Contrafreeloading in Rats Is Adaptive and Flexible: Support for an Animal Model of Compulsive Checking

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Abstract
Contrafreeloading involves working unnecessarily to obtain a reward that is otherwise freely available. It has been observed in numerous species and can be adaptive when it provides an organism with updated information about available resources. Humans frequently update their knowledge of the environment through checking behaviors. Compulsive checking occurs when such actions are performed with excessive frequency. In a putative animal model of compulsive checking, rats treated chronically with the dopamine agonist quinpirole display exaggerated contrafreeloading for water. Although this effect has been attributed to behavioral rigidity, some evidence suggests the behavior remains somewhat flexible and may be adaptive under certain conditions. We assessed the ability of quinpirole-treated rats with contrafreeloading experience to adapt to changing contingencies by requiring them to alternate between response levers. Rats treated with quinpirole or saline were first trained to obtain water by pressing either of two levers. Next, free water was made available for 8 days, and contrafreeloading was measured. Rates of contrafreeloading were significantly higher in the drug-treated rats than in controls. On the following 5 days, each reward caused the associated lever to become inactive until a reward was earned from the alternate lever. Quinpirole-treated rats learned this new response requirement more quickly than controls. Thus, exaggerated checking behavior induced by chronic quinpirole treatment can be advantageous when environmental contingencies change. These results provide support for this animal model of compulsive checking and hint at the presence of a specialized neural checking module involving the dopamine system.

Keywords
contrafreeloading, compulsive checking, animal model, dopamine

Date received: June 22, 2017; Accepted: September 14, 2017

Many animals will continue to perform behaviors that result in the delivery of a resource (e.g., food or water) even when the same resource is freely available. This seemingly unnecessary work is known as contrafreeloading (Jensen, 1963). Many species have been shown to contrafreeload, including rats (Jensen, 1963), pigeons (Neuringer, 1969), starlings (Bean, Mason, & Bateson, 1999; Inglis & Ferguson, 1986), chimpanzees (Menzel, 1991), Japanese macaques (Ogura, 2011), and humans (Singh, 1970; Tarte, 1981). This behavior is most often studied in operant chambers after the operant response has been trained, but it has also been observed without prior training (Neuringer, 1969). This finding suggests that contrafreeloading is not merely due to the persistence of a previously rewarded behavior.

The widespread occurrence of contrafreeloading presents a paradox, since it seems to run counter to both evolutionary theories regarding foraging and common sense. Needlessly expending precious energy resources in pursuit of a resource would seem to put organisms at a disadvantage relative to those who opt to consume the free resource. On the other hand, if contrafreeloading is maladaptive, why is it so commonly observed in so many species? Absent any negative consequences, freeloading would seem to be more adaptive than contrafreeloading because it obtains the same benefits while expending less energy. This idea, often referred to as the principle of least effort, was introduced by the French Philosopher...
Guillaume Ferrero (1894) and expanded on by Linguist George Kingsley Zipf (1949). The principle received empirical support from work by early behavioral psychologists conducting studies of instrumental learning (Tsai, 1932; Waters, 1937). It was not until the introduction of operant chambers that evidence for contrafreeloading emerged (Jensen, 1963), casting doubt on the ubiquity of the principle of least effort. Jensen (1963) suggested a proximate explanation for his observations, specifically that the act of performing the operant response has intrinsic value for the organism. However, it would be several decades before a plausible ultimate explanation was articulated in the form of an evolutionary theory.

The leading theory concerning the functional utility of contrafreeloading was put forth by Inglis, Forkman, and Lazarus (1997). Known as the “information primacy approach,” it suggests that a contrafreeloading organism gains, not only the acquired resource but also potentially valuable information about resource availability. In natural environments, animals who periodically investigate multiple resources will have an advantage over those who stop sampling their environment after finding one “free” resource. Experimental work in starlings by Bean, Mason, and Bateson (1999) has confirmed that contrafreeloading is greatly diminished when the availability of the ‘earned’ resource can be assessed visually, thus making the information to be gained by contrafreeloading redundant. Currently, the experimental evidence across species is consistent with the idea that contrafreeloading represents a form of information gathering that may involve the collection of new resource-relevant information (exploration) or the reassessment of previously encountered resources (checking).

