rats. Sunde (2021) used a combination-design where the results of 14 male Sprague-Dawley rats in two within-subjects experimental conditions (one non-contingent, the other performance-contingent) were compared to those of a control group in an ABABA design alternating between unrewarded baseline conditions and the two rewarded experimental conditions. The study was designed to imitate that by Lepper et al., (1973), which similarly used expected reward, unexpected reward, and no-reward conditions (Sunde, 2021; Lepper et al., 1973). In the two experimental conditions, free-running produced 50% sucrose solution (0.1 ml) on a FR-15 revolution schedule; while in the baseline condition, the same 15 revolutions produced 0.1 ml of water. Each of the experimental subjects were assigned to one of the two experimental groups, which remained consistent across the experiment.

For both experimental conditions, the rates of wheel running systematically increased significantly as a result of the reinforcement effect of the sucrose, but the rates of wheel running did not decrease significantly below the baseline measures when sucrose was removed (Sunde, 2021). Thus, an undermining effect was not observed. Sunde rationalized that this result was likely due to rats lacking higher cognitive factors relevant to the overjustification hypothesis in reward delivery. This result could also support the cognitive-evaluation theory in the same way due to the relevance of higher cognitive factors in that explanation as well (Deci & Ryan, 1980; Deci et al., 1999).

The Present Study

Wheel running has been demonstrated to be an automatically-reinforced behavior in rats (Belke & Pierce, 2014; 2015; Belke et al., 2015), and sucrose solution has been demonstrated to function as a tangible extrinsic reinforcer for wheel running

(Belke & Pierce, 2014; 2015; Belke et al., 2015; Belke et al., 2017). It then follows that an expected sucrose reinforcement, when removed, could serve to demonstrate an undermining effect decreasing the intrinsic motivation for wheel running. The present study evaluated the effect of sucrose reinforcement on automatically-reinforced wheel running in rats. Specifically, wheel-running rates were measured prior to and subsequent to sucrose reinforcement being delivered contingent upon wheel running on an FI 60-second schedule. In addition to comparing wheel-running rates on the FI schedule before, during, and after the administration of an extrinsic reinforcement (i.e., 25% sucrose), the rats also ran freely in the running wheel for 20 min prior to the onset of the FI schedule and for 20 minutes following completion of the FI schedule. Since running during these pre- and post-operant free running periods was never exposed to extrinsic reinforcement, it represents running maintained by the automatic reinforcement effect of wheel running and as such provides a second baseline against which any effects of removal of sucrose solution reinforcement can be assessed.

Method

Subjects

Eight female Long-Evans rats were sourced from Charles River Canada. To allow for weight control, each rat was housed in an individual polycarbonate cage. Despite being housed individually, each rat was provided with weekly social enrichment with other rats, and the individual cages were kept together in one colony room. This room was kept on a 12:12 hour light-dark cycle (lights on at 0730). All rats had free access to clean, distilled water at all times, though food quantity was controlled for each rat to maintain a weight of 260 +/- 10g.

Apparatus

Subjects NA5, NA6, NA13 and NA14 ran in two Wahmann activity wheels (35 cm diameter), while subjects NA7, NA8, NA15 and NA16 ran in Med Associates (ENV42) activity wheels (37 cm diameter). Both types of wheels had metal exterior and interior rims, and the wheels themselves were formed of wire mesh (5 mm x 5 mm). The entrance of the wheel (90 mm high x 70 mm wide) was closed with an aluminum panel (170 mm high x 170 mm wide x 2 mm thick), attached via two 2 in. spring clamps in order to cover the opening and hold a cylindrical liquid dispenser (37 mm diameter x 40 mm long) with a metal clamp during sessions. Liquid from this dispenser was administered on computer command via a solenoid valve.

Procedure

Before beginning the experiment, initial training consisted of 30-min free running periods every day for 17 days. This initial exposure to the running wheel, in addition to allowing wheel running to develop and stabilize, was also important in order for the rats to reliably consume sucrose delivered contingent upon running. Prior exposure for these wheel running-naïve rats was required for the development of habituation to the nausea-inducing properties of wheel running (Baysari & Boakes, 2004; Nakajima, 2016; Nakajima et al., 2006; Salvy et al., 2002). Following training, the first experimental condition began. At the beginning of each session, the brake released and the wheel was free to turn for 20 min. During this initial free-running period, the chamber that the wheel was located in was dark as the lights at the side of the wheels were not illuminated. Wheel revolutions were recorded in 10 successive two-min intervals during this 20-minute period. Following completion of this 20-min initial free-

running period, the brake was engaged for two seconds and the lights at the side of the wheel were illuminated. The onset of the lights and the release of the brake signalled the onset of the FI 60-s schedule. The first revolution after 60 s engaged the brake, turned off the lights for one second, and released a drop of solution into the liquid receptacle. The brake remained engaged and the light remained off for 3 s to allow time for consumption of the delivered solution. Revolutions on the FI 60-s schedule were recorded in successive 5-s segments of the 60-s reinforcement interval for each reinforcement, and cumulatively across all twenty 60-s reinforcement intervals. For the first condition, the solution delivered was 0.1 ml of water (0% sucrose). After 20 drops of solution had been delivered on the FI 60-s schedule, the brake released, but the lights at the side of the wheel remained off to signal the commencement of a 20-min free-running period. As before, revolutions were recorded in 10 successive two-min intervals. The session ended when this 20-min post-reinforcement schedule free-running period was completed.

In the next experimental condition, the 0% sucrose solution was changed to 25% sucrose solution. All other aspects of the experimental session remained the same. Twenty 0.1 ml of 25% sucrose solution were delivered on the FI 60-s schedule in each experimental session for 25 sessions. Following completion of 25 sessions with 25% sucrose being delivered, the solution was changed back to 0% sucrose (water) for another 25 sessions. For each condition, sessions commenced every morning at approximately 8:15 AM (+/- 15 min) when each rat would be placed inside a wheel in a controlled environment with fans to ventilate the chamber and generate noise to reduce the likelihood of the rats reacting to any extraneous noise. Panels also covered each

compartment in which a wheel was located to prevent the rats from being affected by extraneous stimulation.

