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The Effects of Response Prevention and Response Resistance on Activity-Based Anorexia in Rats

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Abstract Activity-based anorexia (ABA) in animals has been suggested as an animal model of human anorexia nervosa in that many of the core behavioral components of the disorder such as restriction of food consumption, dramatic weight loss, and increased drive for physical activity are present in ABA. Experiment 1 demonstrated the general ABA effect of increased wheel running and decreased weight in rats over a 14 day period of wheel access and food restriction. Experiment 2 examined the effects of response prevention and response resistance on the maintenance of ABA. After one week of food restriction and running with either low or high wheel resistance, half of the rats received three days of response prevention, followed by three recovery days of normal wheel access. Rats that received the response prevention produced significantly lower response rates on the recovery days than subjects that received no response prevention. The degree of wheel resistance influenced the amount of responding, independent of response prevention, with higher resistance resulting in greater levels of wheel running than low resistance. A third experiment replicated the effect of resistance, and found that a shift to high resistance after experience with low resistance produced significantly higher final response levels that a shift from high to low resistance. These findings support the notion that learning and motivational variables affect behavioral processes involved in ABA.

Keywords Response Prevention, Activity-Based Anorexia, Wheel Running, Response Interference

1. Introduction

An often replicated paradoxical finding in animal research is that rats receiving food deprivation with a limited daily access to food and the ability to respond freely on a running wheel will over time demonstrate a significant increase in running behavior with a concomitant decrease in weight (e.g., Routtenberg & Kuznesof, 1967), to the degree that if continued long enough the animals may die of starvation (Hall & Hanford, 1954). Because of the decreased eating, increased activity, and decrease in weight, this behavioral phenomenon has been suggested as a potential animal model of anorexia nervosa (e.g., Epling, Pierce, & Stefan, 1983), and has been labeled activity-based anorexia (ABA).

Explanations of this phenomenon have suggested that exercise interferes with the subject's ability to adapt to a new restricted feeding schedule (e.g., Dwyer & Boakes, 1997), or that the running activity becomes sufficiently reinforcing so as to interfere with adequate food intake (e.g., Epling & Pierce, 1988; Pierce, Epling, & Boer, 1986). There has even been an explanation of the effect proposed from an evolutionary perspective suggesting that this behavioral pattern is consistent with a model of anorexia that states behaviors such as increased activity and decreased feeding are consistent with our nomadic ancestors' need to migrate during conditions of famine (e.g., Guisinger, 2003).

Attempts to identify the variables involved in ABA have clearly suggested a role for conditioned associations that are developed either directly with the running response or with the aftereffects of running. For example, it has been demonstrated that running in a wheel can effectively serve as the unconditioned stimulus in a conditioned taste aversion paradigm (e.g., Lett & Grant, 1996; Nakajima, Hayashi, & Kato, 2000). Lett and Grant (1996) exposed rats to a novel flavored fluid followed by 30 minutes of running in a wheel, and the rats subsequently drank less of that flavor compared to controls. Conversely, Hughes and Boakes (2008) reported that pairing a flavor with the aftereffects of running produced a preference for that taste cue. This general finding with taste conditioning is a robust one that occurs in hungry, thirsty, or nondeprived rats, (Lett & Grant, 1996; Lett, Grant, & Gabarko, 1998) and can be achieved with as little as 15 minutes running (Nakajima et al., 2000). Liang, Bello, and Moran (2011) recently extended these findings to the ABA effect by demonstrating a conditioned taste aversion effect with taste-running pairings occurring while the rats were under a food restriction regimen.

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Other research supporting an association role for wheel running and its aftereffects has been presented using place preference conditioning. Several studies have demonstrated that some of the same temporal effects that produce conditioned taste aversion are operative in the conditioning of context place preference (e.g., Belke & Wagner, 2005; Lett, Grant, Byrne, & Koh, 2000; Masaki & Nakajima, 2008). For instance, Lett et al. (2000) reported that either 22.5 hours or 2 hours in a running wheel followed by 30 minutes exposure to a distinctive context resulted in a conditioned place preference for that context. This presumed aftereffect of the running experience has been shown to persist over short (0-10 minutes), but not long (30 minutes) delays (Lett, Grant, & Koh, 2002). Conversely, when exposure to a context was followed by the opportunity to run in a wheel, rats developed an aversion to that context (Masaki & Nakajima, 2008). In other research, both conditioned taste aversion and place preference were demonstrated contingent on wheel running in the same experiment (Lett, Grant, Koh, & Smith, 2001).