It is the checking component of contrafreeloading that has received the most attention in recent years, as researchers have sought to develop more effective in vivo models for the compulsive checking seen in human patients with obsessive–compulsive disorder (OCD). Current animal models of OCD include marble burying and nestlet shredding (Witkin, 2008), but it is not clear how these behaviors translate to human patients with OCD, the behavior of quinpirole-treated rats has been observed with pramipexole, a selective D2/D3 agonist with a D3 preferred profile (Schepisi, De Carolis, & Nencini, 2013). Quinpirole treatment has previously been shown to cause a general pattern of behavioral repetition that includes preservative responding during extinction (Kurylo, 2004) and repetitive checking of behavioral features similar to compulsive checking (Szechtman et al., 1998). A persistent preoccupation with one location in the environment is another commonly observed effect (Alkhatib, Dvorkin-Gheva, & Szechtman, 2013). However, the behavior of quinpirole-treated rats is not entirely fixed as it often changes when the environment is altered (Szechtman et al., 2001; Zadicario, Ronen, & Eilam, 2007). Thus, as with compulsions in patients with OCD, the behavior of quinpirole-treated rats has been characterized as “flexible, yet recurrent” (Szechtman et al., 1998). Furthermore, there is evidence that this behavior, like that of patients displaying compulsive actions, is motivated by a desire for safety and security (Szechtman et al., 1998, Szechtman & Woody, 2004).

The precise manner in which quinpirole-induced contrafreeloading remains flexible in response to environmental changes has received limited attention. Under certain conditions, a high degree of persistence in checking behaviors combined with some level of flexibility might prove advantageous, particularly when the optimal strategy for resource acquisition requires awareness of more than one resource. We hypothesized that quinpirole-treated rats with experience contrafreeloading would display an advantage over controls when the continued acquisition of rewards required the activation of more than one response lever, since more frequent checking should enable these rats to more quickly learn the new contingencies.

**Method**

**Animals**

The experiment was performed using 24 male Sprague-Dawley rats and was conducted at a liberal arts college in the northeastern United States. All procedures were approved by the local Institutional Animal Care and Use Committee and were in compliance with current principles of laboratory animal care. On arrival, rats were 56 days old and weighed 220–250 g. Rats were housed individually in polycarbonate cages and maintained on a 12-hr light/dark cycle (lights on at 7:00). During the first week, water and food were available ad libitum.
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Apparatus
Each of the 24 rats was placed in an operant conditioning chamber (Lafayette Instrument Company, Lafayette, IN) for 30 min per day. The chamber was outfitted with two response levers, and a water dispenser situated between the response levers delivered water reinforcement on a programmable schedule. A program capable of controlling the reinforcement schedule and recording both responses and reinforcements during each session was created using MATLAB R2012a (The MathWorks, Inc.). At the opposite end of the chamber, a small hole allowed the experimenter to add or remove a nozzle-type water bottle similar to the one in the rats’ home cages. This allowed for the presence of ad libitum water during the contrafreeloading sessions.

Experimental Phases

Training. Twenty-four rats were placed on a water deprivation schedule to motivate them to work for water rewards. Each rat received 30 min free water access each day after completion of the experimental session. Sessions lasted for 30 min each day, during which rats were trained to press either of two levers to receive a reward (0.1 ml of water). Shaping by successive approximations was applied until the rats were consistently performing the operant response. Next, the schedule of reinforcement was gradually increased from continuous reinforcement fixed ratio one (FR-1) to a fixed ratio five (FR-5) schedule. All rats were observed earning rewards on both the left and right levers in the operant conditioning chamber. At the end of the 2-week training period, all 24 rats were consistently earning between 125 and 225 rewards per session on the FR-5 schedule.