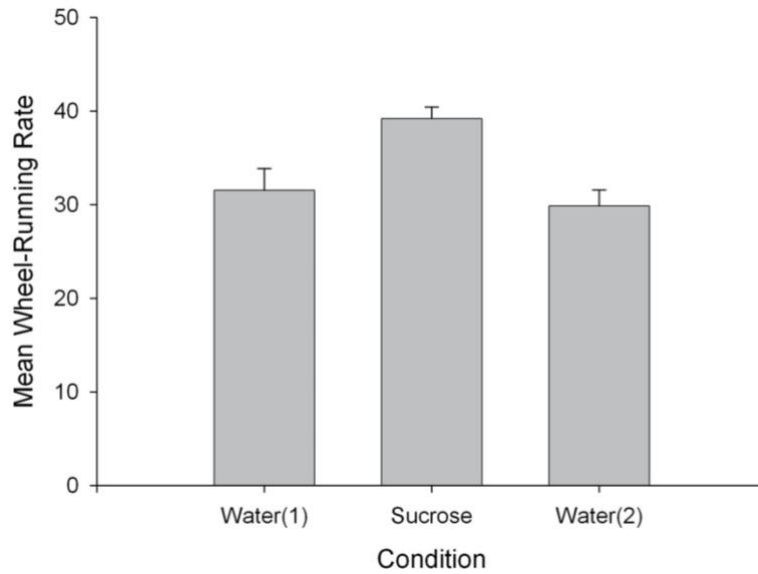
Results

Figure 1 depicts session level operant wheel-running rates for the first water, sucrose, and second water conditions. Inspection of this figure suggests that sucrose systematically increased operant wheel running relative to the two water conditions. An initial paired *t*-test comparison of the first and second water conditions showed no significant difference, $t(7) = 0.96$, $p = .367$, two-tailed. Consequently, operant wheel-running rates were averaged across the two water conditions prior to comparison with the sucrose conditions. As suggested by the figure, 25% sucrose solution effectively reinforced operant wheel running. Wheel-running rate in the sucrose condition increased by 21.64% compared to the wheel-running rate for the collapsed water conditions, $t(7) = -4.63$, $p = .001$, one-tailed, Cohen's $d = 5.412$.

Figure 2 depicts the average postreinforcement pause (PRP (s)) per reinforcement across the first water, sucrose, and second water conditions. As with operant wheel-running rates, mean PRP duration increased with the change to sucrose as an outcome, then returned to its prior level with the shift back to water. A paired *t*-test comparing the two water conditions revealed no significant difference, $t(7) = 0.04$, $p = .97$, two-tailed; consequently, the values for the two water conditions were averaged for comparison to the sucrose values. With sucrose as the outcome for operant wheel running, PRP duration significantly increased, $t(7) = -3.67$, $p = .004$, one-tailed, Cohen's $d = 4.951$.

Figure 1

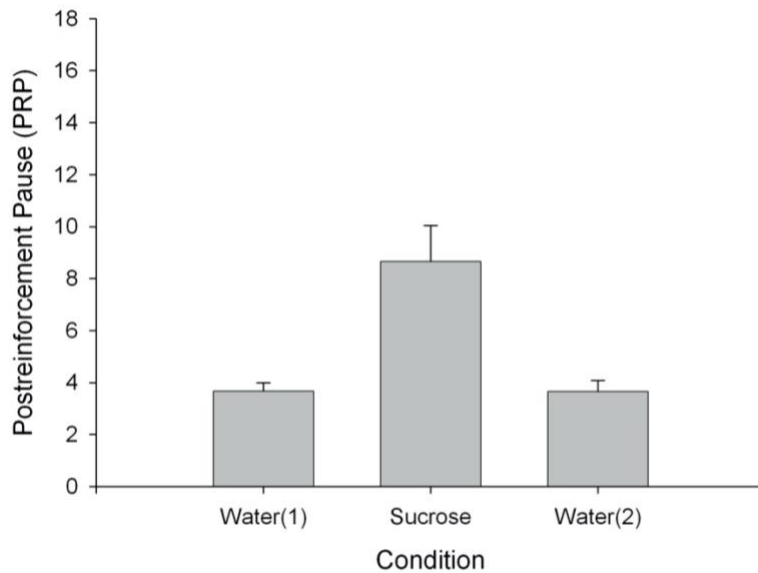
Mean Total Wheel Running Rate Across Conditions



Note. Running is presented in revolutions per minute.

Figure 2

Mean Post-Reinforcement Pause (PRP) Across Conditions

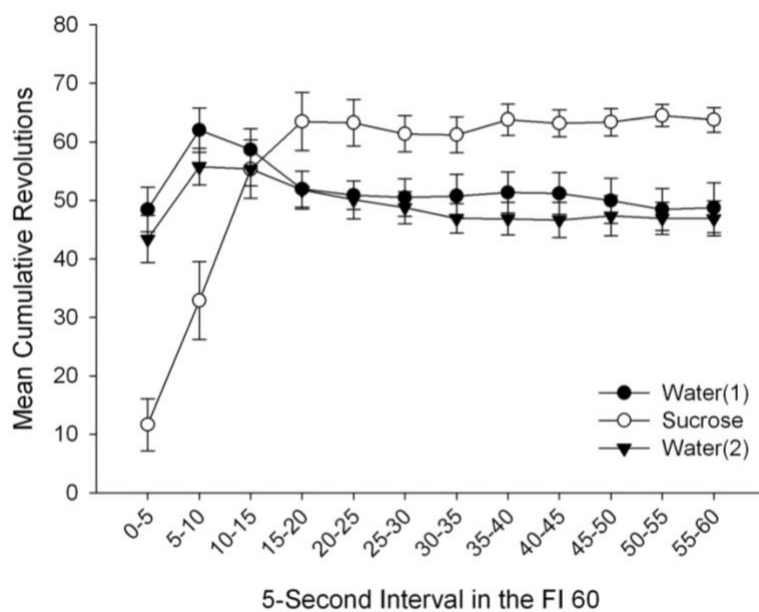


Note. PRP is presented in seconds.