Although a significant amount of research on ABA has been conducted investigating the reinforcing properties of wheel running as well as the factors contributing to the influence of food restriction, little research has been reported examining manipulations designed to restrict running behavior and the effects of such manipulations as response prevention on the maintenance of the ABA effect. It is certainly the case that in clinical cases of anorexia nervosa in humans, excessive physical activity is often observed, particularly running. For example, Brewerton, Stellefson, Hibbs, Hodges, and Cochrane (1994) reported that a significant number of anorexics' exercise regimens are excessive enough to refer to them as compulsive exercisers. Although there has been a suggestion of a high comorbidity between obsessive-compulsive disorder and anorexia (e.g., Milos, Spindler, Ruggiero, Klaghofer, & Schnyder, 2002), and given extensive research reported in the behavior therapy treatment literature on the effectiveness of response prevention for anxiety and obsessive-compulsive disorders (e.g., Foa, Steketee, & Milby, 1980; Franklin & Foa, 2014; Steinglass et al., 2011), it is interesting that not as many controlled experimental studies are available examining response prevention and interference in reducing the excessive activity and exercising behavior in anorexia (e.g., Kennedy, Katz, Neitzert, Ralevski, & Mendlowitz, 1995). Mavissakalian (1982) reported some success (i.e., weight gain) after pairing exercise prevention with food exposure in two anorexic patients, though the sustaining aftereffects of the response prevention on subsequent excessive exercising behavior was not investigated. In more recent research with rats in an ABA design, Ratnovsky & Neuman (2011) found that response prevention (access to a locked wheel) during an anorexia recovery phase did not produce more weight gain (when food was no longer restricted) than that produced with wheel running access, though follow-up effects of the response prevention on later wheel responding were not investigated.

Inasmuch as response prevention has been viewed as a viable way to treat obsessive-compulsive disorders (Franklin & Foa, 2014), as well as anorexia nervosa (Steinglass et al., 2011), and given the clear powerful contribution of the wheel running response in the ABA phenomenon, one of the goals of the present research was to investigate the impact of a response-prevention manipulation on subsequent wheel running within an ABA design. A second goal was to examine the effects of response effort through manipulations of the running wheel resistance. Research demonstrating a general deterrent effect of effort on operant responding in animal research has been around for many years (e.g., Collier, Hirsch, Levitsky, & Leshner, 1975; Collier & Levitsky, 1968). Haddad, Szalda-Petree, Karkowski, Foss, & Berger (1994) reported that higher levels of wheel resistance resulted in slower acquisition and lower asymptotic responding in rats than that found with less response resistance. In addition, research by Kirshenbaum and colleagues (e.g., Kirshenbaum, Szalda-Petree, & Haddad, 2000, 2003) demonstrated that increased wheel running effort resulted in greater risk avoidance in the rat's choice behavior, which they suggested may be reflective of an altered foraging strategy being adopted when response effort is increased. The present studies will extend this wheel effort research to the food restriction ABA model.

2. Experiment 1

A preliminary experiment was conducted to examine whether the findings reported previously in the literature demonstrating an activity-based anorexia effect could be replicated under our laboratory conditions. Specifically rats received two weeks of access to a running wheel during which food was available only during a restricted period of the day. Daily wheel responses and weight were recorded. It was hypothesized that over this period wheel running responses would increase while weight decreased.

2.1. Method

2.1.1. Subjects

All procedures were approved by the USC Aiken Institutional Animal Care and Use Committee. The subjects were 10 experimentally naïve male Sprague-Dawley rats, approximately 120 days old, from the USC Aiken Psychology Department Animal Vivarium.