Operant conditioning. No free water was available in the chamber during this phase. Both levers were set to trigger reinforcement on independent FR-5 schedules. Drug or saline treatments were administered daily prior to the experimental session. After receiving a subcutaneous injection, each rat was returned to its home cage for 15 min before being transferred to the operant chamber for testing. For 2 days prior to the operant conditioning phase, all 24 rats received subcutaneous saline injections (0.3 ml 0.9% NaCl dissolved in water) in order to establish baseline response rates. Random assignment was used to divide the sample into an experimental and a control group. Beginning on the first day of the operant conditioning phase, 12 of the rats received subcutaneous injections of quinpirole (0.5 mg/kg), while the remaining 12 continued to receive saline injections. For 8 days, the response rates for the drug- and saline-treated rats were recorded during 30-min daily sessions. Drug and saline treatments continued to be administered daily throughout the remaining phases of the experiment using the procedures described above.

Contrafreeloading. During the 8 days following the operant conditioning phase, free water was placed in the operant chamber. Water continued to be dispensed when the FR-5 ratio was reached on either lever but was now also available from a nozzle at the other end of the chamber. Drug and saline treatments continued during this phase, and the consumption of both earned and free water was recorded.

Forced lever alternation. During the next 5 days of the experiment, the free water was removed and water could only be obtained by lever pressing on a “forced alternation” schedule. Five presses on either lever would result in water reinforcement, after which the lever would become inactive (still present, but no longer delivering reinforcement). Five total presses on the alternate lever would then be required to deliver the next reinforcement, while additional presses on the first lever would have no effect. After each reward, the active lever alternated, such that in order to continue to earn water the rat would need to frequently switch between the two levers (with the optimal response pattern being five presses at a time on each lever). Drug and saline treatments continued during this phase, and the number of rewards earned was recorded.

Extinction. On the final 3 days of drug and saline treatments, free water was once again available in the operant conditioning chamber. Both response levers were set to extinction such that no water was dispensed in response to lever presses. Free water consumption and the number of lever presses were recorded.

Drugs
Powdered (−)-quinpirole hydrochloride (Sigma-Aldrich, St. Louis, MO) was dissolved in distilled water to a concentration of 0.5 mg/ml. Solutions were prepared immediately before use or prepared and frozen for up to 3 days and thawed prior to use. All injections were administered subcutaneously at a volume of 1 ml/kg. The dose administered (0.5 mg/kg) was consistent with previous research on the behavioral effects of quinpirole (see Amato et al., 2007; Milella et al., 2008; Zadicario et al., 2007).

Data Analysis
Data were analyzed by examining each phase separately using a two-way repeated measures analysis of variance (ANOVA) with one between-subjects factor (drug condition) and one within-subjects factor (day of experimental phase). When Mauchly’s test indicated a violation of the sphericity assumption, Greenhouse–Geisser corrected values were substituted in the analysis. The dependent variables examined were the number of lever presses, rewards earned, and free water consumed. Contrafreeloading was calculated as the fraction of total water consumed that consisted of earned water.

Results
Figure 1a displays the average number of lever presses on each day by the experimental and control groups across the five phases of the experiment. Figure 1b displays the number of lever presses by each group averaged across the days within each experimental phase. Error bars represent ± 2 standard errors of the mean. No significant main effects or interactions
were observed during the 2 days of baseline testing before quinpirole was administered (two-way ANOVA for repeated measures, quinpirole treatment, $F(1, 22) = 3.91, p = .061$; testing day, $F(1, 22) = 1.45, p = .241$; Treatment × Day interaction, $F(1, 22) = .02, p = .888$).

During the operant conditioning phase, quinpirole initially suppressed lever-pressing leading to a significant group difference (two-way ANOVA for repeated measures, quinpirole treatment, $F(1, 22) = 27.65, p < .001$; testing day, $F(2.48, 54.64) = 21.48, p < .001$; Treatment × Day interaction, $F(2.48, 54.64) = 10.06, p < .001$). Response rates gradually recovered, such that by the eighth day of the operant conditioning phase there was no significant difference between the drug and control groups. This is consistent with previous research, which has established that repeated exposure to quinpirole produces a characteristic response pattern in rats that includes an initial suppression of locomotor activity, followed by a gradual increase over several days (Foley, Fudge, Kavaliers, & Ossenkopp 2006). This is known as behavioral sensitization, wherein the behavioral response to a given dose of quinpirole tends to increase across repeated exposure to the drug (Dvorakin, Perreault, & Szechman, 2006). When rates of lever pressing were pooled across sessions and the baseline and operant phases were compared, the drug-treated animals displayed fewer presses per day during the operant phase ($M = 260.24, SD = 80.12$) than during the baseline phase ($M = 397.73, SD = 42.26$), as a result of the initial suppression of locomotor activity that occurs when drug-naïve animals are first exposed to quinpirole, paired-samples $t$ test, $t(11) = 5.62, p < .001$. Conversely, the control animals displayed more presses per day during the operant phase ($M = 409.71, SD = 66.89$) than during the baseline phase ($M = 365.08, SD = 40.47$), likely as a result of additional practice with the task, paired-samples $t$ test, $t(11) = -3.05, p < .05$.