Figure 3 depicts the pattern of cumulative revolutions in successive 5-s segments across the FI 60 for all three conditions. For analyses comparing sucrose conditions with water conditions on the FI 60-s schedule, the water conditions were collapsed due to non-significance in differences between their wheel-running rates. A two-way repeated measures analysis of variance (ANOVA) with water condition (first, second) and two-min interval as within-subject variables found no significant difference in wheel-running rate between the water conditions, $F(7, 77) = 1.47, p = .264$; nor any significant interaction between condition and five-second interval on the FI 60, $F(7, 77) = 1.29, p = .249$. A significant difference was found between patterns of responding across 5-s intervals on the FI 60, $F(7, 77) = 6.20, p < .001, \eta_p^2 = 0.470$; however, this does not affect the capability to collapse water conditions for comparison to the sucrose condition.

Figure 3

Mean Cumulative Revolutions Across 5-s Intervals in the FI 60-s Schedule



The validity of the present investigation of an undermining effect is predicated on the existence of a tangible reinforcement effect of 25% sucrose solution on operant wheel running. But, with all 5-s intervals during the FI 60-s schedule included in a two way repeated-measures ANOVA, no significant difference was found between the sucrose and the collapsed water conditions, $F(7, 77) = 4.06, p = .084$. While there was no main effect of condition between water (first, second) and sucrose, there was a significant main effect of 5-s intervals on the FI 60, $F(7, 77) = 25.39, p < .001, \eta_p^2 = 0.784$; as well as significant interactions between condition and 5-s interval on the FI 60, $F(7, 77) = 28.63, p < .001, \eta_p^2 = 0.804$. Mean cumulative revolutions for the sucrose and collapsed water conditions were 55.63, and 50.40 revolutions, respectively. For the main effect of 5-s intervals, mean cumulative revolutions for the 0-5, 5-10, 10-15, 15-20, 20-25, 25-30, 30-35, 35-40, 40-45, 50-55, and 55-60 s intervals were 28.77, 45.87, 56.17, 57.65, 55.49, 55.02, 56.44, 56.03, 56.01, 56.08, and 55.78 revolutions, respectively. Tukey HSD comparisons showed that revolutions during the 0-5 s interval were significantly lower than revolutions in all other 5-s intervals, all $ps < .001$; and that revolutions during the 5-10 s interval were significantly lower than all subsequent 5-s intervals, all $ps < .005$. Finally, for the interaction, Tukey HSD comparisons showed that for the collapsed water condition, revolutions in the 5-10 s interval were significantly higher than those in the 0-5 s interval, $p = .02$. By contrast, for the sucrose condition, revolutions in the 0-5 s interval were significantly less than all subsequent intervals, all $ps < .001$; and revolutions in the 5-10 s interval were significantly less than in all subsequent intervals, $ps < .001$.

Although this analysis found no main effect consistent with a reinforcement effect of sucrose on wheel running, inspection of the figure suggests otherwise. Over the final 45 seconds of the 60-s reinforcement interval, wheel revolutions for the sucrose condition were systematically higher than those in the water conditions – consistent with a reinforcement effect. Where the water and sucrose functions differ most, as suggested by the interaction, is during the first 10-15 s. Revolutions for the collapsed water conditions started at a higher level during the 0-5 s interval, then increased during the 5-10 s interval followed by a slight decline during the 10-15 s interval, and then remained relatively constant over the remainder of the 60-s reinforcement interval. By contrast, revolutions in the sucrose condition started very low in the 0-5 s interval, then rose rapidly over the subsequent three intervals to a level higher than that of revolutions during the water conditions; remaining relatively constant over the remainder of the 60-s reinforcement interval. The reason for the marked difference between the water and sucrose conditions at the beginning of the interval is an artifact arising from the observation that rats did not consume the water that was delivered and began to run as soon as the brake released. In contrast, rats consumed the delivered sucrose and were still consuming sucrose when the brake released. By virtue of this consumption, revolutions were low in the 0-5 s interval and then rapidly increased as rats shifted quickly from consumption to running. This difference in the rats' behavior is also documented by the systematically longer mean PRP durations per reinforcement in the sucrose condition, as was previously analysed.

Based on this analysis of the difference in revolutions during the initial portion of the reinforcement interval, the first three 5-s intervals of the FI 60-s reinforcement

interval were excluded, and a two way repeated measures ANOVA was conducted on cumulative revolutions over the final 45 seconds of the 60-second reinforcement interval. This analysis revealed a significant main effect of condition, $F(7, 56) = 29.98$, $p = .001$, $\eta_p^2 = 0.811$, with higher revolutions for the sucrose condition compared to the collapsed water conditions. Mean revolutions for the sucrose and water conditions were 63.08 and 49.22 revolutions, respectively, Tukey's HSD, $p = .001$. Contrary to the previous analysis, no significant difference was found for patterns of responding across the last nine 5-s intervals on the FI 60, $F(7, 56) = 0.56$, $p = .808$; nor any significant interaction between condition and 5-s interval on the FI 60, $F(7, 56) = 0.68$, $p = .708$.

In addition to measures on the rates of operant wheel running within the FI 60, wheel-running rates were also collected from the 20-min pre-operant and post-operant periods. Measures within these periods have the potential to represent a clearer depiction of intrinsic motivation due to a lack of potential effects of constraint on operant wheel running present on the FI 60. A comparison of the wheel-running rates for the pre-operant running period prior to and following the sucrose condition showed a significant reduction in wheel-running rate. The wheel-running rate in the second water condition ($M = 29.80$, $SD = 3.56$) decreased by 7.89% from the wheel-running rate in the first condition ($M = 32.35$, $SD = 4.30$), $t(7) = 3.20$, $p = .007$, one-tailed, Cohen's $d = 1.830$. Unlike the findings for operant wheel running during the FI 60, this result suggests the presence of an undermining effect. Due to the significant difference between the wheel-running rates in the pre-operant period for the two water conditions, wheel-running rates could not be collapsed. Separate paired t -tests showed that the pre-operant wheel running rate during the sucrose condition ($M = 33.45$, $SD = 3.32$), was not significantly

higher than the rate during the first water condition, $t(7) = .92, p = .19$, one tailed, but was significantly higher than during the second, $t(7) = 3.59, p = .004$, one tailed, Cohen's $d = 3.001$.