2.1.2. Apparatus

The primary apparatus consisted of four identical Med-Associates wheel boxes (ENV-046), each having a plastic home cage and attached running wheel. Access to and from the wheel could be blocked by inserting a manual door and the wheel could be locked allowing access but no running. The home cage measured 48.26 cm x 26.67 cm x 20.32 cm. The attached wheel was 35.56 cm in diameter with 0.48 cm stainless steel grid rods spaced 1.57 cm apart. The wheel and cage were housed in a light and sound attenuating chamber with a houselight that provided illumination on a 12 hour light:dark cycle. Total daily wheel responses were recorded with a PC and Med-Associates software. Animals were kept individually in the apparatus during the experiment and had continuous water access through a bottle inserted into the cage.

2.1.3. Procedure

The general procedure followed that used by other research to produce the ABA effect (e.g., Routtenberg & Kuznesof, 1967): A habituation phase (Days 1-4) was followed by food restriction and wheel responding (Days 5-14). During habituation, all subjects received 24 hr access to ad lib food and water in the apparatus. Access to the running wheels was allowed for all groups and wheel resistance was set on the lowest value (12 g). Beginning on Day 5, and continuing through the remainder of the experiment, all subjects were placed on a restricted feeding schedule. Food was administered for a 90 min period daily, beginning one hr after the start of the light cycle. Wheel running was prevented during the feeding period by locking the wheel. At the end of the 90-min period any remaining food was removed and access to run the wheel was reinstated for the remaining 22.5 hr period.

The total number of wheel rotations each day and daily weight were recorded and analyzed using an alpha level of .05.

2.2. Results and Discussion

The results indicated that daily wheel responses significantly increased from Day 4 to Day 14 (Ms=3558, 7908), $t(9)=2.20$, $p=.05$. Across these same days, average body weight for the group significantly decreased (Ms=316g, 267g), $t(9)=9.22$, $p<.01$. The present experiment therefore successfully replicated the basic components of the ABA phenomenon (Routtenberg & Kuznesof, 1967). When food access was limited to one 90 min period each day, the average weight of the rats decreased by 16% and the average daily wheel responses more than doubled.

3. Experiment 2

The present experiment was designed to utilize the general procedures that produced an ABA effect in Experiment 1 and investigate the impact of a response-prevention treatment and a response-interference manipulation (effort) on wheel running. It was hypothesized that response prevention may be effective in reducing subsequent running behavior and that increasing the effort required to run might interfere with the response and perhaps decrease wheel running behavior, thereby attenuating the ABA effect. Effort was manipulated by altering the drag resistance of the wheel whereas response prevention was administered by allowing access to the running wheel but the wheel was locked to prevent any responding.

3.1. Method

3.1.1. Subjects

All procedures were approved by the USC Aiken Institutional Animal Care and Use Committee. The subjects were 40 experimentally naïve male Sprague-Dawley rats, approximately 120 days old, from the USC Aiken Psychology Department Animal Vivarium. The study was a 2 x 2 factorial design, with subjects randomly assigned to one of two levels of wheel resistance (High Resistance, HR; Low Resistance, LR), and one of two levels of response prevention (Response Prevention, RP; No Response Prevention, NRP), yielding four groups: HR-RP, HR-NRP, LR-RP, LR-NRP.

3.1.2. Apparatus

The apparatus was the same as in Experiment 1.

3.1.3. Procedure

The procedure consisted of four phases: Habituation, Food Restriction and Wheel Responding, Response Prevention, and Recovery.

Habituation: During habituation, all subjects received 24 hr access to ad lib food and water in the apparatus. Access to the running wheels was allowed for all groups and wheel resistance was set either on the lowest value for the LR groups (12 g) or the highest value for the HR groups (80 g). This wheel resistance setting remained in place throughout the entire experiment.

Food Restriction and Wheel Responding: Beginning on Day 5, and continuing through the remainder of the experiment, all subjects were placed on a restricted feeding schedule. Food was administered for a 90 min period daily, beginning one hr after the start of the light cycle. Wheel running was prevented during the feeding period by locking the wheel. At the end of the 90-min period any remaining food was removed and to the ability to run in the wheel was reinstated for the remaining 22.5 hr period.