When free water was made available during the contrafreeloading phase, all of the rats noticed and drank from the free water source within a few minutes of being placed in the chamber. When comparing pooled rates of responding during the contrafreeloading phase to those during the operant phase, a significant decrease was observed in the control group, paired-samples $t$ test, $t(11) = 23.79, p < .001$, but not in the experimental group, paired-samples $t$ test, $t(11) = 1.53, p = .154$. Throughout the contrafreeloading phase the quinpirole-treated rats continued to lever press at relatively high rates as compared to the controls (two-way ANOVA for repeated measures, quinpirole treatment, $F(1, 22) = 21.86, p < .001$; testing day, $F(3.07, 67.54) = 9.73, p < .001$; no significant interaction).

Our initial intent was to collect and measure any earned water left in the dispensers at the end of each experimental session, since it has been reported that rats treated with quinpirole frequently earn more water rewards than they consume (Amato et al., 2006; Milella et al., 2008). However, examination of the dispensers did not reveal any unconsumed water at the end of any experimental session, and the animals were observed to consume each reward within a few seconds after it was dispensed. We therefore calculated water consumption based on the number of earned rewards and the amount of free water consumed.

Total water consumption during the contrafreeloading phase did not differ between the experimental and control groups (two-way ANOVA for repeated measures, quinpirole treatment, $F(1, 22) = 1.96, p = .175$; testing day, $F(7, 154) =$

![Figure 1](image-url)
Figure 2. The mean free and earned water consumed by the two groups on each day of the contrafreeloading phase. Error bars represent ±2 standard errors of the mean.

6.68, p < .001; no significant interaction). However, those treated with quinpirole consumed relatively more earned water (two-way ANOVA for repeated measures, quinpirole treatment, $F(1, 22) = 21.34, p < .001$; testing day, $F(3.06, 67.22) = 9.87, p < .001$; no significant interaction) and relatively less free water (two-way ANOVA for repeated measures, quinpirole treatment, $F(1, 22) = 12.24, p = .002$; testing day, $F(4.03, 88.75) = 12.38, p < .001$; no significant interaction) than the control group. Thus, while all the rats consumed both free and earned water, chronic quinpirole administration resulted in a considerably higher rate of contrafreeloading. Figure 2 displays the mean free and earned water consumed by the two groups on each day of the contrafreeloading phase. Error bars represent ±2 standard errors of the mean.

On the first day of the forced lever alternation phase, both groups increased lever pressing to compensate for the lack of available free water. As compared to the final day of the contrafreeloading phase, the average number of presses increased from 42.25 to 481.25 in the control group, paired-samples $t$ test, $t(11) = 6.01, p < .001$, and from 190.67 to 608.67 in the experimental group, paired-samples $t$ test, $t(11) = 11.66, p < .001$. Throughout this phase of the experiment, the number of rewards earned gradually increased across the first 3 days as rats in both groups learned the new behavioral requirement. The drug-treated group acquired the lever alternation behavior more quickly, causing them to earn significantly more rewards than the control group (two-way ANOVA for repeated measures, quinpirole treatment, $F(1, 22) = 4.53, p < .05$; testing day, $F(2.34, 51.40) = 15.96, p < .001$; Treatment × Day interaction, $F(2.34, 51.40) = 3.29, p < .05$). Pairwise comparisons revealed significant group differences in the number rewards earned on day 1, independent-samples $t$ test, $t(22) = -3.02, p < .01$; day 2, independent-samples $t$ test, $t(22) = -2.62, p < .05$; and day 3, independent-samples $t$ test, $t(22) = -2.32, p < .05$, such that the quinpirole-treated animals earned a greater number of rewards on these days than the controls. This group difference was not observed on days 4 or 5, during which the reward rates of both groups approached an upper limit of approximately 60 rewards earned per 30 min session. These data suggest that both groups had fully learned the new behavioral requirement by day 4. Figure 3 summarizes the results from the forced lever alternation phase as a function of testing day. The bar graph on the right represents the average across the 5 days. Error bars represent ±2 standard errors of the mean.