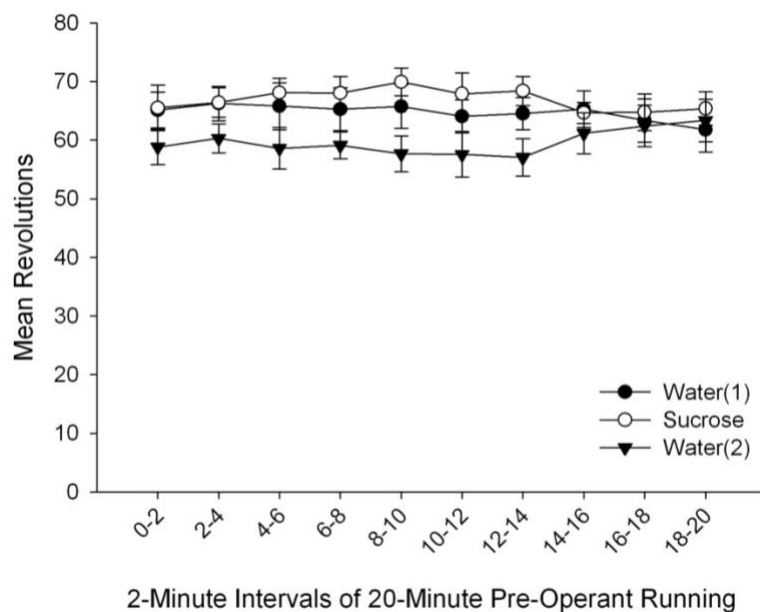
Figure 4 depicts the pattern of change in wheel-running rates across successive two-min intervals of the 20-min pre-operand running period across the first water, sucrose, and second water conditions. Of greatest importance for these data is an analysis of the two water conditions. A two-way repeated measures ANOVA with water condition (first, second) and two-min interval as within-subject variables confirmed a significant main effect of condition, $F(7, 63) = 10.22, p = .015, \eta_p^2 = 0.593$; but no significant main effect of two-min interval $F(7, 63) = 0.39, p = .933$; nor a significant interaction between condition and two-min interval, $F(7, 63) = 1.52, p = .159$. A Tukey HSD comparison showed a significant difference between revolutions per two-minute interval for the first water ($M = 64.71$) and second water ($M = 59.60$) conditions, $p = .015$.

Unlike in the pre-operand period, no significant reduction in wheel-running rate occurred in the 20-min post-operand period for the second water condition relative to the first condition. The wheel-running rate in the second water condition ($M = 29.00, SD = 5.48$) did not differ from the wheel-running rate in the first water condition ($M = 29.59, SD = 4.36$), $t(7) = 0.355, p = .733$, two-tailed. Consequently, the two water conditions were collapsed ($M = 29.29, SD = 4.37$) and compared to the sucrose condition ($M = 32.63, SD = 5.65$). A paired t -test showed that wheel running in the post-operand interval during the sucrose condition was significantly greater than that for the collapsed water conditions, $t(7) = 2.00, p = .043$, one tailed, Cohen's $d = 1.865$. Figure 5 depicts mean

revolutions in successive two-min intervals of the 20-min post-operand period for the first water, sucrose, and second water conditions.

Figure 4

Mean Total Revolutions Across 2-Min Intervals of the Pre-Operant Period



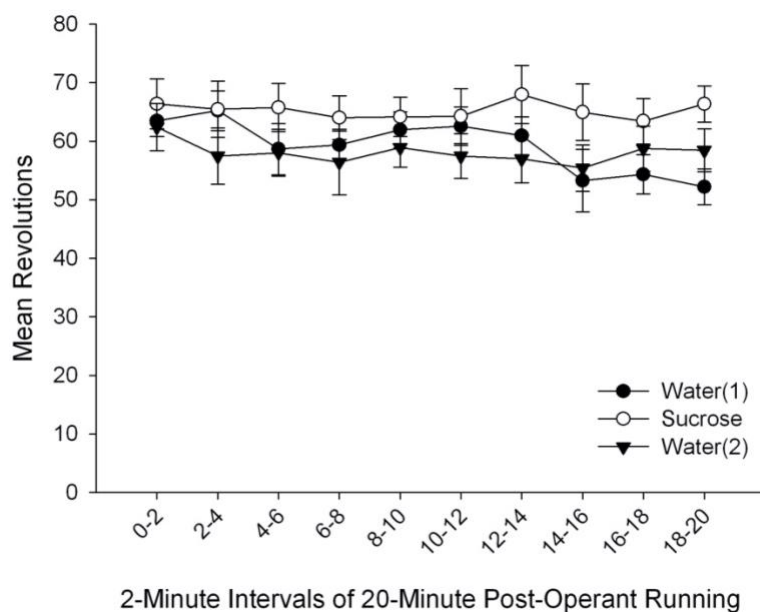
Note. Running is presented in revolutions per two-minute period.