Response Prevention: On Days 8-11 two groups (HR-RP, LR-RP) received a response prevention manipulation in which the wheel was accessible but continuously locked so that no running could occur at any time during these four days. For two other groups running in the wheel was permitted at their original resistance, HR or LR. Food was restricted to one 90-min session daily.

Recovery: For the last three days of the experiment (12-14), all groups had access to wheel running under the same conditions as before the response prevention treatment, with Groups HR-RP, and HR-NRP continuing to run under a High Resistance condition and Groups LR-RP, and LR-NRP running with Low Resistance. As on all other days, feeding continued on the restricted schedule.

The total number of wheel rotations each day, baseline difference scores, and daily weight were analyzed with 2 (Resistance) x 2 (Response Prevention) factorial design ANOVA.

3.2. Results

As was the case in Experiment 1, the basic findings consistent with an ABA effect were obtained. Average body weight for all groups significantly decreased from Day 1 to Day 14 (Ms=332g, 278g), $F(1,36)=622.83$, $p<.01$. There were no group differences in weight loss, *F*s < 1.0. In addition, analysis of total wheel responding comparing Day 1 and 7 (before the response prevention manipulation occurred) indicated a significant increase in responding across all groups (Ms=4117, 6389), $F(1,36)=17.12$, $p<.01$, and no significant group differences in responding were yet present over these days, *Fs* < 1.

On the last day of habituation (prior to food restriction) there were no significant differences among the groups in total responding, $Fs(1,36) < 1.55$, *p*s>05. For all remaining analyses, difference (change) scores were calculated by subtracting the total wheel responses on this baseline (Day 4) from the total responses on each subsequent day (5-14), with higher values reflecting increased wheel running.

Figure 1 presents the mean change in responding on the three recovery days (Days 12-14) after the response prevention manipulation. Several interesting findings are present. First, the response prevention manipulation appeared to be effective in reducing subsequent wheel responding, as the two RP groups demonstrated lower response rates than their corresponding NRP groups. Also, an effect of the resistance manipulation emerged. Wheel running with a high resistance throughout the experiment produced higher responding at the end of the experiment than running with a low resistance (HR groups vs. LR groups).

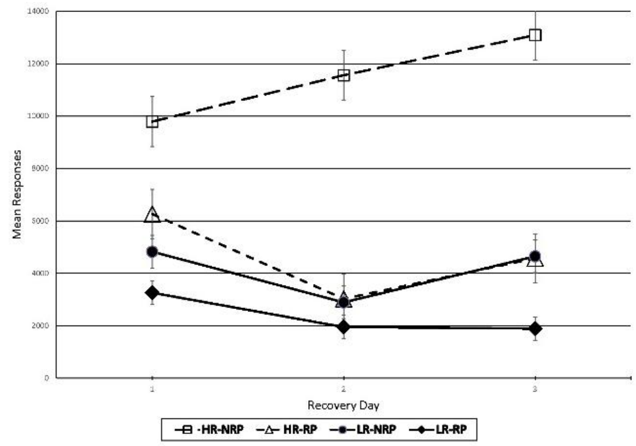

Figure 1. Experiment 2. Mean difference in responses from baseline for all groups on the last 3 recovery days of treatment. HR = High Resistance, LR = Low Resistance, RP = Response Prevention, NRP = No Response Prevention

Repeated measures analysis of variance tests were conducted on the response difference scores over Days 12-14, with Resistance (HR, LR) and Response Prevention (RP, NRP) as the between-subjects factors and Days as the within-subjects factor. This analysis revealed a significant Resistance effect, $F(1,36)=4.84$, $p=.03$, a marginal Prevention effect, $F(1,36)=4.84$, $p=.056$, and marginal Days effect, $F(2,72)=2.84$, $p=.065$. There also was a significant Prevention x Days interaction, $F(2,72)=3.83$, $p=.03$, and a significant Resistance x Prevention x Days interaction, $F(2,72)=3.13$, $p=.05$. Because of the interactions, 2 x 2 (Resistance x Prevention) ANOVAs were performed separately for each Day 12-14. On Day 12, there was only a marginal effect of Resistance, $F(1,36)=3.17$, $p=.08$ with no other significant effects, *F*s<1.30. On Day 13, the effects of Resistance, $F(1,36)=5.35$, $p=.03$, and Prevention, $F(1,36)=5.06$, $p=.03$, were significant and the interaction approached significance, $F(1,36)=3.25$, $p=.08$. The final day, Day 14, revealed similar results, with significant effects of Resistance, $F(1,36)=4.99$, $p=.03$, and Prevention, $F(1,36)=5.12$, $p=.03$, while the interaction was not significant, $F(1,36)=1.34$, $p=.26$.