When comparing the average number of presses relative to the number of rewards earned, both groups improved their efficiency across the 5 days of forced alternation (two-way ANOVA for repeated measures, testing day, $F(1.11, 24.41) = 4.42, p < .05$; quinpirole treatment, $F(1, 22) = 3.80, p = .064$; Treatment × Day interaction, $F(1.11, 24.41) = 3.83, p = .058$). Although the difference in reward-earning efficiency between the groups did not reach significance ($p = .064$), the experimental group was generally more efficient and consistent in terms of minimizing presses-per-reward ($M = 12.69, SD = 1.61$) compared to the control group ($M = 27.85, SD = 26.91$). During the extinction phase, rates of bar-pressing decreased in both groups but remained somewhat higher in the experimental group (two-way ANOVA for repeated measures, quinpirole treatment, $F(1, 22) = 38.26, p < .001$; testing day, $F(1.42, 31.13) = 30.88, p < .001$; Treatment × Day interaction, $F(1.42, 31.13) = 14.97, p < .001$). Consumption of the free water did not differ significantly between the two groups during this phase (two-way ANOVA for repeated measures, quinpirole treatment, $F(1, 22) = .21, p = .654$; testing day, $F(2, 44) = 3.22, p = .049$; no significant interaction).

**Discussion**

The results of this experiment lend support to the use of quinpirole-enhanced contrafreeloading as an animal model of human compulsive checking behavior. Following a period of sensitization, drug-treated rats were shown to lever press for water at a rate similar to that of saline-treated rats. When free water was introduced, the saline-treated animals shifted their preferences toward the free resource, while the drug-treated animals continued to press both the left and right levers on a
regular basis. One potential explanation is that the drug confers behavioral rigidity, leading the rats to continue their habitual lever-pressing despite altered environmental contingencies. However, the behavior of the experimental group was unlikely to be due to a failure to recognize the free water, since all the rats were observed to quickly notice and drink from the free water bottle. Rather, as compared to controls, the drug-treated rats appeared to find the act of rechecking the levers to be more reinforcing.

If quinpirole-treated animals remain capable of adjusting to new environmental demands, why has their behavior so often been interpreted as rigid? We suggest that the drug may facilitate the development of a behavioral routine, which is then frequently repeated. During the contrafreeloading phase, the quinpirole-treated animals tended to regularly visit and interact with both levers, as well as with the free water. Perhaps the drug caused the animals to more evenly distribute their time among the stimuli in the chamber. However, it should be noted that in open-field tests, rats treated chronically with quinpirole have been observed to preferentially visit one or a few locations more frequently than others (Zadicario et al., 2007). Thus, while the sampling may not always occur evenly across the environment, quinpirole-treated animals show a propensity toward more frequent checking of environmental features and are not simply preoccupied with a single feature. This tendency to regularly update knowledge of resource-relevant stimuli becomes an advantage when reward optimization requires alternating between such stimuli. It also bears a striking resemblance to the compulsive checking behavior seen in some patients with OCD.

Our results suggest that the effects of quinpirole on contrafreeloading involve an enhancement of the dopaminergic reward system in response to a “successful check” (i.e., one that confirms the availability of a potential alternative resource). Thus, the drug-treated animals prefer to sample a variety of potential resources rather than opt for the one most readily available. Contrafreeloading demonstrates that the value of a reward is not entirely determined by the biological utility of the physical resource obtained. Premack (1959) and others have suggested that the act of engaging in a behavior can be inherently rewarding. In the case of quinpirole-enhanced contrafreeloading, it seems that the act of pressing a lever is not sufficiently rewarding in itself to maintain responding. Rather, the behavior must periodically lead to a successful check that is followed by a physical reward. Perhaps the dopaminergic reward system is particularly sensitive to external rewards that are triggered by the performance of a learned behavior. If so, chronic quinpirole treatment may selectively enhance this effect causing such contingent rewards to take greater precedence over freely available ones.