A two-way repeated measures ANOVA confirmed a lack of significant difference between wheel-running rates in the first and second water conditions, $F(7, 63) = 0.13, p = .733$. There were, however, significant differences in patterns of responding across the two-min intervals, $F(7, 63) = 4.94, p < .001, \eta_p^2 = 0.413$; as well as a significant interaction between condition and two-min interval, $F(7, 63) = 3.46, p = .001, \eta_p^2 = 0.331$. For the main effect of two-min intervals, the mean revolutions for the 0-2, 2-4, 4-6, 6-8, 8-10, 10-12, 12-14, 14-16, 16-18, and 18-20-minute intervals were 62.91, 61.33, 58.31, 57.88, 60.40, 59.99, 58.94, 54.31, 56.51, and 55.31 revolutions, respectively. Tukey HSD comparisons showed that revolutions for the 0-2-min interval were significantly higher than those for the 14-16, 16-18, and 18-20-min intervals, all ps

< .05. Revolutions for the 2-4-min interval were significantly higher than those during the 14-16 and 18-20-min intervals, both $ps < .05$. Revolutions for the 8-10 and 10-12-min intervals were both significantly higher than those for 14-16-min interval, both $ps < .05$.

Figure 5

Mean Total Revolutions Across 2-Min Intervals of the Post-Operant Period



Note. Running is presented in revolutions per two-minute period.

For the interaction between water condition and two-min intervals, Tukey HSD comparisons showed revolutions during the 0-2 and 2-4-min intervals were significantly higher than revolutions during the 14-16, 16-18, 18-20-min intervals, all $ps < .05$.

Revolutions during the 8-10 and 10-12-min intervals were also significantly higher than revolutions during the 14-16 and 18-20-min intervals, all $ps < .05$. Finally, revolutions during the 12-14-min were significantly higher than revolutions during the 18-20-min interval, $p = .045$. In contrast, for the second water condition, Tukey HSD comparisons revealed no significant differences.

Discussion

To summarize the key findings, a significant increase in operant wheel running response during the experimental condition was found when operant wheel running was reinforced with 25% sucrose solution. This suggests that a reinforcement effect occurred, which is critical for the other analyses to have the potential of describing an undermining effect. While no difference was found in wheel-running rates between the neutral water conditions during the FI 60-s schedule, or during post-operant running periods; wheel running systematically decreased by 7.89% in the second water condition compared to the first. This suggests a potential undermining effect of sucrose reinforcement on operant wheel running in rats during the pre-operant period.

Comparisons of these findings to past research by Garland and Staff (1979) and Sunde (2021) are complicated due to the fact that neither measured rates of wheel running outside of the reinforcement schedule. As mentioned previously, measures within these pre-operant and post-operant wheel-running periods have the potential to represent a clearer depiction of intrinsic motivation to run due to a lack of potential effects of constraint on operant wheel running present in the FI 60, or any other potential confounding variables related to reinforcement schedule.

As a preface, Garland and Staff (1979) did not observe a significant reinforcement effect during the experimental condition of their study. Nonetheless, as one of the only other studies of an undermining effect in non-human species, relevant comparisons to the present study can be drawn. A decrease in wheel-running rates resembling an expected undermining effect occurred during the FI 20 in the extinction condition despite this lack of measured reinforcement. Control subjects exhibited a

significant increase in wheel running during the extinction trials despite no theoretical change in condition. Garland and Staff (1979) briefly acknowledged this ambiguity, but little to no explanation was provided aside from the weak potential influence of muscle development on wheel-running rates; something which should theoretically be controlled by the 11 habituation sessions. Regardless, due to the present use of a within-subjects design where each rat served as its own control, the present study does not have the potential to replicate the discrepancy in wheel-running rates between experimental and control groups in the extinction period. If what Garland and Staff (1979) measured was indeed an undermining effect, it is possible that their finding could be replicated in future between-subjects research of this kind, preferably with a larger sample size.

The investigation by Sunde (2021) was, similarly to the present study, based partly on theoretical methodology by Lepper et al. (1973) in the study of undermining effects in children. Contrary to the present study and that of Garland and Staff (1979), no undermining effect was observed during any part of Sunde's (2021) experiment. This is potentially misleading however, because unlike the present study, Sunde (2021) did not measure wheel running during any pre-operant or post-operant periods. The lack of observation of an undermining effect during the reinforcement schedule is consistent with the present findings. Thusly, a notable question is whether Sunde (2021) would have found an undermining effect if they had measured pre-operant wheel running rather than exclusively FR-15 responding. Is it possible that the distinction between their study which used an FR-15 schedule, and the present study and study by Garland and Staff (1979) which used FI 60 and FI 20 schedules, respectively, could be significant as

well? As aforementioned, schedule effects related specifically to constraint of running on fixed intervals may be relevant to the present analysis.

As with Garland and Staff (1979), it is also worth acknowledging questionable elements of the study by Sunde (2021). Specifically, for reasons that are unclear, the rates of wheel running of Sunde's (2021) rats were shockingly low across all conditions, averaging at approximately 2.50 revolutions per min during baseline conditions compared to the approximate 30 revolutions per min observed in the present study. There are no clear contextual differences that would soundly explain this difference, which suggests the possible presence of extraneous variables at play. Additionally, due to an error in communication, the rats in Sunde's (2021) study were reinforced with a 50% sucrose solution, as opposed to the intended 15% sucrose solution more consistent with the concentrations generally used in previous research on operant wheel running.

Sunde's (2021) discontinuous conclusion that the undermining effect is a consequence of sociocognitive factors, and thus, not present in rats, is contradictory to the findings of the present study. As indicated by Garland and Staff (1979) four decades prior, higher cognitive explanations (such as the cognitive evaluation theory (Deci & Ryan, 1980; Deci et al., 1999)) for an undermining effect exclude children and animals, and are thus contradicted by studies finding an undermining effect in children (Lepper et al., 1973) or non-human animals. The present findings would serve to at least partially support this perspective.