3.3. Discussion

This experiment attempted to determine if, after experience with a running wheel and limited food access, sessions where wheel running was prevented would subsequently produce a decrease in running behavior when the ability to do so was reinstated. The results suggest that a response prevention treatment was effective in reducing later response rates. Subjects that were not allowed to respond on Days 8-11 (response prevention) demonstrated significantly lower subsequent response rates than subjects receiving no response prevention. A second major finding in the present study was that the degree of wheel resistance influenced the amount of wheel responding, independent of response prevention. There were significant effects of the resistance manipulation, although not in the direction anticipated. High wheel resistance actually producing *higher* levels of wheel running during the final three days than that observed with low wheel resistance. This resistance effect was maintained despite the response prevention treatment.

4. Experiment 3

Although Experiment 2 included a high resistance manipulation with an expectation that more response effort might enhance any effect of response prevention (e.g., Haddad et al., 1994), high wheel resistance actually produced significantly greater responding than low resistance under both response prevention and no prevention conditions. Experiment 3 was designed to examine the effects of a shift in wheel resistance after a week of running. Subjects were again given restricted food availability and wheel access, and began the experiment with seven days of running under either high or low resistance. They then were shifted to the other resistance for the remaining seven days. Wheel resistance levels and daily food restriction protocol were the same as Experiment 2.

4.1. Method

4.1.1. Subjects

All procedures were approved by the USC Aiken Institutional Animal Care and Use Committee. The subjects were 20 experimentally naïve male Sprague-Dawley rats, approximately 120 days old, from the USC Aiken Psychology Department Animal Vivarium. The subjects were randomly assigned to one of two groups whose resistance levels were shifted midway through the study, HR-LR (High Resistance shifted to Low Resistance) and LR-HR (Low Resistance shifted to High Resistance).

4.1.2. Apparatus

The apparatus was the same as in Experiment 1 and 2.

4.1.3. Procedure

The general procedure was similar to that of the first two experiments. A habituation phase (Days 1-4) was followed by food restriction and wheel responding (Days 5-14). During habituation, all subjects received 24 hr access to ad lib food and water in the apparatus. Access to the running wheels was allowed for all groups and wheel resistance was set either on the lowest value for Group LR-HR (12 g) or the highest value for Group HR-LR (80 g). Beginning on Day 5, and continuing through the remainder of the experiment, all subjects were placed on the restricted feeding schedule. Food was administered for a 90 min period daily, beginning one hour after the start of the light cycle. Wheel running was prevented during the feeding period by locking the wheel. At the end of the 90-min period any remaining food was removed and access to run in the wheel was reinstated for the remaining 22.5 hour period.

Beginning on Day 8 the two groups had their wheel resistance changed for the remainder of the experiment. Group HR-LR had their resistance changed from High to Low (80 g shifted to 12 g) and Group LR-HR changed from Low to High (12 g shifted to 80 g).

4.2. Results and Discussion

Once again an increase in responding and decrease in weight was observed. Average body weight for all groups significantly decreased over the two-week period (Ms=337g, 283g), $F(1,18)=216.90$, $p<.01$, and there was no group difference in weight loss, $F(1,18) < 1.0$. In addition, analysis of total wheel responding comparing Day 1 and 7 (before the resistance shift manipulation occurred) indicated a significant increase in responding across all groups (Ms=2783, 5445), $F(1,18)=1.91$, $p<.01$, and no significant group differences had yet emerged, $Fs < 1$.