We believe that this enhancement of checking-related rewards is a better explanation for the observed behavior of quinpirole-treated rats than explanations based on behavioral rigidity or hyperactivity. While previous research has shown that the drug does impair reversal learning, suggesting an increase in rigidity (Boulougouris, Castañé, & Robbins, 2009), the drug did not prevent the quick discovery of the free water or its consumption in the current study. The decrease in responding observed during extinction also suggests that the behavior is not entirely rigid but remains flexible. This is consistent with previous research demonstrating that quinpirole-treated rats will reduce rates of responding when the ratio schedule of reinforcement becomes more demanding (Milella et al. 2008). Similarly, past research on quinpirole-enhanced contrafreeloading has shown that rats will ignore an inactive lever that does not trigger reinforcement (Amato et al., 2006). Thus, hyperactivity cannot fully explain the seemingly excessive lever pressing.

While compulsive checking is maladaptive by definition, occasional checking of resources can clearly be beneficial.
Furthermore, the optimal frequency of checking is likely to depend on several factors including the relative stability of the environment. More frequent checking is likely to pay off in environments that are undergoing rapid change. We hypothesized that the frequent checking displayed by quinpirole-treated rats in a contrafreeloading paradigm could be advantageous when continued resource acquisition depended on the activation of more than one lever. Thus, we introduced the forced lever alternation phase. Unlike typical reversal learning, this task did not involve the unlearning or inhibition of one response in favor of another but rather required the alternating performance of two behaviors (left and right lever pressing) in succession. We predicted that the quinpirole-treated rats would excel at this task due to their tendency to repeatedly check various resources during the preceding contrafreeloading phase. Our results confirmed this prediction and supported the notion that more frequent checking is adaptive under certain conditions. This notion is consistent with modern conceptualizations of OCD, which view the disorder as a failure of the inhibitory neural mechanisms that keep the performance of certain ordinarily adaptive behaviors at reasonable frequencies (Penadés et al., 2007). When this inhibition fails, the behavior is repeated despite the increased costs and decreased benefits of doing so.

The idea that many psychopathologies represent adaptive behaviors occurring in nonadaptive contexts is a core concept in evolutionary medicine. As described by Marks and Nesse (1994), anxiety disorders are thought to involve the dysregulation of ordinary defensive responses. These authors note that the behavioral routines observed in patients with OCD are typically exaggerated parodies of ordinary, healthy habits. In healthy individuals, a habitual act is performed to completion, which is then followed by a sense of accomplishment and satisfaction such that the person does not feel compelled to repeat the behavior immediately. James (1893) referred to this completion event as a “flat.” However, in patients with OCD, this feeling of satisfaction never occurs, which leads the individual to perform the action over and over (Marks & Nesse, 1994). Within this framework, checking behaviors are neither inherently adaptive nor maladaptive. Rather, there is an optimal frequency of checking for any given environmental context. In the current study, we have demonstrated that overly frequent checking in an animal model of OCD can in fact be advantageous under certain conditions.

In summary, our results provide support for the use of quinpirole-enhanced contrafreeloading as an animal model for the compulsive checking often observed in humans with OCD. Both can be viewed as adaptive behaviors being performed at maladaptive frequencies, and both remain somewhat flexible and responsive to changes in the environment. By more closely examining this model in future studies, researchers will be able to gain a better understanding of the underlying neural mechanisms involved, as well as to design more effective behavioral and pharmacological treatments for human patients. Additionally, such work may provide new insights into the evolutionary origin and function of checking behaviors.

Acknowledgments
The authors would like to thank Professors Douglas Weldon and Jonathan Vaughan for their help in setting up the equipment and software, as well as the following research assistants: Summer Bottini, Hallie Brown, Liza Gergenti, and Scott Pillette.

Declaration of Conflicting Interests
The author(s) declared no potential conflicts of interest with respect to the research, authorship, and/or publication of this article.

Funding
The author(s) received no financial support for the research, authorship, and/or publication of this article.

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