Attempts must be made to justify why an undermining effect may be found in the pre-operant periods, but not found on the FI 60 reinforcement schedule. Constraint theory posits that the constraint of wheel revolutions for operant wheel running

behaviour in rats can account for differences in wheel-running rate (Belke et al., 2020). Specifically, Belke et al. (2020) found that rates of operant wheel running changed systematically with constraint, such that higher constraint may be expected to elicit higher rates of wheel running. One explanation for the present results could be that the extrinsic constraint on running during the FI 60 into 60-second intervals may be responsible for an increased rate of running that may have eliminated what otherwise could have been a significant difference in wheel-running rates as a function of changes in intrinsic motivation between the water conditions. Moreover, the context of the FI 60 was distinct from the pre-operant and post-operant periods due to the illumination of the chamber lights and initiation of wheel brakes at the end of each 60-second interval. It is possible that these contextual cues of reinforcement (that remained present during the FI 60 despite the absence of sucrose reinforcement) could delay changes in wheel running between water conditions that may otherwise have been observed in longer conditions. This seems unlikely given the distinction between water and sucrose conditions evident in the decrease between the sucrose condition and second water condition; but it could still be a variable to consider in future studies that alternate between a lack of stimulus and a reinforcing stimulus, rather than alternating between neutral (water) and reinforcing (sucrose) stimuli.

Some suggestions for future research include a replication of the current design, but using a different reinforcement schedule in order to address the concern of constraint of running potentially affecting the expression of an undermining effect. A replication using 25% sucrose reinforcement delivered on an alternative schedule to fixed-interval may potentially find different results if constraint due to schedule effects is significant.

Moreover, the same problem could be addressed by using a longer fixed-interval duration; for example, an FI 3-min, FI 5-min, or a longer schedule. It is also worth noting that while the between-subjects design of Garland and Staff (1979) limits generalizability due to the small sample size, a within-subjects design (such as was used in the present study) where each subject acts as their own control does not have this problem. However, a replication using a combination of within and between subjects design could still be worthwhile, allowing for a separate control group to be assessed without reinforcement in order to isolate any potential priming of running as a consequence of the pre-operant running period (Belke et al., 2021); provided that the sample size was increased to accommodate the between-subjects nature of the experiment.

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Appendix

Table 1

Mean Wheel-Running Rate by Subject Across Condition

Rat	Water(1)	Sucrose	Water(2)	Water(1+2)
NA5	25.99	44.61	23.18	24.58
NA6	30.05	36.74	27.35	28.70
NA7	39.23	42.11	38.15	38.69
NA8	33.43	39.50	33.75	33.59
NA13	40.14	41.15	28.35	34.25
NA14	22.23	33.57	25.40	23.82
NA15	25.92	37.48	30.08	28.00
NA16	35.28	38.32	32.68	33.98
<i>M</i>	31.53	39.18	29.87	30.70

Note. Running is presented in revolutions per minute.

Table 2*Mean Post-Reinforcement Pause (PRP) by Subject Across Condition*

Rat	Water(1)	Sucrose	Water(2)	Water(1+2)
NA5	3.94	10.57	5.29	4.62
NA6	4.45	5.95	3.74	4.10
NA7	3.38	5.91	2.53	2.96
NA8	4.43	11.48	3.52	3.97
NA13	2.42	3.40	3.31	2.87
NA14	4.29	15.89	2.89	3.59
NA15	4.36	7.37	5.67	5.02
NA16	2.00	8.74	2.20	2.10
<i>M</i>	3.66	8.66	3.64	3.65

Note. PRP is presented in seconds.

Table 3

Mean Cumulative Revolutions Across 5-s Intervals of the FI 60-s Schedule for the Water(1) Condition.

Rat	0-5	5-10	10-15	15-20	20-25	25-30	30-35	35-40	40-45	45-50	50-55	55-60
NA5	34.2	58.6	55.1	50.5	48.5	44.2	44.9	40.1	40.1	38.5	38.0	38.9
NA6	42.5	56.5	56.7	45.5	47.9	49.0	46.0	48.9	51.0	49.3	44.8	41.6
NA7	47.2	65.2	69.1	65.2	62.0	61.4	61.5	62.4	63.0	65.7	60.5	67.9
NA8	45.9	61.8	61.0	53.4	53.3	52.4	52.6	56.3	53.4	49.4	50.8	51.9
NA13	57.3	77.2	74.2	63.1	56.2	64.1	67.3	63.9	63.8	63.4	62.3	61.3
NA14	52.9	54.4	43.8	42.4	42.4	39.2	37.1	39.1	39.7	38.0	35.4	33.4
NA15	39.2	46.2	47.9	42.0	42.3	40.9	41.1	43.2	40.7	39.7	41.4	40.6
NA16	68.2	76.0	61.5	53.2	54.4	52.6	55.6	56.7	57.9	55.6	54.3	54.5
<i>M</i>	48.4	62.0	58.7	51.9	50.9	50.5	50.8	51.3	51.2	50.0	48.4	48.8

Table 4*Mean Cumulative Revolutions Across 5-s Intervals of the FI 60-s Schedule for the Sucrose Condition*

Rat	0-5	5-10	10-15	15-20	20-25	25-30	30-35	35-40	40-45	45-50	50-55	55-60
NA5	6.3	35.1	56.5	66.1	71.1	70.9	73.9	73.7	69.9	69.2	71.3	66.9
NA6	11.3	44.5	55.5	56.0	55.3	57.6	58.0	62.3	62.1	57.6	66.7	67.7
NA7	11.2	27.3	61.2	71.5	70.3	71.3	70.6	73.0	73.9	75.6	71.9	74.2
NA8	2.4	11.0	54.5	77.7	74.3	65.5	60.1	60.6	57.3	56.1	60.1	55.3
NA13	41.4	67.6	67.8	66.8	65.8	64.6	66.6	69.3	66.7	66.3	65.9	64.5
NA14	4.2	9.6	22.1	32.3	39.3	44.4	47.9	52.2	54.9	60.0	58.8	59.9
NA15	11.7	40.9	60.6	65.2	65.6	58.5	57.7	57.8	59.0	62.3	62.1	59.9
NA16	4.5	26.9	64.4	72.1	64.3	58.1	54.7	61.3	61.4	59.9	58.9	61.4
<i>M</i>	11.6	32.9	55.3	63.5	63.3	61.4	61.2	63.8	63.2	63.4	64.5	63.7

Table 5*Mean Cumulative Revolutions Across 5-s Intervals of the FI 60-s Schedule for the Water(2) Condition*