On the last day prior to the resistance shift (Day 7), there was no significant difference between the groups in total responding, $F(1,18) < 1$. For the remaining analyses, difference (change) scores were calculated by subtracting the total wheel responses on this baseline day (Day 7) from the total responses on each subsequent day (8-14), with higher values reflecting increased wheel running.

Figure 2 presents the mean responding on the seven post-shift days (Days 8-14) after the resistance shift manipulation. Once again an effect of resistance was observed. After seven days of wheel running with low resistance, once Group LR-HR was shifted to high resistance a subsequent increase in daily responding was observed. For the group that was shifted from high to low resistance (HR-LR), daily response rate did not change throughout the remaining days of the experiment.

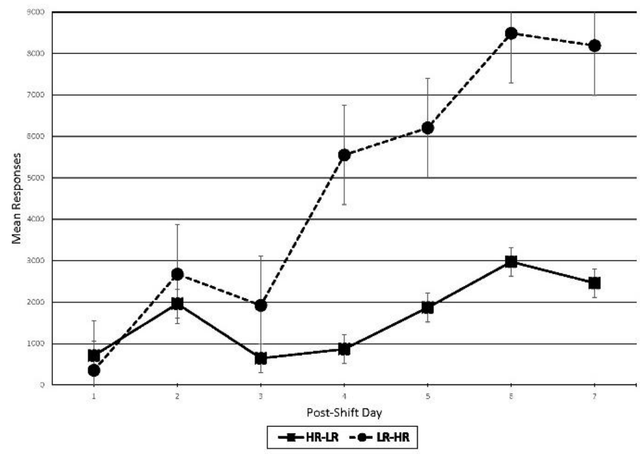

Figure 2. Experiment 3. Mean difference in responses from baseline on the last 7 days of treatment. HR = High Resistance, LR = Low Resistance

A 2 x 7 repeated measures ANOVA was conducted on the daily response difference scores during Days 8-14 (post shift), with Groups as the between-subjects variable and Days as the within-subjects factor. This analysis revealed a significant effect of Days, $F(6,108)=5.61$, $p<.01$, a significant Days x Groups interaction effect, $F(6,108)=2.28$, $p<.05$, and a marginal Groups effect, $F(1,18)=3.27$, $p=.087$. Because of the interaction, separate repeated measures ANOVAs were conducted for each group over Days. These indicated a significant Days effect in Group LR-HR, $F(6,54)=4.45$, $p<.01$, reflecting the increase in responding in this group from the resistance shift through the end of the experiment. There was no significant change over Days in Group HR-LR, $F(6,54)=1.67$, $p>.05$.

5. General Discussion

Activity-based anorexia (ABA) refers to a robust finding in animal research that rats receiving food deprivation with a limited daily access to food and the ability to respond freely on a running wheel will over time demonstrate a significant increase in running behavior and a concomitant decrease in weight (e.g., Routtenberg & Kuznesof, 1967). The present research was designed to investigate the effects of two manipulations on the potential reduction of the excessive wheel running observed in the ABA effect: Response prevention and response interference.

Given that response prevention has been a successful technique in the clinical treatment of various disorders involving inappropriate or maladaptive instrumental responses (e.g., Franklin & Foa, 2014), the high comorbidity of obsessive-compulsive disorder and anorexia (e.g., Milos et al., 2002), as well as the excessive exercise behavior pattern often observed in anorexic patients (e.g., Brewerton et al., 1994), one of the goals of the current research was to examine the use of response prevention within the general ABA design. After demonstrating the general ABA effect of increasing response rates and decreasing weight in the present laboratory, food-restricted rats received seven days of wheel running with either high or low wheel resistance. Then half of the subjects received four days of wheel exposure with running blocked, following by three recovery days of free responding with the original wheel resistance. For both the high resistance and low resistance conditions, the response prevention resulted in significantly lower subsequent responding on the three recovery days as compared to the comparable no-prevention groups (see Fig. 1). Although it appeared that the effect of response prevention was greater under high resistance than low, that interaction was not significant.