Rat	0-5	5-10	10-15	15-20	20-25	25-30	30-35	35-40	40-45	45-50	50-55	55-60
NA5	44.6	61.1	56.4	51.3	45.8	38.7	34.9	32.2	31.1	32.1	35.5	35.7
NA6	44.0	60.1	50.5	46.9	43.9	44.2	45.1	43.0	40.9	43.5	44.3	42.6
NA7	48.0	61.2	66.6	70.2	69.6	61.8	56.0	59.4	58.4	64.8	60.3	61.5
NA8	39.6	56.8	64.6	57.6	55.7	54.8	53.7	50.4	50.7	53.0	53.0	54.7
NA13	34.0	49.7	53.5	48.2	44.8	44.7	44.1	48.6	45.9	42.8	44.2	44.9
NA14	49.7	45.7	42.1	39.8	41.6	42.1	41.6	42.8	43.4	42.5	40.3	39.2
NA15	24.2	42.8	50.4	53.3	52.4	49.4	47.4	47.4	47.7	47.7	47.4	45.7
NA16	63.0	68.7	58.7	46.9	47.1	54.5	52.7	51.2	55.0	52.4	50.7	50.9
<i>M</i>	43.4	55.8	55.4	51.8	50.1	48.8	46.9	46.9	46.6	47.4	47.0	46.9

Table 6*Mean Cumulative Revolutions Across 5-s Intervals of the FI 60-s Schedule (Water(1+2))*

Rat	0-5	5-10	10-15	15-20	20-25	25-30	30-35	35-40	40-45	45-50	50-55	55-60
NA5	39.4	59.9	55.8	50.9	47.2	41.5	39.9	36.2	35.6	35.3	36.8	37.3
NA6	43.3	58.3	53.6	46.2	45.9	46.6	45.6	46.0	46.0	46.4	44.6	42.1
NA7	47.6	63.2	67.9	67.7	65.8	61.6	58.8	60.9	60.7	65.3	60.4	64.7
NA8	42.8	59.3	62.8	55.5	54.5	53.6	53.2	53.4	52.1	51.2	51.9	53.3
NA13	45.7	63.5	63.9	55.7	50.5	54.4	55.7	56.3	54.9	53.1	53.3	53.1
NA14	51.3	50.1	43.0	41.1	42.0	40.7	39.4	41.0	41.6	40.3	37.9	36.3
NA15	31.7	44.5	49.2	47.7	47.4	45.2	44.3	45.3	44.2	43.7	44.4	43.2
NA16	65.6	72.4	60.1	50.1	50.8	53.6	54.2	54.0	56.5	54.0	52.5	52.7
<i>M</i>	45.9	58.9	57.0	51.8	50.5	49.6	48.9	49.1	48.9	48.7	47.7	47.8

Table 7

Mean Wheel Revolutions during the 20 min Pre-Operant Period by Subject Across First Water, Sucrose, Second Water as well as the Combined Water Conditions

Rat	Water(1)	Sucrose	Water(2)	Water(1+2)
NA5	535.0	701.1	510.2	522.6
NA6	603.4	604.6	519.0	561.2
NA7	760.3	732.1	707.7	734.0
NA8	631.7	684.9	597.9	614.8
NA13	765.7	727.4	629.7	697.7
NA14	558.4	536.2	526.8	542.6
NA15	629.9	678.4	646.0	638.0
NA16	692.5	687.7	630.9	661.7
<i>M</i>	647.1	669.1	596.0	621.6

Note. Running is presented in total revolutions over 20 minutes.

Table 8

Mean Revolutions Across Successive Two-Min Intervals of the Pre-Operant Period for the Water(1) Condition

Rat	0-2	2-4	4-6	6-8	8-10	10-12	12-14	14-16	16-18	18-20
NA5	52.0	57.1	60.4	50.8	50.5	51.4	55.9	52.4	51.9	52.6
NA6	60.0	66.1	55.7	58.3	58.7	58.4	60.9	59.4	58.6	67.3
NA7	81.3	66.2	78.3	78.4	77.5	72.1	75.4	75.9	76.9	78.3
NA8	65.2	60.4	61.4	58.4	64.3	64.0	61.0	65.1	69.6	62.3
NA13	67.4	82.8	82.8	80.6	82.0	76.7	76.0	76.4	74.7	66.2
NA14	59.0	58.0	54.4	63.1	58.5	60.0	56.3	58.2	48.6	42.3
NA15	68.9	68.9	57.5	63.6	62.4	63.4	64.0	62.8	58.1	60.3
NA16	67.1	70.5	75.9	69.0	71.9	66.3	66.7	72.1	68.3	64.7
<i>M</i>	65.1	66.3	65.8	65.3	65.7	64.0	64.5	65.3	63.3	61.8

Note. Running is presented in revolutions per two-minute period.

Table 9*Mean Wheel Revolutions Across Successive Two-Min Intervals of the Pre-Operant**Period for the Sucrose Condition*

Rat	0-2	2-4	4-6	6-8	8-10	10-12	12-14	14-16	16-18	18-20
NA5	75.8	74.7	65.7	69.7	75.6	73.6	74.0	65.2	65.4	61.4
NA6	52.5	61.2	66.4	62.9	61.8	57.8	61.4	58.2	58.4	63.9
NA7	85.2	66.5	69.2	78.7	75.4	74.5	71.3	65.2	73.7	72.3
NA8	63.1	61.0	68.9	62.1	72.7	74.0	75.6	69.7	68.9	68.8
NA13	68.1	80.0	77.3	76.8	77.2	76.9	70.0	69.9	62.9	68.3
NA14	52.8	61.0	54.2	54.5	59.0	49.0	54.5	55.9	47.3	48.0
NA15	66.1	65.2	75.8	68.4	69.4	64.2	68.2	67.8	67.1	66.2
NA16	60.5	61.8	67.1	71.0	68.3	73.1	72.0	65.4	74.4	74.1
<i>M</i>	65.5	66.4	68.1	68.0	69.9	67.9	68.4	64.7	64.8	65.4

Note. Running is presented in revolutions per two-minute period.

Table 10*Mean Wheel Revolutions Across Successive Two-Min Intervals of the Pre-Operant**Period for the Water(2) Condition*

Rat	0-2	2-4	4-6	6-8	8-10	10-12	12-14	14-16	16-18	18-20
NA5	58.0	51.8	44.4	50.6	53.8	50.3	52.6	52.1	47.7	48.9
NA6	59.1	58.1	49.7	52.9	44.6	39.8	48.9	59.1	52.5	54.3
NA7	73.5	64.0	66.3	66.5	67.3	72.0	70.9	77.3	76.3	73.6
NA8	44.8	51.9	47.5	59.5	57.8	60.0	59.7	70.1	70.1	76.5
NA13	62.6	69.8	65.9	58.4	61.8	63.3	63.3	52.8	63.2	68.6
NA14	52.0	62.1	62.8	53.6	46.6	46.2	43.0	50.9	55.5	54.1
NA15	63.8	69.0	71.6	64.5	66.5	66.5	63.5	57.3	62.1	61.2
NA16	56.8	55.7	60.6	66.9	62.9	62.4	54.6	69.6	71.9	69.5
<i>M</i>	58.8	60.3	58.6	59.1	57.7	57.6	57.1	61.2	62.4	63.3

Note. Running is presented in revolutions per two-minute period.

Table 11

Mean Wheel Revolutions during the 20 min Post-Operant Period by Subject Across

First Water, Sucrose, Second Water as well as the Combined Water Conditions

Rat	Water(1)	Sucrose	Water(2)	Water(1+2)
NA5	476.2	634.6	393.4	434.8
NA6	581.6	668.5	527.1	554.4
NA7	702.1	813.4	762.3	732.2
NA8	615.2	716.3	625.8	620.5
NA13	703.7	658.4	516.6	610.2
NA14	483.4	409.9	587.9	535.7
NA15	548.5	661.9	565.3	556.9
NA16	622.9	657.4	662.0	642.5
<i>M</i>	591.7	652.6	580.1	585.9

Note. Running is presented in total revolutions over 20 minutes.

Table 12

Mean Revolutions Across Successive Two-Min Intervals of the Post-Operant Period for the Water(1) Condition

Rat	0-2	2-4	4-6	6-8	8-10	10-12	12-14	14-16	16-18	18-20
NA5	49.8	61.9	44.3	46.5	49.0	53.2	50.4	38.0	38.4	44.7
NA6	65.9	58.5	59.4	56.7	59.5	56.2	59.9	53.1	56.0	56.4
NA7	70.1	70.4	76.2	69.0	70.7	73.0	73.9	73.2	62.1	63.5
NA8	68.1	62.9	58.4	61.0	63.8	69.0	64.8	54.5	56.3	56.4
NA13	73.1	83.3	72.9	62.7	76.5	76.0	70.5	66.2	67.7	54.8
NA14	58.6	55.1	40.0	60.3	56.9	58.3	47.8	27.2	42.8	36.4
NA15	62.0	56.8	57.1	55.6	56.3	51.2	56.1	50.7	54.5	48.2
NA16	59.9	72.6	60.7	63.1	62.5	63.4	64.0	62.9	56.7	57.0
<i>M</i>	63.4	65.2	58.6	59.4	61.9	62.5	60.9	53.2	54.3	52.2

Note. Running is presented in revolutions per two-minute period.

Table 13*Mean Wheel Revolutions Across Successive Two-Min Intervals of the Post-Operant**Period for the Sucrose Condition*

Rat	0-2	2-4	4-6	6-8	8-10	10-12	12-14	14-16	16-18	18-20
NA5	60.9	64.4	70.7	56.8	57.4	62.3	63.6	64.8	63.3	70.4
NA6	61.6	67.8	63.4	67.8	66.0	71.4	69.4	66.2	66.2	68.7
NA7	80.6	85.6	83.1	81.2	78.4	82.9	89.1	86.8	75.8	69.9
NA8	68.4	73.2	72.5	67.8	72.1	71.7	78.2	70.9	68.7	72.8
NA13	71.6	60.2	66.4	67.1	62.0	63.1	69.0	66.2	64.6	68.1
NA14	41.4	37.7	41.9	44.7	46.6	36.9	40.0	37.2	38.1	45.4
NA15	75.1	66.7	62.8	65.5	63.4	65.8	69.5	65.8	62.6	64.7
NA16	71.2	67.9	65.1	61.1	67.2	59.8	64.9	61.5	68.0	70.7
<i>M</i>	66.4	65.4	65.7	64.0	64.1	64.2	68.0	64.9	63.4	66.3

Note. Running is presented in revolutions per two-minute period.

Table 14*Mean Wheel Revolutions Across Successive Two-Min Intervals of the Post-Operant**Period for the Water(2) Condition*

Rat	0-2	2-4	4-6	6-8	8-10	10-12	12-14	14-16	16-18	18-20
NA5	47.3	30.8	42.6	26.1	42.1	38.9	43.5	39.5	38.8	43.8
NA6	46.6	53.2	50.1	55.4	52.9	45.6	52.0	51.1	62.8	57.4
NA7	81.5	77.1	77.9	80.6	71.0	71.6	78.3	74.7	74.3	75.3
NA8	66.3	61.7	58.1	65.0	62.9	58.7	68.3	60.7	62.4	61.7
NA13	62.1	52.4	52.8	45.1	55.5	58.9	48.6	43.4	51.7	46.1
NA14	68.3	57.0	53.7	56.3	55.6	60.3	50.6	59.7	60.6	65.8
NA15	59.4	58.8	58.4	58.3	61.7	57.0	52.2	52.8	52.5	54.2
NA16	67.6	68.5	70.4	64.4	69.5	68.5	62.1	61.2	66.6	63.2
<i>M</i>	62.4	57.4	58.0	56.4	58.9	57.4	57.0	55.4	58.7	58.4

Note. Running is presented in revolutions per two-minute period.