This experiment provides some support for the notion that a response prevention treatment may reduce subsequent wheel running in the ABA paradigm, and perhaps might be effective in clinical treatments of anorexia nervosa through exposure and response prevention of running or excessive exercise (cf. Mavissakalian, 1982). It should be pointed out that the various phases of treatment employed in the current research were of relatively short durations, and given that a repeated-measures design was employed a more meaningful pattern of results may have been obtained after observing more stability of responding during each phase. For example, three days of response prevention were used, after just one week of original running experience, so it is not clear whether an instrumental response with much stronger response strength would be equally affected by the response prevention. In addition, this study only used three recovery days after the response prevention treatment, so any long-term persistence of response prevention on behavioral suppression was not addressed.

The results of the resistance manipulation were a little less expected. Although there is not a lot of research that has examined the effects of response effort within the traditional ABA design, it was anticipated that an increase in wheel resistance might produce an overall reduction of responding during the two-week period due to the increased effort to respond (e.g., Collier et al., 1975; Haddad et al., 1994). The results, however, indicated an effect of wheel resistance different than expected. In two experiments increasing the drag resistance of the wheel, presumably resulting in greater effort to respond, actually produced a robust effect of increased rates of responding during the second week of treatment in Experiment 2 (Fig. 1). For the groups that did not receive any response prevention, high resistance (wheel drag set at its maximum value, 80 grams) produced significantly greater overall response rates than low resistance (drag set at the minimum value, 12 grams). Although the response prevention treatment attenuated responding compared to no-prevention controls, the main effect of higher responding with high resistance than with low resistance was maintained despite the response prevention attenuation of subsequent running. Although some significant effects were observed here, it may be the case that using sample sizes larger than the current experiment (Ns=10) may have increased the overall power to detect greater group differences.

A follow-up experiment was conducted to further examine this resistance effect. In Experiment 3 rats received one week of wheel access with either high or low resistance (while being maintained on the standard food restriction schedule), and then were switched to the other resistance level for the second week of the treatment. Once again resistance differences produced a significant effect on running. Rats that had their wheel resistance shifted from low to high resistance produced significantly greater daily response rates than the group that started under high resistance and was shifted to low. One observation from this study is that by Day 14 the response rates with high resistance (after first receiving training with low resistance) were not at the level on Day 14 of those in the group that received high resistance throughout in Experiment 2 (Fig. 1 vs. 2). This suggests that the maximum effect of higher resistance to produce increased behavior may take some time to develop in the rat's running regimen.

One major difference in the resistance effects demonstrated in present studies and that of Haddad et al. (1994), which showed an overall degrading effect of resistance on wheel running, was the feeding regimen. Haddad et al. was not examining the ABA phenomenon and therefore did not implement a restricted feeding schedule as used in the current design and other ABA studies. This suggests that there may be something about wheel running when food availability is restricted that actually enhances the motivation to run, and/or the reinforcement for running, under high effort conditions. If increasing wheel running effort increases risk aversion and alters foraging strategy (e.g., Kirshenbaum et al., 2000, 2003), perhaps the food restriction and accompanying weight loss observed in the usual ABA effect serves to motivate even more focused risk aversion foraging and therefore enhanced running in the wheel.

It may be the case that there is some interaction between the effects of running with high effort under food deprivation and the reinforcement for that running behavior. Lydall, Gilmour, & Dwyer (2010) observed that rats valued a reward (sucrose palatability) more when it followed a high-effort response (lever pressing) than when the same reward followed a low-effort response. Given the evidence that the aftereffects of wheel running seem to produce some level of positive associability, or reward (e.g., Belke & Pierce, 2014; Belke & Wagner, 2005; Hughes & Boakes, 2008; Lett et al., 2000), it may be that under conditions similar to those in the present studies post-response reward is enhanced when the response requires more effort. As stated earlier, the sample sizes used in the current experiments may have had a general impact on the overall generalizations that can be made from these results. Inasmuch as the present research (and much of the previous research in this area) utilized a between-subjects mixed design with repeated measures, future investigations may benefit from examining these variables with single-subject design studies, where multiple baseline response periods can be interspersed with different treatments to determine the stability and differences in response trends, potentially resulting in increased reliability and generalizability.

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